MATH 4370/7370 – Linear Algebra and Matrix Analysis

An example from metapopulations

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Outline

Position of the problem

A metapopulation of sources and sinks with explicit movement

The movement matrix

Local analysis of the model

Global behaviour

An interesting special case

Mathematical w.l.o.g. $\neq$ numerical w.l.o.g.

Why do this?

This work is mostly about dynamics

Looping back to our first few lectures: *matrices are everywhere*!

This is a (rather abstract) problem in theoretical ecology (or mathematical ecology?)

We will be using a surprising number of results we have already seen

Rael & Taylor (2018)

A flow network model for animal movement on a landscape with application to invasion, Theoretical Ecology

$$P_i' = P_i B(P_i) + \sum_{j=1}^{N} a_{ji} P_j m(P_j, P_i) - P_i \sum_{j=1}^{N} a_{ij} m(P_i, P_j)$$

where

$$m(P_i, P_j) = \frac{\max\{0, \pi(P_i) - \pi(P_j)\}}{d_{ij}} \qquad \pi(P_i) = \frac{P_i}{K_i}$$

d_{ij} distance from i to j, K_i carrying capacity

$$B(P_i) = \begin{cases} r_i \left(1 - \dfrac{P_i}{K_i}\right) & \text{sources} \\ -r_i & \text{sinks} \end{cases}$$

Bulletin of Mathematical Biology (2019) 81:1916–1942
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Society for Mathematical Biology

Check for updates

Number of Source Patches Required for Population Persistence in a Source–Sink Metapopulation with Explicit Movement

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Position of the problem

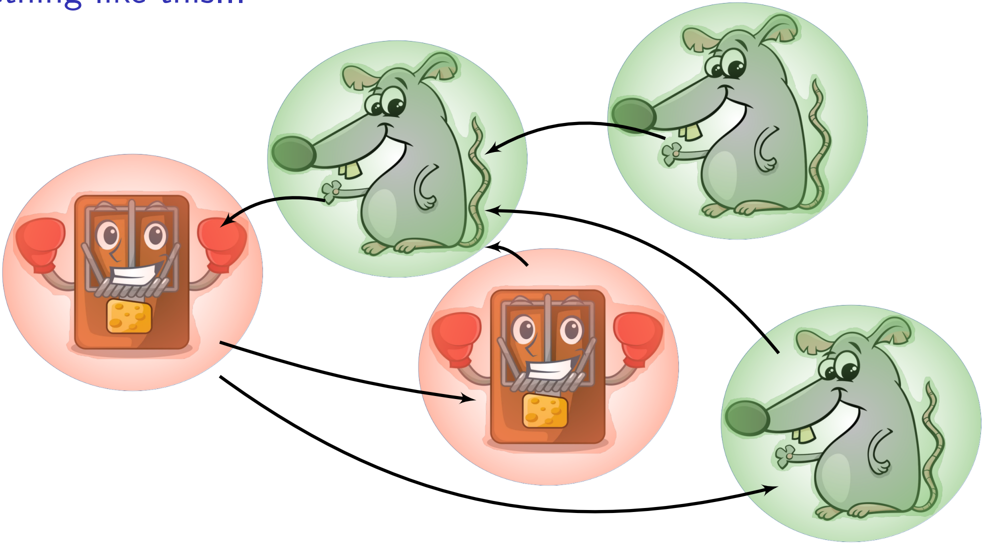
Assume a metapopulation of patches connected through transport of individuals between them

Some patches are sources, others are sinks:

