Appendix C

(The theorem of Perron and Frobenius.)

Irreducible matrix:

- A non-negative square matrix is *irreducible* if its directed graph is *strongly connected*. (i.e., if there is a path from every node to every other node).

Graph of a non-negative square matrix $A = (a_{ij})$:

- Node j is connected to i if and only if $a_{ij} > 0$. We then write $(j) \longrightarrow (i)$

Example.

$$A := \begin{pmatrix} 0 & 0 & a_{13} & a_{14} \\ a_{21} & 0 & 0 & 0 \\ 0 & a_{32} & 0 & 0 \\ 0 & a_{42} & 0 & 0 \end{pmatrix}$$

Matrix.

$a_{13}, a_{14}, a_{21}, a_{32}, a_{42} > 0$.

- $\Downarrow$

$$\begin{tikzcd} ① \arrow[r, "a_{21}"] & ② \arrow[d, "a_{32}"] \arrow[dl, "a_{42}"] \\ ④ \arrow[u, "a_{14}"] & ③ \arrow[ul, "a_{13}"'] \end{tikzcd}$$

Graph.

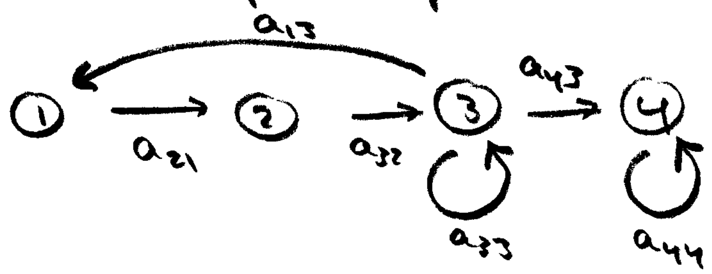
- The graph is obviously strongly connected

So, the matrix is irreducible

Example

Age-structured population with post-reproductive individuals (state 4).

Life-cycle graph:



Not strongly connected, because from (4) you cannot go to (1), (2) or (3).

Matrix:

$$A = \begin{pmatrix} 0 & 0 & a_{13} & 0 \\ a_{21} & 0 & 0 & 0 \\ 0 & a_{32} & a_{33} & 0 \\ 0 & 0 & a_{43} & a_{44} \end{pmatrix}$$

So, the corresponding matrix is not irreducible (i.e., reducible)

Theorem

$A \in \mathbb{R}^{d \times d}$ is irreducible if and only if $(I+A)^{d-1}$ is strictly positive

(**Proof.**
See: Horn & Johnson, 1985, pp. 507-520.)

$\boxed{\text{Primitive matrix}}$

a non-negative matrix A is primitive if it becomes strictly positive if raised to a sufficiently high power.

(i.e., if $\exists k > 0 : A^k > 0$).

Properties

- Any primitive matrix is irreducible.
- An irreducible matrix is primitive if the greatest common division of the lengths of all loops in the directed graph is equal to one.

(→ Rosenblatt, 1957).

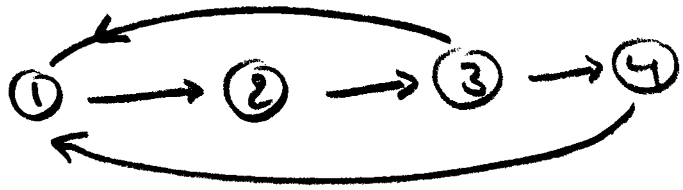
Theorem.

$A \in \mathbb{R}^{d \times d}$ is primitive if and only if $A^{d^2 - 3d + 2}$ is strictly positive.

(Proof.

See: Horn & Johnson, 1985, pp. 507–520.)

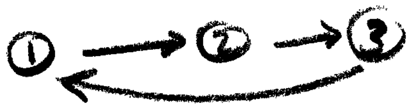
Example.



graph is strongly connected and there are at least two loops (namely ①→②→③ and ①→②→③→④) of lengths 3 and 4, which have a common divisor equal to one.

