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FOURTH AUTUMN COURSE ON MATHEMATICAL ECOLOGY

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"Discrete-Time Population Models with Age and Stage Structure I"

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These are preliminary lecture notes, intended only for distribution to participants.

Discrete-Time Population Models with Age and Stage Structure I

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Outline of Talk

- Age Structure – Leslie Matrix L

$$\vec{n}(t+1) = L\vec{n}(t)$$

- Life Cycle Graph
- Properties of L
  - (1) nonnegative
  - (2) irreducible
  - (3) primitive
- Examples
- Perron-Frobenius Theorems
- Strong Ergodic Theorem
- Relationship to Continuous Model
- Rate of Convergence
- Variations in Leslie Matrix
  - (1) Older Ages
  - (2) Two sexes
  - (3) Spatial Distribution
  - (4) Size or Stage Structure
- Examples
  - (1) Insect
  - (2) Plant
- General Structured Matrix

Age Structure : Leslie Matrix

- Bernadelli (1940), Lewis (1942), Leslie (1945, 1948)
- Only females are considered.
- Population is divided into age classes.

Parameters:

f_i = average number of females born per female of age class i during interval t to $t+1$ that are alive at time $t+1$, $f_i \geq 0$.

p_i = proportion of females in age group i that survive to age $i+1$, $p_i > 0$.

$n_i(t)$ = size of age class i at time t.

$$n_1(t) = f_1 n_1(t) + f_2 n_2(t) + \cdots + f_m n_m(t) = \sum_{i=1}^{m} f_i n_i(t),$$

where m is the oldest age class.

$$n_{i+1}(t+1) = p_i n_i(t), \quad i = 1, \ldots, m-1.$$

Leslie Matrix

In matrix form:

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ \vdots \\ n_m(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & \cdots & f_{m-1} & f_m \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{m-1} & 0 \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_m(t) \end{pmatrix}$$

or

$$\vec{n}(t+1) = L\vec{n}(t).$$

Thus,

$$\vec{n}(t) = L^t \vec{n}(0).$$

The projection matrix L is called the

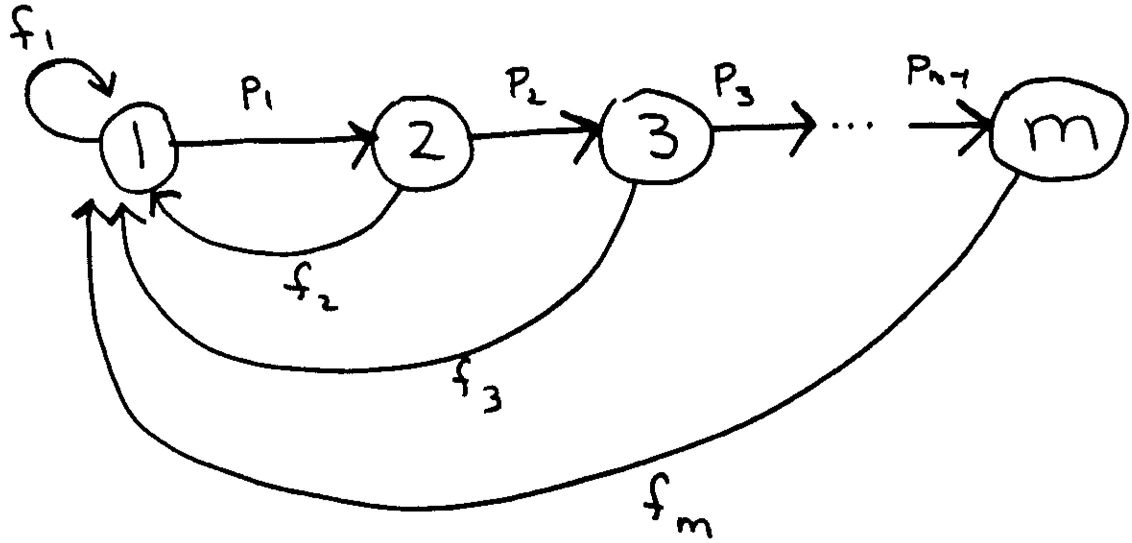
<u>Leslie matrix</u>.

Life Cycle Graphs

The Leslie matrix has an associated life cycle graph.

$$L = \begin{pmatrix} f_1 & f_2 & \cdots & f_{m-1} & f_m \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{m-1} & 0 \end{pmatrix}$$

Life Cycle Graph:



Nice Properties of the Leslie Matrix

- Nonnegative
- Irreducible
- Primitive

Definitions

Def: A matrix $A = (a_{ij})$ is nonnegative if $a_{ij} \geq 0$ for all i, j, $A \geq 0$.
A matrix $A = (a_{ij})$ is positive if $a_{ij} > 0$ for all i, j, $A > 0$.