- Population tends to persist in sources
- Population tends to vanish in sinks

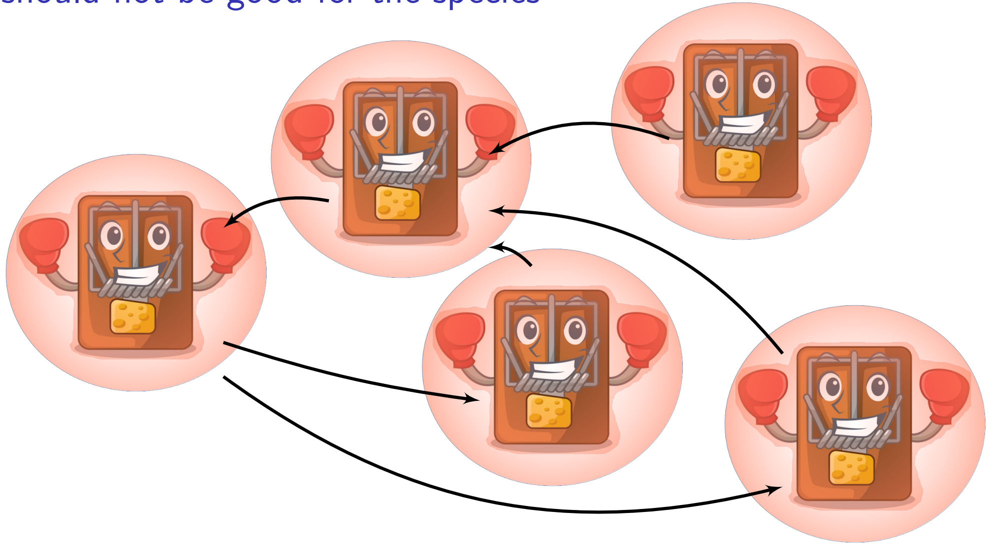
Ceteris paribus, does there exist a ratio of the number of source to sink patches s.t. the population of the coupled system persists?

Something like this...

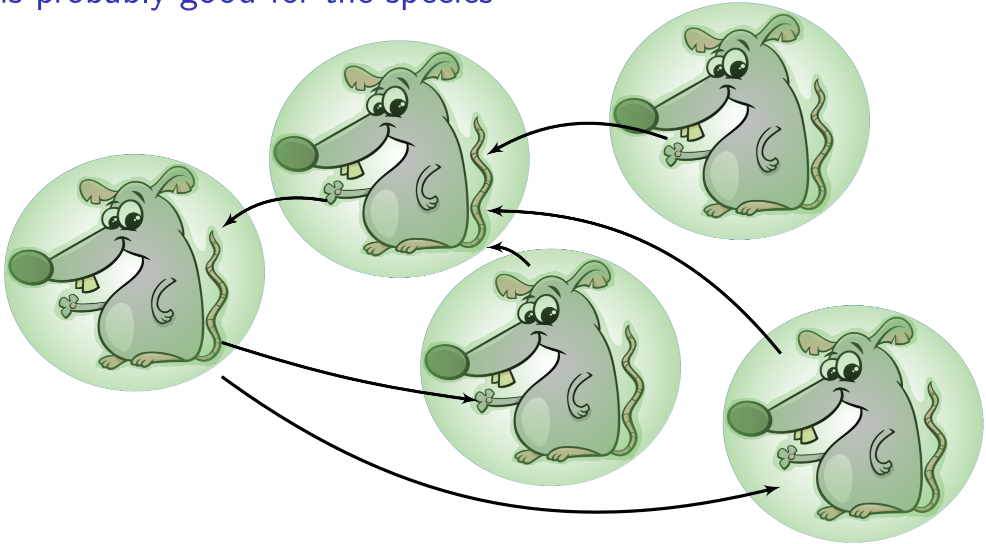


Obvious special cases

This should not be good for the species



This is probably good for the species



Model for N patches

W.l.o.g.: $S \geq 0$ first patches are sources, $N - S$ remaining are sinks [w.l.o.g. but not that trivial nonetheless]

Sources:

$$P_i' = r_i P_i \left(1 - \frac{P_i}{K_i}\right) + \sum_{j=1}^{N} m_{ij} P_j, \quad i = 1, \ldots, S \tag{1a}$$

Sinks:

$$P_i' = -r_i P_i + \sum_{j=1}^{N} m_{ij} P_j, \quad i = S+1, \ldots, N \tag{1b}$$

$$m_{ii} = -\sum_{\substack{j=1 \\ j \neq i}}^{N} m_{ji}$$

Vector form (v1)

$\mathbf{P} = (P_1, \ldots, P_N)^T$

$$\mathbf{P}' = \mathbf{G}(\mathbf{P})\mathbf{P} + \mathcal{M}\mathbf{P}$$

where

$$\mathbf{G}(\mathbf{P}) = \operatorname{diag}\left(r_1\left(1 - \frac{P_1}{K_1}\right), \ldots, r_S\left(1 - \frac{P_S}{K_S}\right), -r_{S+1}, \ldots, -r_N\right)$$

$$\mathcal{M} = \begin{pmatrix} -\sum\limits_{\substack{j=1 \\ j\neq 1}}^{N} m_{j1} & m_{12} & \cdots & m_{1N} \\ m_{21} & -\sum\limits_{\substack{j=1 \\ j\neq 2}}^{N} m_{j2} & \cdots & m_{2N} \\ & & \ddots & \\ m_{N1} & m_{N2} & \cdots & -\sum\limits_{\substack{j=1 \\ j\neq N}}^{N} m_{jN} \end{pmatrix}$$