$\Rightarrow$ The corresponding matrix is <u>primitive</u>.

Example



Strongly connected, but the greatest common divisor is 3.

$\Rightarrow$ Corresponding matrix is irreducible but <u>not</u> primitive.

Perron-Frobenius. (P.F.)

(This is part of the P.F. theorem
Proof in, e.g., Horn & Johnson
1985)

① Suppose $A \in \mathbb{R}^{d \times d}$ is non-negative
and primitive.

Then there exists an eigenvalue
$\lambda_1 > 0$ which is a simple root of
the characteristic equation, and
which has associated left and
right eigenvectors $v_1 > 0$ and $w_1 > 0$
and all other eigenvalues λ_i
$(i \geq 2)$ satisfy $\lambda_1 > |\lambda_i|$.

② Suppose $A \in \mathbb{R}^{d \times d}$ is non-negative
and irreducible.

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of the characteristic equation and which has associated left and right eigenvectors $v_1 > 0$ and $w_1 > 0$, and all other eigenvalues λ_i $(i \geq 2)$ satisfy

$\lambda_1 \geq |\lambda_i|$, but if $\lambda_1 = |\lambda_i|$ for some $i \neq 1$, then λ_i is complex and has complex eigenvectors.

<u>Dominant eigenvalue</u>

The eigenvalue λ_1 above is called <u>the dominant</u> eigenvalue.

Application (discrete time)

Consider the discrete time invader dynamics

$$\boxed{m(t+1) = A\, m(t)} \in \mathbb{R}^d \quad (d>1).$$

where A is a constant, non-negative and primitive matrix, with eigenvalues $\lambda_1, \dots, \lambda_d$ and corresponding right eigenvectors $w_1, \dots, w_d$.

From the PF theorem we know that A has a dominant eigenvalue, which we can choose to be denoted λ_1.

Write

$$\Lambda = \begin{pmatrix} \lambda_1 & & 0 \\ & \ddots & \\ 0 & & \lambda_d \end{pmatrix} \quad \text{and} \quad W = (w_1, \dots, w_d).$$

Both are $d \times d$ matrices, and

$$\boxed{AW = W\Lambda}$$

Assume that W is nonsingular (i.e., $w_1, \dots, w_d$ are linearly independent)

Then

$$\boxed{A = W \Lambda W^{-1}}$$

and hence

$$\boxed{W^{-1} m(t+1) = \Lambda \cdot W^{-1} m(t)}$$

which is a system of decoupled difference equations with solution

$$\boxed{W^{-1} m(t) = \Lambda^t W^{-1} m(0)}$$

and so

(*) $$\boxed{m(t) = W \Lambda^t W^{-1} m(0)}$$

where

$$\boxed{\Lambda^t = \begin{pmatrix} \lambda_1^t & & 0 \\ & \ddots & \\ 0 & & \lambda_d^t \end{pmatrix}}$$

Since the eigenvectors $w_1, \dots, w_d$ are assumed to be lin. indep there exists a (complex-valued) vector $c = (c_1, \dots, c_d)$ such that

$$\boxed{m(0) = c_1 w_1 + \dots + c_d w_d = Wc}$$

Substitution into (*) gives

$$\boxed{m(t) = W\Lambda^t \cancel{W^{-1}} \cancel{W} c = W\Lambda^t c}$$

that is,

$$\boxed{m(t) = \sum_{i=1}^{d} c_i \lambda_i w_i}$$

Since $\lambda_1 > 0$ (P.F.) we can write

$$\boxed{\frac{m(t)}{\lambda_1^t} = c_1 w_1 + \sum_{i \geq 2} c_i \left(\frac{\lambda_i}{\lambda_1}\right)^t w_i}$$

and since $\lambda_1 > |\lambda_i| \ \forall i \geq 2$ (P.F) $(\lambda_i/\lambda_1)^t \to 0$ as $t \to \infty$, and hence

