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I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

SMR.478 - 4

THIRD AUTUMN COURSE ON MATHEMATICAL ECOLOGY

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"Matrix Population Models"

Hal CASWELL
Woods Hole Oceanographic Institution
Department of Biology
Woods Hole, MA 02543
U.S.A.

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

Matrix Population Models

Hal Caswell

General references

H. Caswell 1989 Matrix Population Models $\boxed{\text{MPM}}$
Sinauer Associates, Sunderland, MA, 01375
U.S.A.

H. Caswell 1986 Life cycle models for plants
Lectures on Mathematics in the Life Sciences
18:171-233

Software

MATLAB (MS-DOS, Macintosh, Sun, Vax, ... Cray)
The MathWorks Inc.
21 Eliot St.
South Natick MA 01760
U.S.A.

Life cycle of the individual

life cycle stages

vital rates
[survival
growth
reproduction
development
migration
infection,
etc.]

Demographic models

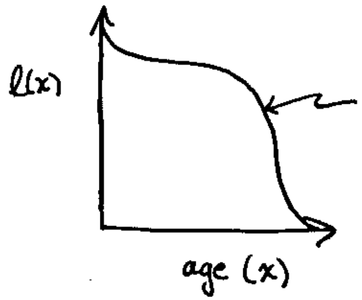
stages	time	models
discrete	discrete	matrix models
discrete	continuous	delay-differential equations (Nisbet & Gurney 1982)
continuous	continuous	partial differential equations (Metz & Diekmann 1986)

Dynamics of the population

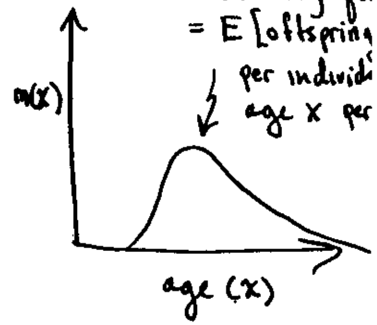
asymptotic dynamics
persistence / extinction
transient dynamics
perturbation analysis
selection / evolution

Classical Demography

Graunt 1662
Euler 1760
Lotka 1911



survivorship = P[survival from birth to age x]



maternity fc
= E[offspring
per individu
age x per

$B(t)$ = number of births at time t

$$= \int_0^\infty B(t-x)\, l(x)\, m(x)\, dx$$

conjecturing that $B(t) \longrightarrow Q e^{rt}$

$$1 = \int_0^\infty l(x)\, m(x)\, e^{-rx}\, dx$$

- exponential growth at rate r
- convergence of age distribution to stable form (ergodicity)

Pearl
Lack
Deevey
Birch
Park
⋮

Leslie Matrix

Leslie 1945, 1948
Bernardelli 1941
Lewis 1942

age classes $i = 1, 2, \dots, s$ (uniform width)

projection interval = age class width

P_i = P[survival from i to $i+1$ over interval t to $t+1$] = survival probability

F_i = E[age class 1 individuals at $t+1$ per age class i individual at t] = fertility

$\boxed{\text{$P_i$ and F_i calculated from $\ell(x)$ and $m(x)$ — see MPM, Chapter 2}}$

$$n_1(t+1) = \sum_i F_i n_i(t)$$

$$n_i(t+1) = P_{i-1} n_{i-1}(t) \qquad i = 2, 3, \dots s$$

$$\begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_s \end{pmatrix}(t+1) = \underbrace{\begin{pmatrix} F_1 & F_2 & \cdots & F_s \\ P_1 & 0 & \cdots & 0 \\ 0 & P_2 & \cdots & 0 \\ \vdots & & \ddots & \\ 0 & 0 \cdots & P_{s-1} & 0 \end{pmatrix}}_{\text{Leslie matrix}} \begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_s \end{pmatrix}(t)$$

Population projection matrices (general, stage-classified)

life cycle stages (size classes, age classes, developmental stages, instars, ...)

life cycle graph

j i nodes = stages $1, 2, \dots, s$

arc connecting n_j to n_i $\Leftrightarrow$ stage j at time t can contribute individuals to stage i at time $t+1$ → projection interval!