Vector form (v2)

$$\mathbf{P}_s = (P_1, \ldots, P_S)^T \text{ (sources)}, \quad \mathbf{P}_t = (P_{S+1}, \ldots, P_N) \text{ (sinks)}$$

$$\begin{aligned}
\mathbf{P}_s' &= \mathbf{G}_s(\mathbf{P}_s)\mathbf{P}_s + \mathcal{M}_s\mathbf{P}_s + \mathcal{M}_{st}\mathbf{P}_t \\
\mathbf{P}_t' &= -\mathcal{D}_t\mathbf{P}_t + \mathcal{M}_{ts}\mathbf{P}_s + \mathcal{M}_t\mathbf{P}_t
\end{aligned}$$

where

$$\begin{aligned}
\mathbf{G}_s(\mathbf{P}_s) &= \operatorname{diag}\left(r_1\left(1-\frac{P_1}{K_1}\right), \ldots, r_S\left(1-\frac{P_S}{K_S}\right)\right) \\
\mathcal{D}_t &= \operatorname{diag}\left(r_{S+1}, \ldots, r_N\right) \\
\begin{pmatrix} \mathcal{M}_s & \mathcal{M}_{st} \\ \mathcal{M}_{ts} & \mathcal{M}_t \end{pmatrix} &= \mathcal{M}
\end{aligned} \tag{2}$$

Main result we want to get to

Theorem 8.1

$\exists$ a unique critical interval $\mathcal{S}_{int} \subset (0, N) \subset \mathbb{R}$ s.t. if the number of source patches $S < \min(\mathcal{S}_{int})$, the population-free equilibrium (PFE) $(P_1, \ldots, P_N) = (0, \ldots, 0)$ of (1) is locally asymptotically stable and if $S > \max(\mathcal{S}_{int})$, the PFE is unstable

If, additionally, the digraph of patches is strongly connected, then $\mathcal{S}_{int}$ reduces to a single point S^c and the PFE is globally asymptotically stable in the case that $S < S^c$; in the case that $S > S^c$, there is a unique component-wise positive equilibrium $\mathbf{P}^*$ that is GAS with respect to $\mathbb{R}_+^N \setminus \{0\}$

Properties of the movement matrix $\mathcal{M}$

Lemma 8.2

1. $0 \in \sigma(\mathcal{M})$ *corresponding to left e.v.* $\mathbb{1}^T$ *[σ spectrum]*
2. $-\mathcal{M}$ *is a singular M-matrix*
3. $0 = s(\mathcal{M}) \in \sigma(\mathcal{M})$ *[s spectral abscissa]*
4. *If* $\mathcal{M}$ *irreducible, then* $s(\mathcal{M})$ *has multiplicity 1*

Proof of Lemma 8.2

1. The result is obvious: all column sums of $\mathcal{M}$ equal zero, i.e., $\mathbb{1}^T \mathcal{M} = 0\mathbb{1}^T$

3. Using the Gershgorin Disk Theorem A.3 on $\mathcal{M}$ indicates that all Gershgorin disks are tangent to the imaginary axis at $(0, 0)$. As 0 is an eigenvalue of $\mathcal{M}$, it follows that $s(\mathcal{M}) = 0$

4. This is a direct consequence of using the Perron-Frobenius Theorem A.5 on the essentially nonnegative matrix $\mathcal{M}$

Proof of Lemma 8.2 (cont'd)

2. From the Gershgorin Disk Theorem A.3, all eigenvalues of $-\mathcal{M}$ belong to disks that lie to the right of the imaginary axis and, from the zero column sums, are tangent to that axis at $(0, 0)$

Now consider $-\mathcal{M} + \varepsilon\mathbb{I}$, for $\varepsilon > 0$. This shifts the centers of all Gershgorin disks to the right by ε Theorem A.1 but does not change their radii, so all disks now lie strictly to the right of the imaginary axis

Thus all eigenvalues of $-\mathcal{M} + \varepsilon\mathbb{I}$ have positive real parts

Furthermore, $-\mathcal{M}$ and $-\mathcal{M} + \varepsilon\mathbb{I}$ are of class Z_n (Definition A.6). Theorem A.7(18) $\implies -\mathcal{M} + \varepsilon\mathbb{I}$ is of class K, i.e., an M-matrix. Since this is true for all $\varepsilon > 0$, Theorem A.8(1) implies that $-\mathcal{M}$ is of class K_0. So $-\mathcal{M}$ is an M-matrix and it is singular