Def: A permutation of a square matrix A is a permutation of the rows of A combined with the same permutation of columns.

Def: A square matrix A is called reducible if there is a permutation that puts it into the form

$$\begin{pmatrix} B & O \\ C & D \end{pmatrix},$$

where B and D are square matrices and O is the zero matrix.
Otherwise A is irreducible.

<u>Def$^{\prime}$R</u> A square matrix $A = (a_{ij})_{i,j=1}^{n}$ is called <u>reducible</u> if the index set $1, 2, \ldots, n$ can be split into two nonempty complementary sets: $i_1, \ldots, i_\mu$; $k_1, \ldots, k_\nu$ $(\mu + \nu = n)$ such that

$$a_{i_\alpha j_\beta} = 0$$

$\alpha = 1, \ldots, \mu$, $\beta = 1, \ldots, \nu$.

<u>Def</u> If an irreducible matrix $A \geq 0$ has h eigenvalues of maximal modulus r $(|\lambda_1| = |\lambda_2| = \cdots = |\lambda_h| = r)$, then A is called <u>primitive</u>. if $h = 1$ and <u>imprimitive</u> if $h > 1$. The number h is called the <u>index of imprimitivity</u> of A.

• Gantmacher (1964)

Reducible and Irreducible Leslie Matrices

$$L = \begin{pmatrix} f_1 & f_2 & \cdots & f_{m-1} & f_m \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{m-1} & 0 \end{pmatrix}$$

- If $f_m = 0$, then L is reducible.

  Apply Def R: $L = \left(\begin{array}{c|c} B & \begin{matrix} 0 \\ \vdots \\ 0 \end{matrix} \\ \hline C & 0 \end{array}\right)$

- If $f_m \neq 0$, then L is irreducible.

  Apply Def R': no nonempty index sets.

Generally, it is assumed that age class m is the last reproductive age class. If there are post reproductive age classes (k classes), then

$$\underset{(m+k)\times(m+k)}{M} = \left(\begin{array}{c|c} L_{m\times m} & 0 \\ \hline C & D_{k\times k} \end{array}\right),$$

where L is a Leslie matrix, D is lower triangular, $D^t = 0$ for $t \geq k$. Postreproductive age classes are dead by the time k units have elapsed.

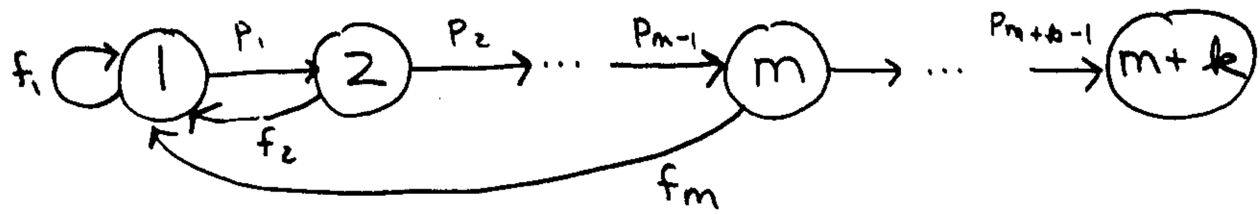
$$M^t = \left(\begin{array}{c|c} L^t & 0 \\ \hline \sum_0^{t-1} D^i C L^{t-1-i} & D^t \end{array}\right)$$

Reducible and Irreducible Leslie Matrices in terms of the Life Cycle Graph

Def: A nonnegative matrix A is irreducible if its life cycle graph is strongly connected, i.e., if there is a path in the graph from every node to every other node.

A reducible life cycle graph contains at least one age that does not contribute to another age.

Example



If there are k postreproductive age classes, $k \geq 1$, then there is no path from age class $m+j$, $1 \leq j \leq k$ to age class i, $1 \leq i \leq m$. The Leslie matrix L is reducible.

• Caswell (1989)

Characteristic Equation of the Leslie Matrix

$$L = \begin{pmatrix} f_1 & f_2 & \cdots & f_{m-1} & f_m \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{m-1} & 0 \end{pmatrix}$$

$$|\lambda I - L| = 0 \qquad \text{or}$$

$$\lambda^m - f_1\lambda^{m-1} - p_1 f_2 \lambda^{m-2} - \cdots - p_1 p_2 \cdots p_{m-1} f_m = 0$$

By Descarte's Rule of Signs the matrix L has only one positive real root, λ_1.