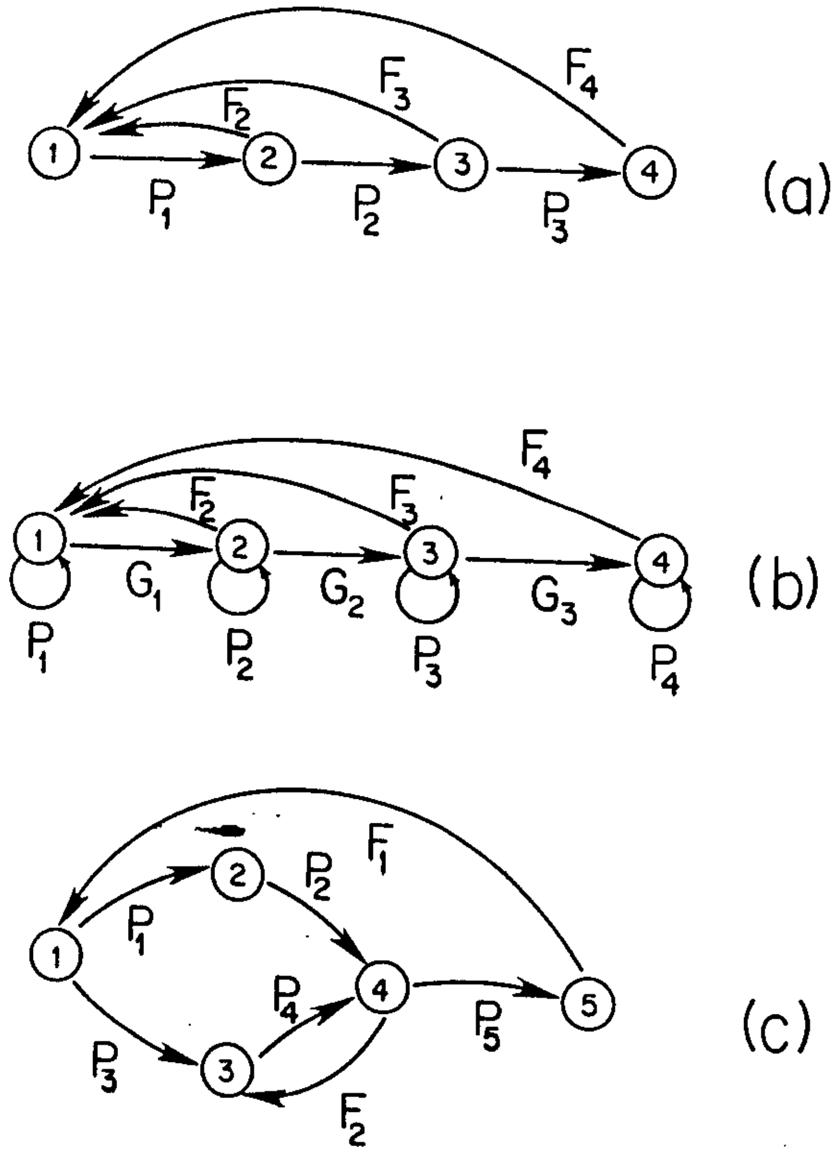
$j \longrightarrow i$

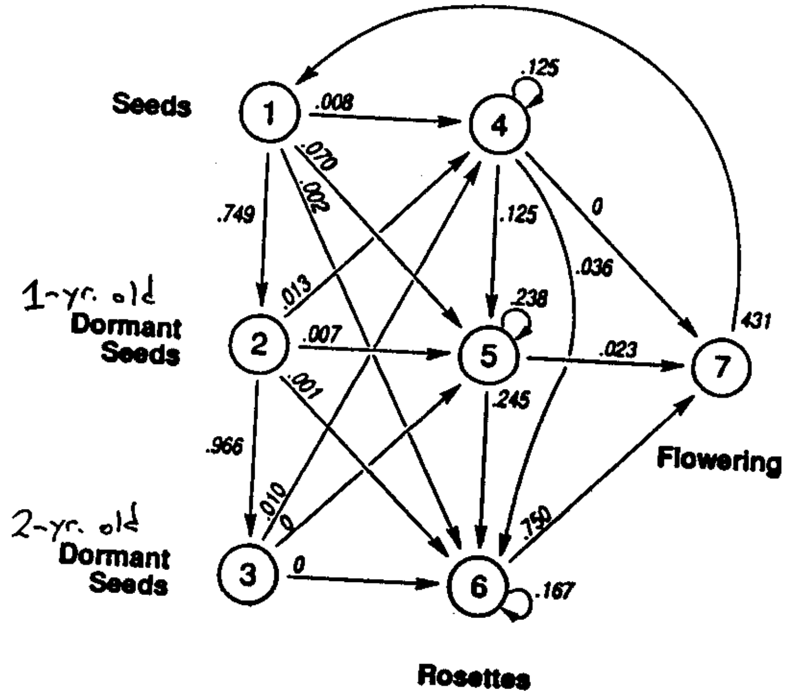
coefficient on arc from n_j to n_i = number of individuals in stage i at $t+1$ per individual in stage j at time t