Properties of the movement matrix $\mathcal{M}$ (cont'd)

Proposition 8.3 (D a diagonal matrix)

1. $s(\mathcal{M} + d\mathbb{I}) = d$, $\forall d \in \mathbb{R}$
2. $s(\mathcal{M} + D) \in \sigma(\mathcal{M} + D)$ *associated to* $\mathbf{v} > \mathbf{0}$. *If* $\mathcal{M}$ *irreducible,* $s(\mathcal{M} + D)$ *has multiplicity 1 and is associated to* $\mathbf{v} \gg \mathbf{0}$
3. $\mathrm{diag}(D) \gg \mathbf{0} \implies D - \mathcal{M}$ *invertible M-matrix and* $(D - \mathcal{M})^{-1} > \mathbf{0}$
4. $\mathcal{M}$ *irreducible and* $\mathrm{diag}(D) > \mathbf{0} \implies D - \mathcal{M}$ *nonsingular irreducible M-matrix and* $(D - \mathcal{M})^{-1} \gg \mathbf{0}$

Proof of Proposition 8.3

1. From Lemma 8.2(3), $s(\mathcal{M}) = 0$. Therefore, using a "spectrum shift" Theorem A.1, $s(\mathcal{M} + d\mathbb{I}) = d$

2. These are direct consequences of applying the Perron-Frobenius Theorem A.5 to the essentially nonnegative matrix $\mathcal{M} + D$

Proof of Proposition 8.3 (cont'd)

3. Define $\underline{d} = \min_{i=1,\dots,N} d_{ii}$. Then

$$\mathrm{diag}(D) \gg \mathbf{0} \implies \underline{d} > 0 \implies -\mathcal{M} \leq d\mathbb{I} - \mathcal{M} \leq D - \mathcal{M}$$

From Theorem A.8(5), $d\mathbb{I} - \mathcal{M}$ is an M-matrix. Since $s(\mathcal{M}) = 0$, using a "spectrum shift", all eigenvalues of $d\mathbb{I} - \mathcal{M}$ have real parts larger than $\underline{d}$, so $\underline{d}\mathbb{I} - \mathcal{M}$ is a nonsingular M-matrix. In turn, Theorem A.7(4) $\implies$ $D - \mathcal{M}$ nonsingular M-matrix and Theorem A.7(11) leads to the conclusion

4. Suppose $\mathcal{M}$ irreducible. Let $\overline{d} = \max_{i=1,\dots,N} d_{ii} > 0$. Then $D - \mathcal{M}$ is irreducible and diagonally dominant with all columns $k = 1, \dots, N$ such that $d_{kk} = \overline{d}$ satisfying the strict diagonal dominance requirement. (Other columns with nonzero entries in D also satisfy the requirement.) As a consequence, [**?**, Theorem 1.11] implies that $D - \mathcal{M}$ nonsingular and inverse positivity follows from Theorem A.9

$-\mathcal{M}$ is also the Laplacian matrix of a digraph

Note that $-\mathcal{M}$ is also the Laplacian matrix of a directed graph

As such, finer estimates of the location of eigenvalues are available; see, e.g., [**?**]

However, the main concern here is with the spectral abscissa, so this is not needed

The *population-free equilibrium* (PFE)

We find the PFE $\mathbf{P}_s = \mathbf{P}_t = \mathbf{0}$

At the PFE,

$$J^S_{\mathrm{PFE}} = \mathcal{M} + (\mathcal{D}_s \oplus -\mathcal{D}_t) \tag{3}$$

where $\mathcal{D}_s = \mathbf{G}_s(\mathbf{0}) = \mathrm{diag}(r_1, \ldots, r_S)$

The matrix

$$\mathcal{D}_s \oplus -\mathcal{D}_t = \mathrm{diag}(r_1, \ldots, r_S, -r_{S+1}, \ldots, -r_N)$$

has S diagonal entries > 0 and $N - S$ diagonal entries < 0

Mechanism of the existence proof

Start with $S = 0$ (only sinks)
$\implies \mathcal{D}_s$ vacuous and $\mathcal{D}_s \oplus -\mathcal{D}_t = \mathrm{diag}(-r_1, \ldots, -r_N)$
$\implies s(J^S_{PFE}) < 0$