The eigenvector associated with λ_1 has positive coordinates:

$$L\vec{v}_1 = \lambda_1 \vec{v}_1$$

$$\vec{v}_1 = \begin{pmatrix} 1 \\ \frac{p_1}{\lambda_1} \\ \frac{p_1 p_2}{\lambda_1^2} \\ \vdots \\ \frac{p_1 p_2 \cdots p_{m-1}}{\lambda_1^{m-1}} \end{pmatrix}$$

Characteristic Equation of the Leslie Matrix

$$\lambda^m - f_1\lambda^{m-1} - p_1 f_2 \lambda^{m-2} - \cdots - p_1 p_2 \cdots p_{m-1} f_m = 0$$

Rewrite the characteristic equation of L:

$$1 = \frac{f_1}{\lambda} + \frac{p_1 f_2}{\lambda^2} + \cdots + \frac{p_1 p_2 \cdots p_{m-1} f_m}{\lambda^m}$$

The quantity

$$R = f_1 + p_1 f_2 + \cdots + p_1 p_2 \cdots p_{m-1} f_m$$

is called the net reproductive rate – i.e., the expected number of daughters born to a female.

If $R > 1$, then $\lambda_1 > 1$.

If $R < 1$, then $\lambda_1 < 1$.

Primitive Leslie Matrices

Theorem P1: A matrix $A \geq 0$ is primitive if and only if some power of A is positive,

$$A^p > 0$$

for some $p \geq 1$. (Gantmacher, 1964).

Theorem P2: An irreducible Leslie matrix is primitive if and only if

$$\text{g.c.d.}\{i \mid f_i > 0\} = 1.$$

(Proof - See Pollard, 1973)

Sometimes the definition of primitive is given as some power is positive. (Theorem P1)

$$L_1 = \begin{pmatrix} 0 & \frac{3}{2}\alpha^2 & \frac{3}{2}\alpha^3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix} \qquad \alpha > 0$$

Characteristic equation:

$$\lambda^3 - \frac{3}{4}\alpha^2\lambda - \frac{1}{4}\alpha^3 = 0$$

Net reproductive rate:

$$R = \frac{3}{4}\alpha^2 + \frac{1}{4}\alpha^3$$

Eigenvalues:

$$\lambda_1 = \alpha \qquad \lambda_{2,3} = -\frac{\alpha}{2}$$

$$\lambda_1 > |\lambda_2| = |\lambda_3|$$

Eigenvector associated with λ_1:

$$\vec{v}_1 = (1, \ 1/2\alpha, \ 1/6\alpha^2)^T$$

Matrix L_1 is <u>primitive</u>.

Example 2

$$L_2 = \begin{pmatrix} 0 & 0 & 6\alpha^3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}$$

Characteristic equation :

$$\lambda^3 - \alpha^3 = 0$$

Net Reproductive Rate :

$$R = \alpha^3$$

Eigenvalues :

$$\lambda_1 = \alpha, \quad \lambda_{2,3} = \frac{\alpha}{2}\left(-1 \pm i\sqrt{3}\right)$$

$$\lambda_1 = |\lambda_2| = |\lambda_3|$$

Eigenvector associated with λ_1 :

$$\vec{V_1} = \left(1, \ 1/2\alpha, \ 1/6\alpha^2\right)^T$$

Matrix L_2 is imprimitive, with index of imprimitivity equal to 3.

heorems of Perron and Frobenius

<u>Theorem PF1</u> : If A is positive, or nonnegative and primitive, then there exists a real eigenvalue $\lambda_1 > 0$ which is a simple root of the characteristic equation. This eigenvalue is strictly greater than the magnitude of any other eigenvalue, $\lambda_1 > |\lambda_k|$, $k \neq 1$. The right and left eigenvectors $\vec{v}_1$ and $\vec{w}_1$ corresponding to λ_1 are real and strictly positive.

(For a general nonnegative primitive matrix A, λ_1 may not be the only real positive eigenvalue but it is the largest one and the only one with nonnegative eigenvectors.)

<u>Theorem PF2</u> If A is irreducible but imprimitive with index of imprimitivity h, then there exists a real eigenvalue $\lambda_1 > 0$ which is a simple root of the characteristic equation, and has associated right and left positive eigenvectors $\vec{v}_1$ and $\vec{w}_1$. The eigenvalues λ_k $k \neq 1$ satisfy $\lambda_1 \geq |\lambda_k|$. There are h-1 eigenvalues equal in magnitude to λ_1 :

$$\lambda_l = \lambda_1 \exp\left(\frac{2\pi l i}{h}\right) \quad l = 1, \dots, h-1.$$

Eigenvalue λ_1 is called the <u>dominant</u> <u>eigenvalue</u>. (Gantmacher, 1964; Caswell, 1989)

Strong Ergodic Theorem

Ergodic implies the asymptotic population behavior is independent of initial conditions. Eventually the population "forgets" its past.

