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 $j \rightarrow i$. 
**Example.**

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

**Matrix:**

\[ a_{13}, a_{14}, a_{21}, a_{32}, a_{42} > 0 \]

**Graph:**

The graph is obviously **strongly connected**.

So, the matrix is **irreducible**.
Example

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

Life-cycle graph:

\[ 
\begin{array}{c}
1 \\
\downarrow a_{21} \\
3 \\
\downarrow a_{32} \\
4 \\
\uparrow a_{43} \\
\end{array} 
\]

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

Matrix:

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

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:**


**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

\[ A \in \mathbb{R}^{d \times d} \text{ is primitive if and only if } A^{m-1} \neq 0 \text{ for some } m \text{ and } A^{m-1} \text{ is strictly positive.} \]

Proof

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

$$
\begin{array}{ccccc}
1 & \rightarrow & 2 & \rightarrow & 3 & \rightarrow & 4 \\
& \nearrow & & \nwarrow & & \searrow & \\
4 & \leftarrow & 3 & \leftarrow & 2 & \leftarrow & 1
\end{array}
$$

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

$\Rightarrow$ The corresponding matrix is **primitive**.

Example

$$
\begin{array}{ccc}
1 & \leftrightarrow & 2 & \rightarrow & 3 \\
& \swarrow & & \searrow & \\
3 & \leftarrow & 2 & \leftarrow & 1
\end{array}
$$

Strongly connected, but the greatest common divisor is 3.

$\Rightarrow$ Corresponding matrix is **irreducible** but not **primitive**.
Perron–Frobenius (P.F.)

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

1. Suppose $A \in \mathbb{R}^{n \times n}$ 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 $\lambda_i$ ($i > 2$) satisfy $\lambda_i > 12 \lambda_1$.

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

Then there exists an eigenvalue $\lambda_1 > 0$ which is a simple root.
of the characteristic equation and which have associated left
and right eigenvectors \( v, \geq 0 \) and \( w, \geq 0 \), and all other eigen-
values \( \lambda_i \ (i \neq 2) \) satisfy
\[ \lambda_i \geq 12;1, \text{ but if } \lambda_i = 12;1 \text{ for some } i \neq 1, \text{ then } \lambda_i \text{ is complex and has complex eigenvectors.} \]

---

**Dominant eigenvalue**

The eigenvalue \( \lambda_1 \) above is called the **dominant eigenvalue**.
Application (discrete time)

Consider the discrete time invader dynamics

\[ \mathbf{w}(t+1) = A \mathbf{w}(t) \quad \in \mathbb{R}^d \quad (d \geq 1) \]

where \( A \) is a constant, non-negative and primitive matrix, with eigenvalues \( \lambda_1, \ldots, \lambda_d \) and corresponding right eigen vectors \( \mathbf{w}_1, \ldots, \mathbf{w}_d \).

From the Perron-Frobenius theorem we know that \( A \) has a dominant eigenvalue, which we can choose to be denoted \( \lambda_1 \).

Write

\[ \Lambda = \begin{pmatrix} \lambda_1 & \mathbf{0} \\ \mathbf{0} & \lambda_d \end{pmatrix} \quad \text{and} \quad \mathbf{W} = \begin{pmatrix} \mathbf{w}_1 \\ \vdots \\ \mathbf{w}_d \end{pmatrix} \]

Both are \( d \times d \) matrices, and

\[ A \mathbf{W} = \mathbf{W} \Lambda \]

Assume that \( W \) is nonsingular (i.e., \( w_1, \ldots, w_d \) are linearly independent)
Then
\[ A = W W^{-1} \]
and hence
\[ W^{t} m(t+1) = \Lambda W^{t} m(t) \]
which is a system of decoupled difference equations, with solution
\[ W^{t} m(t) = \Lambda^{t} W^{t} m(0) \]
and so
\[ m(t) = W^{t} W^{-1} m(0) \]
where
\[ \Lambda^{t} = \begin{pmatrix} 2^{t} & 0 \\ 0 & 2^{t} \end{pmatrix} \]
Since the eigenvectors \( w_{1}, \ldots, w_{d} \) are assumed to be l.u. indep, there exists a (complex-valued) vector \( c = (c_{1}, \ldots, c_{d}) \) such that
\[ m(0) = c_{1} w_{1} + \cdots + c_{d} w_{d} = Wc \]
Substitution into \( \star \) gives
\[ w(t) = W^t W^T Wc = W^t c \]