Finish with $S = N$ (only sources)
$\implies \mathcal{D}_t$ vacuous and $\mathcal{D}_s \oplus -\mathcal{D}_t = \mathrm{diag}(r_1, \ldots, r_N)$
$\implies s(J^S_{PFE}) > 0$

Eigenvalues of J^S_{PFE} depend continuously of entries of J^S_{PFE}, so $s(J^S_{\mathrm{PFE}})$ changes signs, we are done.. if we are happy with a lot of uncertainty about behaviour of $s(J^S_{\mathrm{PFE}})$

Continuous perturbation of the spectrum

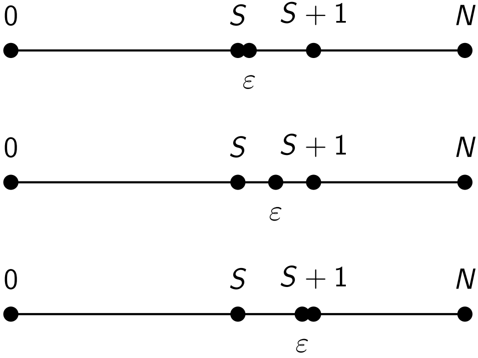
We have assumed that patches are ordered so that the first S patches are sources and the remaining $N-S$ are sinks

From previous argument, as S varies from 0 to N, there should be a point where $s(J^S_{\mathrm{PFE}})$ changes signs

Thinking about it, $s(J^S_{\mathrm{PFE}})$ can probably be made to vary continuously

We need to describe a continuous perturbation of the spectrum of J^S_{PFE} as S varies from 0 to N

For $S \in \{0, \dots, N-1\}$



$$J_{\mathrm{PFE}}^{S,\varepsilon} = \mathcal{M} + \mathrm{diag}(r_1, \dots, r_S, \varepsilon, -r_{S+2}, \dots, -r_N)$$

where $\varepsilon \in [-r_{S+1}, r_{S+1}]$ is in $(S+1)^{\mathrm{th}}$ position

For $S \in [0, N]$

$$J_{\mathrm{PFE}}^{S} = J_{\mathrm{PFE}}^{\xi,\varepsilon}, \quad \text{with} \quad \xi = \lfloor S \rfloor, \quad \varepsilon = 2(S - \lfloor S \rfloor) r_i - r_i \tag{4}$$

where $i = \lfloor S \rfloor + 1$ if $S < N$ and $i = N$ when $S = N$

Generally we vary ζ continuously in each $[-r_{S+1}, r_{S+1}]$

$$J_{\mathrm{PFE}}^{S,-r_{S+1}} = J_{\mathrm{PFE}}^{S} \quad \text{and} \quad J_{\mathrm{PFE}}^{S,r_{S+1}} = J_{\mathrm{PFE}}^{S+1}$$

(4) translates a continuous value of S into a pair (ξ, ε) giving the actual (integer) number ξ of source patches and an "offset" ε

The spectral abscissa $s(J^S_{\mathrm{PFE}})$ switches signs

Lemma 8.4

Let $\underline{r} = \min_{i=1,\ldots,N}\{r_i\}$

Then $s(J^0_{PFE}) \leq -\underline{r} < 0$ *and* $s(J^N_{PFE}) \geq \underline{r} > 0$

Proof of Lemma 8.4

If $S = 0$, then

$$J^0_{\mathrm{PFE}} = \mathcal{M} + \mathrm{diag}(-r_1, \ldots, -r_N)$$

From Proposition 8.2(3), $s(\mathcal{M}) = 0$. Note that this follows from using the Gershgorin Disk Theorem A.3, where for $\mathcal{M}$, all Gershgorin disks are left of the imaginary axis and tangent to origin of the complex plane

Then the centres of the Gershorin disks of $\mathcal{M} + \mathrm{diag}(-r_1, \ldots, -r_N)$ are shifted left by $r_1, \ldots, r_N$ while the radii remain the same

As a consequence, the closest disk(s) to the origin of the complex plane have centre(s) $-\underline{r}$ and thus $s(\mathcal{M} + \mathrm{diag}(-r_1, \ldots, -r_N)) \leq -\underline{r} < 0$

Proof of Lemma 8.4 (cont'd)

If $S = N$, then

$$J^N_{\mathrm{PFE}} = \mathcal{M} + \mathrm{diag}(r_1, \dots, r_N)$$

For $i = 1, \dots, N$, define $e_i = r_i - \underline{r} \geq 0$, then

$$J^N_{\mathrm{PFE}} = \mathcal{M} + \underline{r}\mathbb{I} + \mathrm{diag}(e_1, \dots, e_N)$$

where, by Proposition 8.3(1), $s(\mathcal{M} + \underline{r}\mathbb{I}) = \underline{r} > 0$