<u>Theorem SE1</u> If A is positive, or nonnegative and primitive, then

$$\lim_{t \to \infty} \frac{A^t}{\lambda_1^t} = \vec{v}_1 \vec{w}_1^T,$$

where $\vec{v}_1$ and $\vec{w}_1$ are right and left eigenvectors associated with the dominat eigenvalue λ_1, $\vec{w}_1^T \vec{v}_1 = 1$. If $\|\vec{v}_1\| = 1$, then

$$\lim_{t \to \infty} \frac{\vec{n}(t)}{\|\vec{n}(t)\|} = \vec{v}_1 .$$

$(\|\vec{n}(t)\| = |n_1(t)| + |n_2(t)| + \cdots + |n_m(t)| = L_1 \text{ norm}).$

If $\vec{n}(0)$ and $\vec{n}'(0)$ are different initial conditions, eventually $\vec{n}(t)$ and $\vec{n}'(t)$ grow at the same rate, λ_1 (<u>stable growth rate</u>) and they approach the same age structure, $\vec{v}_1$ (<u>stable age structure</u>). If $\lambda_1 = 1$ the population is called <u>stationary</u>.

(Cohen, 1979)

Example 1 Revisited
(primitive)

Let $\alpha = 2$.

$$L_1 = \begin{pmatrix} 0 & 6 & 12 \\ 1/2 & 0 & 0 \\ 0 & 1/3 & 0 \end{pmatrix}$$

$$\lambda_1 = 2, \quad \lambda_2 = -1 = \lambda_3$$

$$\vec{v}_1 = \frac{1}{31}\begin{pmatrix} 24 \\ 6 \\ 1 \end{pmatrix} \simeq \begin{pmatrix} .774 \\ .194 \\ .032 \end{pmatrix}$$

$$\begin{array}{ccccccccc}
t & 0 & 1 & 2 & 3 & & 10 & 11 \\
\vec{n}(t) & \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix} & \begin{pmatrix} 18 \\ 1/2 \\ 1/3 \end{pmatrix} & \begin{pmatrix} 7 \\ 9 \\ 1/6 \end{pmatrix} & \begin{pmatrix} 56 \\ 7/2 \\ 3 \end{pmatrix} & \cdots & \begin{pmatrix} 4959 \\ 1273 \\ 202 \end{pmatrix} & \begin{pmatrix} 10064 \\ 2480 \\ 424 \end{pmatrix} \\
\|\vec{n}(t)\| & 3 & 18.83 & 16.17 & 62.5 & & 6434 & 12968 \\
\frac{\vec{n}(t)}{\|\vec{n}(t)\|} & \begin{pmatrix} .333 \\ .333 \\ .333 \end{pmatrix} & \begin{pmatrix} .955 \\ .026 \\ .018 \end{pmatrix} & \begin{pmatrix} .433 \\ .557 \\ .010 \end{pmatrix} & \begin{pmatrix} .896 \\ .056 \\ .048 \end{pmatrix} & \cdots & \begin{pmatrix} .771 \\ .198 \\ .031 \end{pmatrix} & \begin{pmatrix} .776 \\ .191 \\ .033 \end{pmatrix}
\end{array}$$

$$\frac{\|\vec{n}(11)\|}{\|\vec{n}(10)\|} \approx 2.015$$

$\|\vec{n}\| = |n_1| + |n_2| + \cdots + |n_m|$.

Example 2 Revisited
(imprimitive)

Let $\alpha = 2$.

$$L_2 = \begin{pmatrix} 0 & 0 & 48 \\ 1/2 & 0 & 0 \\ 0 & 1/3 & 0 \end{pmatrix}$$

$$\lambda_1 = 2 \,, \quad \lambda_{2,3} = -1 \pm i\sqrt{3}$$

$$|\lambda_1| = |\lambda_2| = |\lambda_3| \,, \text{ index of imprimitivity} = 3$$

$$\vec{v}_1 = \frac{1}{31}\begin{pmatrix} 24 \\ 6 \\ 1 \end{pmatrix} \approx \begin{pmatrix} .774 \\ .194 \\ .032 \end{pmatrix}$$