Thus, in,

\[ w(t) = \sum_{i=1}^{N} c_i \lambda_i^t w_i \]

Since \( \lambda_i > 0 \) (P,F) we can write

\[ \frac{w(t)}{\lambda_i^t} = c_i w_i + \sum_{i \geq 2} c_i (\frac{\lambda_i}{\lambda_1})^t w_i \]

and since \( \lambda_i > 1 \), \( \lambda_i \geq 2 \) (P,F)

\( (\lambda_2 / \lambda_1)^t \rightarrow 0 \) as \( t \rightarrow \infty \), and hence

\[ \lim_{t \rightarrow \infty} \frac{w(t)}{\lambda_i^t} \rightarrow c_i w_i \]

In other words, the structure of the population converges to the dominant eigen vector as \( t \rightarrow \infty \), which is known as the strong ergodic theorem.

Taking norms and logarithms in ** and then dividing by \( t \) gives
\[
\lim_{t \to 0} \frac{\log \mu(t) s(t)}{t} - \log \lambda_1 = 0
\]

\[\Rightarrow \text{invasion fitness} = \frac{\log \text{arithmetic dominant eigenvalue}}{\text{discrete tone}}\]
Application (cont'd)

\[ \mathbf{m} = A \mathbf{m} \in \mathbb{R}^d \quad (d \geq 2) \]

where \( A \) is a constant matrix with non-negative off-diagonal elements, and eigen values \( 2, \ldots, 2d \) and corresponding right eigen vectors \( \mathbf{w}_1, \ldots, \mathbf{w}_d \).

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

Note, that this is a condition on \( A \) (not on \( \mu \)), 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 P.F. theorem we know that $A + \mu I$ has a dominant eigenvalue, which we can take to be $\lambda_1 + \mu$. Hence, for all $i \neq 1$:

$$|\lambda_i| = |(\lambda_1 + \mu) - \mu| \geq |\lambda_i + \mu| - |\mu| \geq |\text{Re}(\lambda_i + \mu)| - |\mu| = |\text{Re}\lambda_i|$$

So we show:

$$\lambda_i > \text{Re}\lambda_1 \quad \forall i \neq 1$$

Solving $w_i = A w_i$ given

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

where

$$\Lambda = \begin{pmatrix} \lambda_1 & & \\
& \ddots & \\
& & \lambda_d \end{pmatrix}$$

and $W = (w_1, \ldots, w_d)$
and assuming that \( W \) is not singular.

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

\[
m(0) = \sum_{i=1}^{d} w_i \cdot c_i = Wc
\]

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

Then, from (2) on prev. page,

\[
m(t) = W e^{At} c = \sum_{i=1}^{d} c_i e^{\lambda_i t} w_i
\]

Hence

\[
e^{-\lambda_1 t} m(t) = c_1 w_1 + \sum_{i \neq 1} c_i e^{\lambda_i t} w_i
\]

\[
\rightarrow c_1 w_1, \text{ as } t \rightarrow \infty.
\]

So, the structure of the invader population converges to the dominant eigenvector as \( t \rightarrow \infty \)

(Strong ergodic theorem)
\( e^{-2t} \) maps \( c, w \) on \( t \to \infty \)

Taking norms, logarithms and dividing by \( t \) gives

\[
\log \left| \frac{\| u \|_2}{t} \right| - 2, \quad t \to 0 \quad \text{on } t \to 0
\]

Invasion fitness:

\[
\text{invasion fitness} = \frac{\text{dominant eigenvalue}}{(\text{continuous time})}
\]