Proof of Lemma 8.4 (cont'd)

First, assume $\mathcal{M}$ irreducible

Then J^N_{PFE} is an irreducible essentially nonnegative matrix

Since $J^N_{\mathrm{PFE}} \geq \mathcal{M} + \underline{r}\mathbb{I}$, Theorem A.10(3) $\implies$

$$s(J^N_{\mathrm{PFE}}) \geq s(\mathcal{M} + \underline{r}\mathbb{I}) = \underline{r}$$

with the inequalities being strict if there exists at least one $e_i > 0$

Proof of Lemma 8.4 (cont'd)

Now assume that $\mathcal{M}$ reducible

Then $\exists$ permutation matrix P such that $P^T\mathcal{M}P$ is block upper triangular with irreducible blocks on the diagonal

Call C the number of such blocks, i.e., the number of strong components in the digraph of patches

For $i = 1, \ldots, C$, denote $n(i)$ the number of patches in strong component i and $k(1), \ldots, k(n(i))$ their indices

By abuse of notation, denote $\mathcal{M}_{ii}$ the corresponding diagonal block in the reduced form of $\mathcal{M}$

Proof of Lemma 8.4 (cont'd)

Applying the permutation matrix P to J^N_{PFE} gives a block upper triangular matrix

$$P^T J^N_{\mathrm{PFE}} P$$

with, for $i = 1, \ldots, C$, the $n(i) \times n(i)$ diagonal blocks $\mathcal{M}_{ii} + E_i$ being irreducible and with

$$E_i = \underline{r}\mathbb{I} + \mathrm{diag}\left(e_{k(1)}, \ldots, e_{k(n(i))}\right)$$

Proof of Lemma 8.4 (cont'd)

Fix $i = 1, \ldots, C$ and let $\mathbf{v}$ be a positive right eigenvector of $\mathcal{M}_{ii} + E_i$ corresponding to the spectral abscissa s_1 and $\mathbf{w}$ be a positive left eigenvector of $\mathcal{M}_{ii} + \underline{r}\mathbb{I}$ corresponding to the spectral abscissa s_2. Then

$$\begin{aligned}
s_1 \mathbf{w}^T \mathbf{v} &= \mathbf{w}^T \left(\mathcal{M}_{ii} + \underline{r}\mathbb{I} + \mathrm{diag}(e_{k(1)}, \ldots, e_{k(n(i))}) \right) \mathbf{v} \\
&= \mathbf{w}^T (\mathcal{M}_{ii} + \underline{r}\mathbb{I}) \mathbf{v} + \mathbf{w}^T \mathrm{diag}(e_{k(1)}, \ldots, e_{k(n(i))}) \mathbf{v} \\
&= s_2 \mathbf{w}^T \mathbf{v} + \mathbf{w}^T \mathrm{diag}(e_{k(1)}, \ldots, e_{k(n(i))}) \mathbf{v} \\
&\geq s_2 \mathbf{w}^T \mathbf{v}
\end{aligned}$$

the inequality being strict if at least one of the $e_{k(j)}$, $j = 1, \ldots, n(i)$, is positive. Hence $s_1 \geq s_2$, i.e., $s(\mathcal{M}_{ii} + E_i) \geq s(\mathcal{M}_{ii} + \underline{r}\mathbb{I})$. This is true for all diagonal blocks. Now, since $P^T J^N_{\mathrm{PFE}} P$ is block upper triangular,

$$s(J^N_{\mathrm{PFE}}) = s(P^T J^N_{\mathrm{PFE}} P) = \max\{s(\mathcal{M}_{11} + E_1), \ldots, s(\mathcal{M}_{CC} + E_C)\}$$

Proof of Lemma 8.4 (cont'd)

As $P^T(\mathcal{M}+\underline{r}\mathbb{I})P$ is also block upper triangular,

$$\underline{r} = s(\mathcal{M}+\underline{r}\mathbb{I}) = \max\{s(\mathcal{M}_{11}+\underline{r}\mathbb{I}),\dots,s(\mathcal{M}_{11}+\underline{r}\mathbb{I})\}$$

