

**A comparison theorem
in Population Dynamics**

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based on

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**Applications of Perron-Frobenius
theory to population dynamics**

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A tribute to
IVO MAREK
born 24 January 1933
from Hans Schneider
born 24 January 1927

POPULATION DEMOGRAPHY

Demography is the study of population in terms of its growth and decay, fertility and mortality,

John Impagliazzo, 1984

Models:

Continuous

Alfred J. Lotka [1880 -]

Discrete and Linear

P.H. Leslie, *Econometrica*, (1945, 1948)

E.G. Lewis (1941)

H. Bernadelli (1941)

Single sex

(St)age distribution

Age distribution - Leslie Matrix transition (mortality) matrix,

t_j prob of survival from j to $j + 1$

$$0 \leq t_j \leq 1$$

$$T = \begin{pmatrix} 0 & \cdots & 0 & 0 \\ t_1 & \cdots & 0 & 0 \\ \vdots & \cdots & \vdots & \vdots \\ 0 & \cdots & t_{n-1} & 0 \end{pmatrix}$$

the fertility matrix

f_j no of exp newbrns indiv age j

$$0 \leq f_j$$

$$F = \begin{pmatrix} f_1 & \cdots & f_{n-1} & f_n \\ 0 & \cdots & 0 & 0 \\ \vdots & \cdots & \vdots & \vdots \\ 0 & \cdots & 0 & 0 \end{pmatrix}$$

projection matrix.

$$P = T + F = \begin{pmatrix} f_1 & \cdots & f_{n-1} & f_n \\ t_1 & \cdots & 0 & 0 \\ \vdots & \cdots & \vdots & \vdots \\ 0 & \cdots & t_{n-1} & 0 \end{pmatrix}$$

$$Px = \begin{pmatrix} f_1x_1 + \cdots + f_nx_n \\ t_1x_1 \\ \vdots \\ t_{n-1}x_{n-1} \end{pmatrix}$$

Standard model of population demography:

$$x^0 \geq 0$$

$$x^k = Px^{k-1}, \quad k = 1, 2, \dots$$

“stable solution”

$$Pu = ru, \quad u \geq 0, r > 0$$

Question: does $(P/r)^n x$ tend to stable solution for all initial distributions x ?

Bernadelli, Lewis, Leslie

all unaware of Perron-Frobenius

Reproved P-F in this special case.

$f_j > 0$ implies P is (irred) primitive

Answer: Yes

GENERAL CASE

Stage models

$$T \geq 0, \quad \Sigma_j t_{ij} \leq 1$$

t_{ij} prob trans (j) \rightarrow (i)

$$\lim_k T^k x = 0, \forall x \iff \rho(T) < 1$$

$$F \geq 0$$

f_{ij} av. new by (j) in (i)

$$P = T + F$$

See e.g Caswell(2001)

plant lifecycle with vegetative and
seed reproduction,

$$\mathbf{T} = (1/2) \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix}$$

$$\mathbf{F} = (1/2) \begin{pmatrix} 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix}.$$

$$\mathbf{P} = \mathbf{T} + \mathbf{F} = (1/2) \begin{pmatrix} 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 \\ 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix}$$

Fundamental Theorem of Demography:

Cushing-Yecang (1998)
(aka Perron-Frobenius)

Let P be the projection matrix of a standard population model $x^k = P^k x^0$, $k = 0, 1, \dots$. Suppose that P is primitive with spectral radius $\rho(P) = r$ and has left and right Perron vectors v^t and u resp. normalized so that $v^t u = 1$. Then $(\lim_{k \rightarrow \infty} (P/r)^k = uv^t)$

$$\lim_{k \rightarrow \infty} x^0 / r^k = (v^t x^0) u.$$

Consequently, if $|x^k|$ denotes the total population at time k then

$$\lim_{k \rightarrow \infty} |x^k| = \begin{cases} 0 & \text{if } r < 1, \\ |(v^t x^0) u| & \text{if } r = 1, \\ \infty & \text{if } r > 1. \end{cases}$$

NET REPRODUCTIVE RATE R_0 Fischer(1930)?

Samuelson (1976): "the expected number of female babies that will be born to a representative female baby who throughout her life will be subject to the current age specific mortality and fertility rates"

$$\rho(T) < 1$$

$$I + T + T^2 + \dots = (I - T)^{-1}$$

dist of newborns from init dist over
lifetime

$$Fx + FTx + FT^2x + \dots = F(I - T)^{-1}x$$

$$Q := F(I - T)^{-1}$$

Next Generation matrix

$$R_0 := \rho(Q)$$

Stability and comparison theorem: Assume that a projection matrix $P = T + F$ is irreducible with T and F nonzero. Denote the growth rate $\rho(P)$ by r and the net reproductive rate $\rho(Q)$ by R_0 . Then

$$R_0 > 0,$$

$$\rho(T + F/R_0) = 1,$$

and one of the following holds:

$$1 < r < R_0,$$

$$r = 1 = R_0,$$

$$0 < R_0 < r < 1.$$

cf. Stein-Rosenberg
generalized in Elsner, Frommer,
Nabben, S , Szyld (2003)