$$\begin{array}{cccccccc}
t & 0 & 1 & 2 & 3 & 4 & 5 & 6 \\
\vec{n}(t) & \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix} & \begin{pmatrix} 48 \\ 1/2 \\ 1/3 \end{pmatrix} & \begin{pmatrix} 16 \\ 24 \\ 1/9 \end{pmatrix} & \begin{pmatrix} 8 \\ 8 \\ 8 \end{pmatrix} & \begin{pmatrix} 384 \\ 4 \\ 8/3 \end{pmatrix} & \begin{pmatrix} 128 \\ 192 \\ \frac{4}{3} \end{pmatrix} & \begin{pmatrix} 64 \\ 64 \\ 64 \end{pmatrix} \\
\|\vec{n}(t)\| & 3 & 48.83 & 40.17 & 24 & 390.67 & 321.33 & 192 \\
\dfrac{\vec{n}(t)}{\|\vec{n}(t)\|} & \begin{pmatrix} .333 \\ .333 \\ .333 \end{pmatrix} & \begin{pmatrix} .983 \\ .010 \\ .007 \end{pmatrix} & \begin{pmatrix} .399 \\ .599 \\ .003 \end{pmatrix} & \begin{pmatrix} .333 \\ .333 \\ .333 \end{pmatrix} & \begin{pmatrix} .983 \\ .010 \\ .007 \end{pmatrix} & \begin{pmatrix} .399 \\ .599 \\ .007 \end{pmatrix} & \begin{pmatrix} .333 \\ .333 \\ .333 \end{pmatrix}
\end{array}$$

Periodic Behavior: $\vec{n}(3t+i) = 2^{3t}\,\vec{n}(i) \,, \quad i = 1, 2, 3$

Rate of Convergence

Suppose A is positive or nonnegative and primitive with dominant eigenvalue λ_1 and associated positive left and right eigenvectors, $\vec{w}_1$, $\vec{v}_1$, $\vec{w}_1^T \vec{v}_1 = 1$. In addition, suppose the distinct eigenvalues of A, $\lambda_1, \lambda_2, \ldots, \lambda_g$ are ordered such that $\lambda_1 > |\lambda_2| \geq |\lambda_3| \geq \cdots |\lambda_g|$ and if $|\lambda_2| = |\lambda_3|$, the algebraic multiplicity of λ_2 is at least as great as that of λ_3 or of any other eigenvalue of the same modulus as λ_2. Then

$$A^t = \lambda_1^t \vec{v}_1 \vec{w}_1^T + O(t^{m_2 - 1} |\lambda_2|^t)$$

If $m_2 = 1$, then

$$\left\| \frac{\vec{n}(t)}{\lambda_1^t} - \vec{v}_1 \vec{w}_1^T \vec{n}(0) \right\| \leq k \left(\frac{|\lambda_2|}{\lambda_1} \right)^t.$$

The quantity $\rho = \frac{\lambda_1}{|\lambda_2|}$ is called the <u>damping ratio</u>. Convergence to the stable age distribution will be more rapid the larger λ_1 is in relation to $|\lambda_2|$.

- Caswell (1989)

Relationship Between The Discrete Leslie Model and the Continuous McKendrick von Foerster Equation

- McKendrick (1926) von Foerster (1959)

$n(a,t)$ = age distribution at time t.

$\mu(a)$ = per capita mortality rate at age a.

$m(a)$ = average number of female offspring per female of age a = maternity function.

McKendrick von Foerster

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

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

Leslie

$$n_i(t+1) = P_{i-1}\, n_{i-1}(t)$$
$$n_1(t+1) = \sum_{i=1}^{m} f_i\, n_i(t)$$

Relationship (Continued)

McKendrick von Foerster

$$B = \text{Births}(t, t+1) = \int_0^\infty \int_t^{t+1} m(a)\, n(a,x)\, dx\, da$$

$$\approx \int_0^\infty m(a) \left[\frac{n(a,t) + n(a,t+1)}{2} \right] da$$

$$\approx \frac{1}{2} \sum_{i=1}^{\infty} m_i \left[n_i(t) + n_i(t+1) \right]$$

$$\approx \frac{1}{2} \sum_{i=1}^{\infty} m_i \left[n_i(t) + p_{i-1} n_{i-1}(t) \right]$$

$$\approx \frac{1}{2} \sum_{i=1}^{\infty} \left[m_i + p_i m_{i+1} \right] n_i(t)$$

But

$$n_1(t+1) \approx \ell B$$

ℓ = probability of surviving for ½ time interval

$$n_1(t+1) \approx \sum_{i=1}^{m} \frac{\ell}{2} \left[m_i + p_i m_{i+1} \right] n_i(t)$$

Leslie $$n_1(t+1) \approx \sum_{i=1}^{m} f_i n_i(t)$$

- Caswell (1989)

Leslie $$n_i(t+1) = p_{i-1}\, n_{i-1}(t) = [1-\mu(i-1)]\, n_{i-1}(t)$$

Thus,

$$n_i(t+1) - n_{i-1}(t) = -\mu(i-1)\, n_{i-1}(t)$$

$$\underbrace{n_i(t+1) - n_i(t)} + \underbrace{n_i(t) - n_{i-1}(t)} = -\mu(i-1)\, n_{i-1}(t)$$

$$\Delta_t n \quad + \quad \Delta_i n \quad = -\mu(i-1)\, n_{i-1}(t)$$

$\Delta t = \Delta a = 1$, $a = i$

$$\frac{\Delta_t n}{\Delta t} + \frac{\Delta_a n}{\Delta a} = -\mu(a-\Delta t)\, n_{a-\Delta t}(t)$$