As a consequence, $s(J^N_{\mathrm{PFE}}) \geq \underline{r} > 0$

Thus, S^c necessarily lies in the open interval $(0, N)$. The following lemma is of interest and the method of proof of the second assertion is used again later

Lemma 8.5

1. *For all* $S \in (0, N) \subset \mathbb{R}$,
$$J^0_{PFE} < J^S_{PFE} < J^N_{PFE} \tag{5}$$
2. J^S_{PFE} *is an increasing function of* S*, in the sense that*
$$\forall S_1, S_2 \in [0, N] \subset \mathbb{R} \textit{ such that } S_1 < S_2, \quad J^{S_1}_{PFE} < J^{S_2}_{PFE} \tag{6}$$

Proof of Lemma 8.5

1. Let $S \in (0, N)$ be fixed. Using (4), we get a pair $(\xi, \varepsilon) \in \{0, \dots, N\} \times [-r_i, r_i]$, for $i = 1 \dots N$, such that $J^S_{\mathrm{PFE}} = J^{\xi,\varepsilon}_{\mathrm{PFE}}$. We have

$$
\begin{aligned}
J^{\xi,\varepsilon}_{\mathrm{PFE}} - J^0_{\mathrm{PFE}} &= \mathcal{M} + \operatorname{diag}(r_1, \dots, r_\xi, \varepsilon, -r_{\xi+2}, \dots, -r_N) \\
&\quad - \mathcal{M} - \operatorname{diag}(-r_1, \dots, -r_N) \\
&= \operatorname{diag}(2r_1, \dots, 2r_\xi, \varepsilon + r_{\xi+1}, 0, \dots, 0) \\
&> \mathbf{0}
\end{aligned}
$$

since $\varepsilon \in [-r_{\xi+1}, r_{\xi+1}]$

Computing $J^N_{\mathrm{PFE}} - J^{\xi,\varepsilon}_{\mathrm{PFE}}$ at the other endpoint works similarly, giving (5)

Proof of Lemma 8.5 (cont'd)

2. Use (4) again to obtain two pairs (ξ_1, ε_1) and (ξ_2, ε_2), where, by the assumption $S_1 < S_2$, $\xi_1 \leq \xi_2$. First, assume that $\xi_1 < \xi_2$. Then

$$\begin{aligned}
J_{\mathrm{PFE}}^{\xi_2,\varepsilon_2} - J_{\mathrm{PFE}}^{\xi_1,\varepsilon_1} &= \mathrm{diag}(r_1, \ldots, r_{\xi_2}, \varepsilon_2, -r_{\xi_2+2}, \ldots, -r_N) \\
&\quad - \mathrm{diag}(r_1, \ldots, r_{\xi_1}, \varepsilon_1, -r_{\xi_1+2}, \ldots, -r_N) \\
&= \mathrm{diag}(0, \ldots, 0, r_{\xi_1+1} - \varepsilon_1, 2r_{\xi_1+2}, \ldots, 2r_{\xi_2}, \varepsilon_2 + r_{\xi_2+1}, 0, \ldots, 0) \\
&> \mathbf{0}
\end{aligned}$$

since $\varepsilon_1 \in [-r_{\xi_1+1}, r_{\xi_1+1}]$, and $\varepsilon_2 \in [-r_{\xi_2+1}, r_{\xi_2+1}]$

Now assume $\xi_1 = \xi_2$. Then, since $S_1 < S_2$, we find that $\varepsilon_1 < \varepsilon_2$ and the diagonal matrix in the subtraction $J_{\mathrm{PFE}}^{\xi_2,\varepsilon_2} - J_{\mathrm{PFE}}^{\xi_2,\varepsilon_1}$ takes the form $\mathrm{diag}(0, \ldots, 0, \varepsilon_2 - \varepsilon_1, 0, \ldots, 0) > \mathbf{0}$. So (6) holds

Proposition 8.6

$\mathcal{M}$ *reducible* $\implies s(J^{S}_{PFE})$ *nondecreasing for* $S \in [0, N]$

$\mathcal{M}$ *irreducible* $\implies s(J^{S}_{PFE})$ *increasing for* $S \in [0, N]$

$\implies \exists \mathcal{S}_{int} \subset (0, N)$ (resp. $S^c \in (0, N)$) s.t. PFE LAS if $S < \min(\mathcal{S}_{int})$ (resp. $S < S^c$) and PFE unstable if $S > \max(\mathcal{S}_{int})$ (resp. $S > S^c$)