SOME PROOFS

$R_0 > 0$ follows from

Proposition: Let T and F be nonnegative matrices with $\rho(T) < 1$ and $F \neq 0$. Suppose $T + F$ is irreducible and $Q = F(I - T)^{-1}$. Then, after a permutation similarity,

$$Q = \begin{pmatrix} Q_{11} & Q_{12} \\ 0 & 0 \end{pmatrix},$$

where Q_{11} is a nontrivial irreducible nonnegative matrix, Q_{12} is a nonnegative matrix every column of which has a positive entry, and the 0 rows of Q correspond to the 0 rows of F , if any.

S (1984), Szyld (1985)

$$\mathbf{y}^t \succeq \mathbf{0}, \quad R_0 \mathbf{y}^t = \mathbf{y}^t Q = \mathbf{y}^t F (I - T)^{-1}$$
$$\mathbf{y}^t (T + F/R_0) = \mathbf{y}^t$$

Hence

$$\rho(T + F/R_0) = 1$$

Case $R_0 > 1$

$$T + F/R_0 \preceq T + F \preceq R_0 T + F$$

Hence

$$1 = \rho(T + F/R_0) < \rho(T + F) = r$$

$$r < \rho(R_0 T + F) = R_0$$

INTUITIVE CONTENT

Suppose

$$r = \rho(P) = \rho(T + F) > 1$$

$$P^r x_0 \rightarrow \infty$$

Aim: Stationary Population

Birth/death control

$$(T + F) \longrightarrow (T + F)/r$$

Birth control $\quad \uparrow \downarrow$

$$T + F \longrightarrow T + F/R_0$$

Intuitive:

$$R_0 > r$$

A GENERALIZATION

Achieving a given growth rate s by
scaling F

THEOREM: Let P, T and F satisfy the previous conditions. For $s > \rho(T)$ define

$$q(s) = \rho(F(I - T/s)^{-1})/s.$$

Then $q(s) > 0$. Let $P(s) = T + F/q(s)$. Then its growth rate, $\rho(P(s))$, is s , and its net reproductive rate is

$$R_0(s) = R_0/q(s).$$

Further, one of the following holds:

$$\begin{aligned} 1 &= s = R_0(s), \\ 1 &< s < R_0(s), \\ 0 &< R_0(s) < s < 1. \end{aligned}$$

Population with outside adoption

$$T = \begin{pmatrix} 0 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} \quad F = \begin{pmatrix} 0 & .5 & .5 \\ 0 & .5 & .5 \\ 0 & 0 & 0 \end{pmatrix}$$

$$P = T + F = \begin{pmatrix} 0 & .5 & .5 \\ 1 & .5 & .5 \\ 0 & 1 & 0 \end{pmatrix}$$

$$Q = F(I - T)^{-1} = \begin{pmatrix} 1 & 1 & .5 \\ 1 & 1 & .5 \\ 0 & 0 & 0 \end{pmatrix}$$

$$r = \rho(P) = 1.4376 < 2 = \rho(Q) = R_0$$

$$u = \begin{pmatrix} 0.5898 \\ 1.0000 \\ 0.6956 \end{pmatrix}$$

For growth rate of s divide F by

$$q = \rho(F(I - T/s)^{-1})/s.$$

For growth rate of 1 divide F by R_0 .

In previous example $R_0(T + F) = 2$

$$P_1 = T + F/2 = \begin{pmatrix} 0 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} + \begin{pmatrix} 0 & .25 & .25 \\ 0 & .25 & .25 \\ 0 & 0 & 0 \end{pmatrix}$$

$$\rho(T + F/2) = R_0(T + F/2) = 1$$

$$u_1 = \begin{pmatrix} 0.5000 \\ 1.0000 \\ 1.0000 \end{pmatrix}$$

$$s = 2$$

$$q = \rho(F(I - T/2)^{-1})/2 = 0.5625$$

$$P_2 = T + F/2 = \begin{pmatrix} 0 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} + \begin{pmatrix} 0 & .88.. & .88.. \\ 0 & .88.. & .88.. \\ 0 & 0 & 0 \end{pmatrix}$$

$$u_2 = \begin{pmatrix} 0.6667 \\ 1.0000 \\ 0.5000 \end{pmatrix}$$

$$\begin{pmatrix} r \\ R_0 \\ \\ u \end{pmatrix} \begin{pmatrix} 1.4 & 1 & 2 \\ 2.0 & 1.0 & .56 \\ \\ .59 & .50 & .67 \\ .70 & 1.0 & 1.0 \\ 1.0 & 1.0 & .50 \end{pmatrix}$$

In epidemiology death control

Scale T

Consider $cT + F$

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THANK YOU!