$j \xrightarrow{a_{ij}} i$

$$\underline{n}(t+1) = \underline{A}\, \underline{n}(t)$$

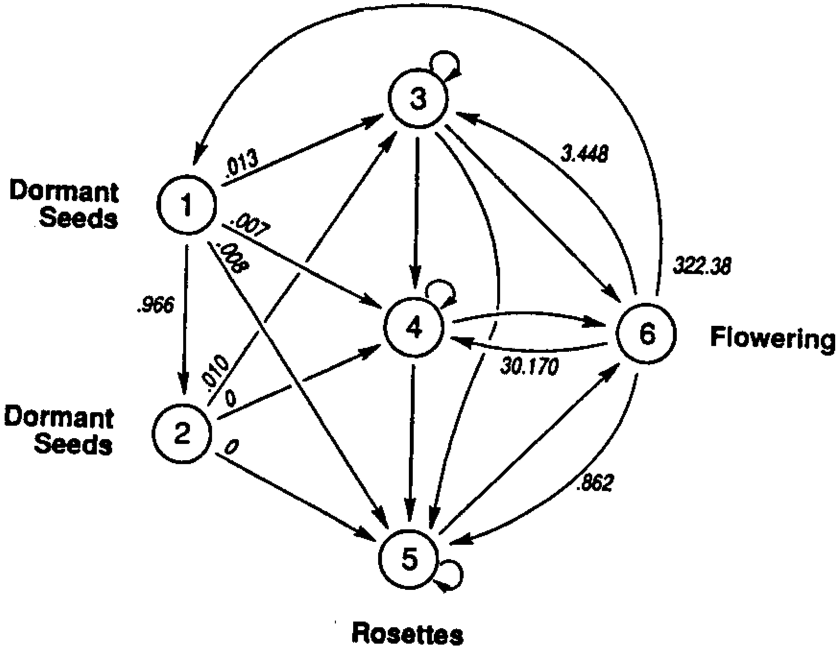
$$\underline{A} = (a_{ij})$$ = population projection matrix





Dipsacus sylvestris

(Werner & Caswell 1977)



State variables in population models

$e(t) \Longrightarrow \boxed{\text{object}} \xRightarrow{r(t)}$

$e(t) \in E$ = environment
excitation
stimulus

$r(t) \in R$ = response

Stimulus – response model

$g: E \to R \qquad r(t) = g(e(t))$ indeterminate (because of history)

State model

$x(t) \in X$ = "state" of object

$G: E \times X \to R \qquad r(t) = G(e(t), x(t))$ determinate (or Markovian)

$F: E \times X \to X \qquad x(t+1) = F(e(t), x(t))$

$$\frac{dx}{dt} = F(e(t), x(t))$$

So a state variable <u>must</u>

(1) summarize all information about object relevant to determining its response to the environment

(2) permit calculation of a new state which will satisfy (1) at the next time

$$\underline{n}(t+1) = \underbrace{\underline{A}\,\underline{n}(t)}_{F[\underline{n}(t),\, e(t)]}$$

state transition function

Metz & Diekman 1986

i-state – state of individual — age, size, sex, hunger, etc.

p-state – state of population = distribution of i-states(*) — age distribution, size distribution

⇒ to decide on a p-state, we can look at i-states

Question: does (age, size, sex, developmental stage, ⋮) determine the vital rates of an individual?

(statistical methods MPM Chapter 3)

(*) provided all individuals in a given i-state experience the same environment (this rules out certain kinds of strong local interaction)

When is age not an adequate state variable

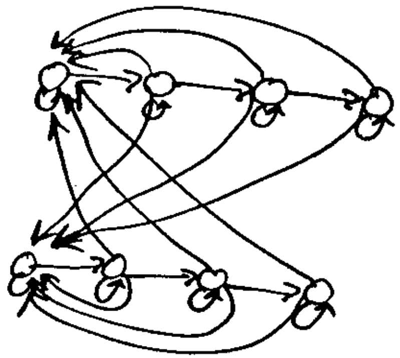
1. size-dependent vital rates + plastic growth
(stage-dependent)

    threshold size for maturity
    size-dependent mortality
    size-dependent reproductive output
    size-dependent sex change

modular construction

2. multiple modes of reproduction

3. spatial subdivision



Habitat 1

Habitat 2

Analysis of matrix models

$\underline{n}(t+1) = \underline{A}\,\underline{n}(t)$

$\underline{A}$: linear, time-invariant

$\underline{A}_t$: time-varying — stochastic / deterministic

$\underline{A}_n$: non-linear — density-dependent / frequency-dependent

$\underline{A}_{n,t}$: time-varying, nonlinear

interpretation?