$\Delta t,\ \Delta a \to 0$

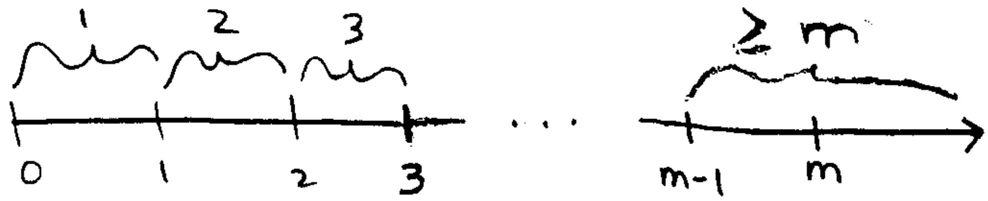
McKendrick Von Foerster $$\frac{\partial n(a,t)}{\partial t} + \frac{\partial n(a,t)}{\partial a} = -\mu(a)\, n(a,t)$$

Some Variations in Leslie Model

Include:

- Older ages ($\geq m$)
- Two sexes, include males and females
- Spatial distribution, multiregional models
- size or stage structure

Include Older Age Classes



p_m = proportion of females in age class $\geq m$ that survive one year.

$$n_i(t+1) = p_{i-1}\, n_{i-1}(t), \quad i = 2, \dots, m-1$$

$$n_m(t+1) = p_{m-1}\, n_{m-1}(t) + p_m\, n_m(t)$$

$$n_1(t+1) = \sum_{i=1}^{m} f_i\, n_i(t)$$

$$\vec{n}(t+1) = \begin{pmatrix} f_1 & f_2 & \cdots & f_{m-1} & f_m \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{m-1} & p_m \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_m(t) \end{pmatrix}$$

(De Angelis et al., 1980)

A Two Sex Model

Let

$$\vec{n}(t) = \left(n_{m_1}(t), n_{m_2}(t), \ldots, n_{m_k}(t), n_{f_1}(t), n_{f_2}(t), \ldots, n_{f_k}(t)\right)^T,$$

where $n_{m_i}(t)$ and $n_{f_i}(t)$ are males and females in age class i.

Three Age Classes:

$$L = \begin{pmatrix} 0 & 0 & 0 & f_{m_1} & f_{m_2} & f_{m_3} \\ p_{m_1} & 0 & 0 & 0 & 0 & 0 \\ 0 & p_{m_2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & f_{f_1} & f_{f_2} & f_{f_3} \\ 0 & 0 & 0 & p_{f_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & p_{f_2} & 0 \end{pmatrix} = \begin{pmatrix} L_{mm} & L_{mf} \\ 0 & L_{ff} \end{pmatrix}$$

This particular model is called <u>female dominant</u> two-sex model.

$$L^t = \begin{pmatrix} L^t_{mm} & g(L_{mm}, L_{mf}, L_{ff}) \\ 0 & L^t_{ff} \end{pmatrix}$$

Matrix L_{ff} is the Leslie matrix.

- Hansen (1989)

Include Spatial Distribution
Multi regional Models

Let

$$\vec{n}(t) = (n_{1,1}(t), n_{2,1}(t), \dots, n_{m,1}(t), \dots, n_{1,k}(t), \dots, n_{m,k}(t))^T$$

where $n_{i,j}(t)$ is the size of age class i in region j. Number of ages: $i = 1, \dots, m$. Number of regions: $j = 1, \dots, k$.

$$L = (L_{ij}),$$

where

L_{ij} represents transfer from region j to i, $j \neq i$

L_{ii} represents births, deaths and transfer out of region i.

Two regions and Three Age Classes:

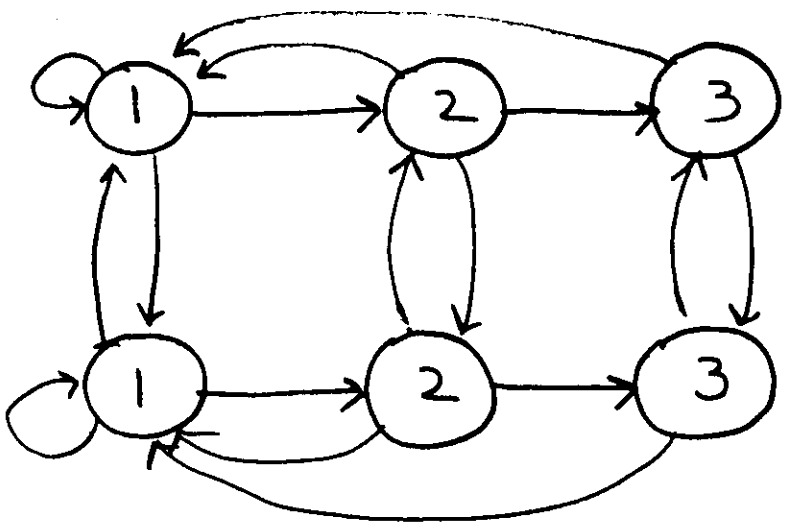
$$L_{ii} = \begin{pmatrix} 1 - d_{1,j,i} + f_{i1} & f_{i2} & f_{i3} \\ p_{i1} & 1 - d_{2,j,i} & 0 \\ 0 & p_{i2} & 1 - d_{3,j,i} \end{pmatrix} \text{region } i$$