(**) $$\boxed{\lim_{t\to\infty} \frac{m(t)}{\lambda_1^t} \to c_1 w_1}$$

In other words, the structure of the population converges to the dominant eigenvector as $t \to \infty$, which is known as the <u>strong ergodic theorem</u>

Taking norms and logarithms in (**) and then dividing by t gives

$$\underbrace{\lim_{t\to\infty} \frac{\log \|u(t)\|}{t}}_{\text{invasion fitness}} - \log \lambda_1 = 0$$

$$\Rightarrow \boxed{\text{invasion fitness} = \text{logarithm dominant eigenvalue}}$$

(discrete time)

Application (cont. time)

$$\dot{m} = A\, m \quad \in \mathbb{R}^d \quad (d \geq 2)$$

where A is a constant matrix with non-negative off-diagonal elements, and eigen values $\lambda_1, \dots, \lambda_d$ and corresponding right-eigen vectors $w_1, \dots, w_d$.

Let $\mu > 0$ such that $A + \mu I$ is non-negative (i.e., also on the diagonal) and suppose $A + \mu I$ is irreducible.

(note, that this is a condition on A (not on μ), and therefore we can also say that A is irreducible even if its diagonal elements may be negative)

The eigenvalues of $A+\mu I$ are $\lambda_1+\mu, \ldots, \lambda_d+\mu$ and the associated eigenvectors $w_1, \ldots, w_d$.

By the PF-theorem we know that $A+\mu I$ has a dominant eigenvalue, which we can take to be $\lambda_1+\mu$. Hence, for all $i \neq 1$:

$$\boxed{\lambda_1} = (\lambda_1+\mu)-\mu \overset{\text{P.F.②}}{\geq} |\lambda_i+\mu| - \mu \overset{\text{triangel inequal.}}{\geq}$$

$$\geq |\mathrm{Re}(\lambda_i+\mu)| - \mu \underset{\text{P.F.②}}{\geq} \mathrm{Re}(\lambda_i+\mu) - \mu = \boxed{\mathrm{Re}\,\lambda_i}$$

In short:

$$(*) \quad \boxed{\lambda_1 > \mathrm{Re}\,\lambda_i \quad \forall i \neq 1}$$

Solving $\dot{m} = A m$ gives

$$(**) \quad \boxed{m(t) = W e^{\Lambda t} W^{-1} m(0)}$$

where

$$\Lambda = \begin{pmatrix} \lambda_1 & & 0 \\ & \ddots & \\ 0 & & \lambda_d \end{pmatrix} \text{ and } W = (w_1, \ldots, w_d)$$

and assuming that W is not singular.

Write $m(0)$ as a linear combination of $w_1, \dots, w_d$:

$$\boxed{m(0) = \sum_{i=1}^{d} w_i c_i = Wc}$$

where $c = (c_1, \dots, c_d) \in \mathbb{C}^d$.

Then, from (**) on prev. page,

$$\boxed{\begin{aligned} m(t) &= W e^{\Lambda t} c = \\ &= \sum_{i=1}^{d} c_i e^{\lambda_i t} w_i \end{aligned}}$$

Hence

$\mathrm{Re}(\lambda_i - \lambda_1) < 0$

$$\boxed{\begin{aligned} e^{-\lambda_1 t} m(t) &= c_1 w_1 + \sum_{i \geq 2} c_i e^{(\lambda_i - \lambda_1)t} w_i \\ &\to c_1 w_1 \quad \text{as } t \to \infty. \end{aligned}}$$

So, the structure of the invader population converges to the dominant eigenvector as $t \to \infty$

(Strong ergodic theorem).

$$\boxed{e^{-\lambda_1 t}\, m(t) \longrightarrow c_1 w_{11}}$$ as $t \to \infty$

Taking norms, logarithm and dividing by t gives

$$\boxed{\underbrace{\frac{\log \|m(t)\|}{t}}_{\text{invasion fitness}} - \lambda_1 \longrightarrow 0}$$ as $t \to \infty$.

In other words:

$$\boxed{\text{invasion fitness} = \text{dominant eigenvalue}}$$

(continuous time).