Linear, time-invariant case

$\underline{n}(0) = \sum_i c_i \underline{w}_i$

$\underline{n}(1) = \underline{A}\,\underline{n}(0)$

$= \sum c_i \lambda_i \underline{w}_i$

$\underline{n}(2) = \sum c_i \lambda_i^2 \underline{w}_i$

$\underline{n}(t) = \sum_i c_i \lambda_i^t \underline{w}_i$

λ_i real, >1 

λ_i real, $\in (0,1)$ 

λ_i real, $\in (-1,0)$ 

λ_i real <-1 

λ_i complex $|\lambda_i|<1$ 

$\underline{A}\,\underline{w}_i = \lambda_i \underline{w}_i$

λ_i = eigenvalues $i = 1,2,\dots s$

$\underline{w}_i$ = right eigenvectors

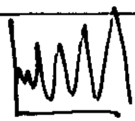
assume λ_i distinct $\Rightarrow \underline{w}_i$ linearly independent

$\underline{v}_i^* \underline{A} = \lambda_i \underline{v}_i^*$

$\underline{v}^*$ = left eigenvector of $\underline{A}$

$\underline{W} = (w_1\ w_2\ \cdots\ w_s)$

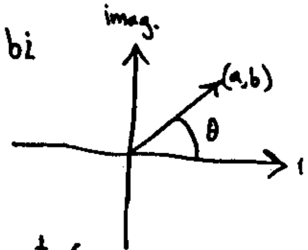
$\underline{V} = \begin{pmatrix} v_1^* \\ v_2^* \\ \vdots \\ v_s^* \end{pmatrix} = \underline{W}^{-1}$

λ_i complex, $|\lambda_i|>1$ 

Analysis (cont'd.)

$\underline{n}(t) = \sum c_i \lambda_i^t \underline{w}_i$

$\lambda_i = a + bi$



$\lambda_i^t = |\lambda_i|^t (\cos\theta t + i \sin\theta$

Perron-Frobenius theorem: describes the eigenvalue spectrum of a non-negative matrix

$\underline{A} \geq 0$

reducible

$\lambda_1 \geq 0$, real

$\lambda_1 \geq |\lambda_i|$ $i = 2,\dots s$

$\left.\begin{array}{l} \underline{w}_1 \geq 0 \\ \underline{v}_1 \geq 0 \end{array}\right\}$ real

irreducible $\Leftrightarrow$ life cycle graph strongly connected

imprimitive

g.c.d. of loop lengths = d
index of imprimitivity

$\lambda_1 > 0$, real

$\lambda_1 = |\lambda_2| = \dots = |\lambda_d|$

$\left.\begin{array}{l} \underline{w}_1 > 0 \\ \underline{v}_1 > 0 \end{array}\right\}$ real

primitive $\Leftrightarrow \underline{A}^k > 0$ for some $k>$

$\lambda_1 > 0$, real

$\lambda_1 > |\lambda_i|, i = 2,\dots s$

$\left.\begin{array}{l} \underline{w}_1 > 0 \\ \underline{v}_1 > 0 \end{array}\right\}$ real

$\Leftrightarrow$ irreducible and greatest common divisor of length of loops in life cycle graph = 1

$$\underline{n}(t) = \sum c_i \lambda_i^t \underline{w}_i$$

Analysis (cont'd)

$\underline{A}$ primitive $\left(\lambda_1 > |\lambda_i|,\ i = 2, \ldots s\right)$

$$\lim_{t \to \infty} \frac{\underline{n}(t)}{\lambda_1^t} = \lim_{t \to \infty} \sum c_i \frac{\lambda_i^t}{\lambda_1^t} \underline{w}_i$$

$$= c_1 \underline{w}_1$$

$\Rightarrow$ asymptotic growth rate λ_1

stable stage distribution $\underline{w}_1$

strong ergodic theorem of demography

$\underline{A}$ imprimitive

- stage distribution oscillates with period d
- mean stage distribution grows at rate λ_1

$\underline{A}$ reducible

- there exists one (or more) subsets of stages that can be analyzed independently: that portion of the population grows at a rate λ_1