$$L_{ij} = \begin{pmatrix} d_{1,i,j} & 0 & 0 \\ 0 & d_{2,i,j} & 0 \\ 0 & 0 & d_{3,i,j} \end{pmatrix}$$

Two regions and Three Age Classes:

$$L = \begin{pmatrix} 1-d_{1,2,1}+f_{11} & f_{12} & f_{13} & d_{1,1,2} & 0 & 0 \\ p_{11} & 1-d_{2,2,1} & 0 & 0 & d_{2,1,2} & 0 \\ 0 & p_{12} & 1-d_{3,2,1} & 0 & 0 & d_{3,1,2} \\ d_{1,2,1} & 0 & 0 & 1-d_{1,1,2}+f_{21} & f_{22} & f_{23} \\ 0 & d_{2,2,1} & 0 & p_{21} & 1-d_{2,1,2} & 0 \\ 0 & 0 & d_{3,2,1} & 0 & p_{22} & 1-d_{3,1,2} \end{pmatrix}$$

Associated Life Cycle Graph:



Region 1

Region 2

- Fahrig and Merriam (1985)

Reproduction is followed by movement to another region.

Two Regions:

$$D = \begin{pmatrix} 1-d_{11} & d_{12} \\ d_{21} & 1-d_{22} \end{pmatrix}$$

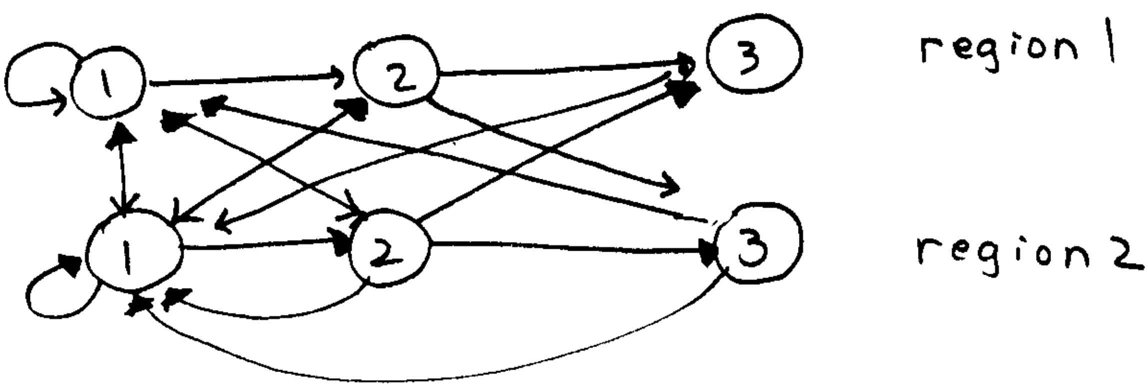
d_{ij} = proprotion of population moving from region j to i $i \neq j$, $0 \leq d_{ij} \leq 1$

$1-d_{ii}$ = proportion staying in region i, $0 \leq d_{ii} \leq 1$

If $d_{11} = d_{21}$ and $d_{12} = d_{22}$, then there is no loss or gain just an exchange of the population between the two regions.

If movement is the same for all age classes

$$D \otimes L = \begin{pmatrix} (1-d_{11})L & d_{12}L \\ d_{21}L & (1-d_{22})L \end{pmatrix}$$



Size or Stage Structure

The population is divided into size or stage classes. Each time unit individuals either stay in the same size or stage class or advance to the next size or stage class. Thus, the Leslie matrix has elements on the main diagonal or on the superdiagonal.

These types of models have applications in forestry, fisheries, pest management, wildlife management, etc. For example, insects have egg, larval, pupal, and adult stages, trees are usually classified in a breast-height diameter class and are harvested according to diameter class, populations in game parks are controlled by culling individuals of a particular age, size, or sex.

- Getz (1988) Getz and Haight (1989)

Insect Example

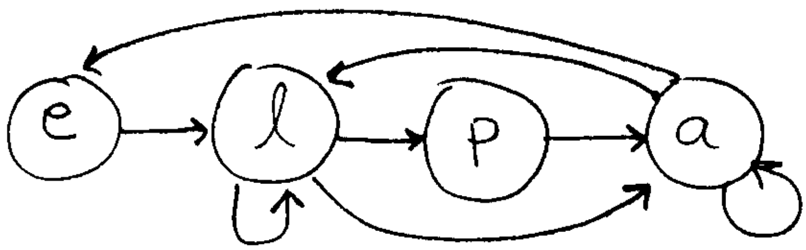
Insects have egg, larval, pupal, and adult stages.

Suppose the length of each stage is:

egg: 4 days
larval: 24 days
pupal: 5 days
adult: no eggs laid during first 8 days.

Suppose the time interval is one week.

$$M = \begin{pmatrix} 0 & 0 & 0 & m_{e,a} \\ m_{\ell,e} & m_{\ell,\ell} & 0 & m_{\ell,a} \\ 0 & m_{p,\ell} & 0 & 0 \\ 0 & m_{a,\ell} & m_{a,p} & m_{a,a} \end{pmatrix}$$



• Usher (1972)

Plant Example

Monocarpic Perennials reproduce once and die.

$$
\begin{array}{cc}
 & \begin{array}{ccc} S & J & F \end{array} \\
M_1 = & \begin{pmatrix} 0 & 0 & f p_0 \\ p_{JS} & p_{JJ} & V \\ 0 & p_{FJ} & 0 \end{pmatrix}
\end{array}
\quad
\begin{array}{l} \text{Seedlings } (S) \\ \text{Juveniles } (J) \\ \text{Flowering } (F) \end{array}
$$

f = number of seeds per plant.

p_0 = emergence rate of seeds.

p_{ij} = transition probability from stage j to stage i.

V = average number vegetatives per flowering plant.

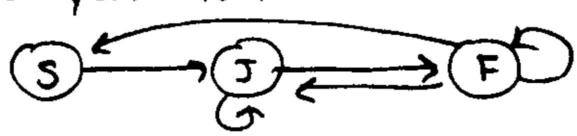
$$f,\ p_0,\ p_{ij} > 0, \quad V \geq 0.$$

M_1 is nonnegative and primitive

Polycarpic Perennials reproduce more than once.

$$
M_2 = \begin{pmatrix} 0 & 0 & f p_0 \\ p_{JS} & p_{JJ} & V \\ 0 & p_{FS} & p_{FF} \end{pmatrix}
$$

p_{FF} = probability flowering plant survives from one year to next.



- Takada and Nakajima (1992)

General Structured Matrix

Let

p_k = probability an individual in class k survives one unit of time.

p_{jk} = probability individual in class k at time t will be in class j at time $t+1$ given that it survives one unit of time.

$t_{jk} = p_k p_{jk}$ = expected fraction of individuals in class j from class k during one unit of time.

Transition Matrix:

$$T = (t_{jk}) \geq 0$$

Let

b_{jk} = expected number of j-class offspring per k class individual during one unit of time.

s_j = probability j class offspring born during any time interval survives to end of time interval.

$f_{jk} = s_j b_{jk}$ = expected number of j class newborns per k-class individuals at time $t+1$ due to births during t to $t+1$.

Fertility Matrix:

$$F = (f_{ij}) \geq 0$$

Let $\quad M = F + T, \quad M\vec{n}(t) = \vec{n}(t+1)$

• Cushing (1988)

Summary of Part

- Age Structure: Leslie matrix (Bernadelli, 1940; Lewis, 1942; Leslie, 1945, 1948)

$$\vec{n}(t+1) = L\vec{n}(t)$$

- Life Cycle Graphs
- Properties of L (Gantmacher, 1964)
  - (1) nonnegative
  - (2) irreducible
  - (3) primitive (Pollard, 1973)
- Examples
- Perron-Frobenius Theorems (Gantmacher, 1964; Caswell, 1989)
- Strong Ergodic Theorem (Cohen, 1979)
- Relationship to Continuous Model (Caswell, 1989 McKendrick, 1926; von Foerster, 1959)
- Rate of Convergence (Caswell, 1989)
- Variations in Leslie Matrix
  - (1) Older Ages (De Angelis et al., 1980)
  - (2) Two Sexes (Hansen, 1989)
  - (3) Spatial Distribution (Fahrig and Merriam, 1985)
  - (4) Size or Stage Structure (Getz, 1988; Getz and Haight, 1989)
- Examples
  - (1) Insect (Usher, 1972)
  - (2) Plant (Takada and Nakajima, 1992)
- General Structured Matrix (Cushing, 1989)

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