Proof of Proposition 8.6

First, assume $\mathcal{M}$ is irreducible. Then, by Lemma 8.5 and the fact that $\mathcal{M}$ is irreducible (and thus so is J^S_{PFE}), Theorem A.10(3) gives the result

Proof of Proposition 8.6 (cont'd)

Now, assume that $\mathcal{M}$ is reducible. $\implies \exists$ permutation matrix P such that $P^T\mathcal{M}P$ block upper triangular. Consider $S \in [0, N] \subset \mathbb{R}$ and use (4) to obtain a corresponding pair $(\xi, \varepsilon) \in \{0, \ldots, N\} \times [-r_\xi, r_\xi]$. Apply the same permutation to $J_{\mathrm{PFE}}^{\xi,\varepsilon}$, giving

$$P^T J_{\mathrm{PFE}}^{\xi,\varepsilon} P = \begin{pmatrix} \mathcal{M}_{11} + E_1 & \mathcal{M}_{12} & \cdots & \mathcal{M}_{1N} \\ 0 & \mathcal{M}_{22} + E_2 & & \\ & & \ddots & \\ 0 & \cdots & 0 & \mathcal{M}_{CC} + E_C \end{pmatrix}$$

where C is the number of strong components in the digraph of patches and

$$E_1 \oplus \cdots \oplus E_C = P^T \mathrm{diag}(r_1, \ldots, r_\xi, \varepsilon, -r_{\xi+2}, \ldots, -r_N) P$$

with matrix on right hand side having ε as $(\xi+1)^{\mathrm{th}}$ diagonal entry. As in the proof of Lemma 8.4, we have denoted $\mathcal{M}_{ii}$ the diagonal blocks in the reduced form of $\mathcal{M}$

Proof of Proposition 8.6 (cont'd)

For $j = 1, \ldots, C$, each of the matrices $\mathcal{M}_{jj}$ is irreducible; $C-1$ of the matrices E_j are diagonal with entries $-r_i$ and r_i on the diagonal (with some having only $-r_i$, some having only r_i and some having both types of entries)

The remaining E_j matrix is diagonal, with potentially $-r_i$ and r_i as the others, but also ε. Call $\eta \in \{1, \ldots, C\}$ the index of the strong component containing the matrix with ε

As a consequence, for all $j = 1, \ldots, C$, $\mathcal{M}_{jj} + E_j$ are irreducible essentially nonnegative matrices, with only matrix $\mathcal{M}_{\eta\eta} + E_\eta$ having an ε added to one of its diagonal entries

Proof of Proposition 8.6 (cont'd)

As $P^T J_{\mathrm{PFE}}^{\xi,\varepsilon} P$ is block upper triangular, we have

$$s\left(P^T J_{\mathrm{PFE}}^{\xi,\varepsilon} P\right) = \max\left\{s(\mathcal{M}_{11} + E_1), \ldots, s(\mathcal{M}_{CC} + E_C)\right\}$$

Except for $\mathcal{M}_{\eta\eta} + E_\eta$, all matrices $\mathcal{M}_{ii} + E_i$ have fixed spectral abscissa. Concerning matrix $\mathcal{M}_{\eta\eta} + E_\eta$, it is clear that the reasoning in the proof of Lemma 8.5(2) carries through and thus,

$$\forall \varepsilon_1, \varepsilon_2 \in [-r_{\xi+1}, r_{\xi+1}],\ \varepsilon_1 < \varepsilon_2 \implies J_{\mathrm{PFE}}^{\xi,\varepsilon_1} < J_{\mathrm{PFE}}^{\xi,\varepsilon_2}$$

Hence $s(J_{\mathrm{PFE}}^{\xi,\varepsilon})$ is the maximum of a set of C functions, $C-1$ of which are constant in ε and one of which is increasing in ε. It now follows that $s(J_{\mathrm{PFE}}^{S})$ is a nondecreasing function of S, as desired

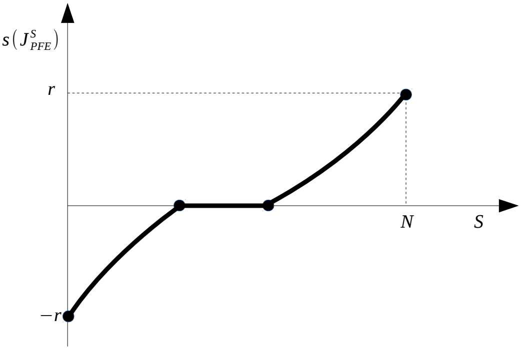
We now can do Part 1 of Theorem 8.9

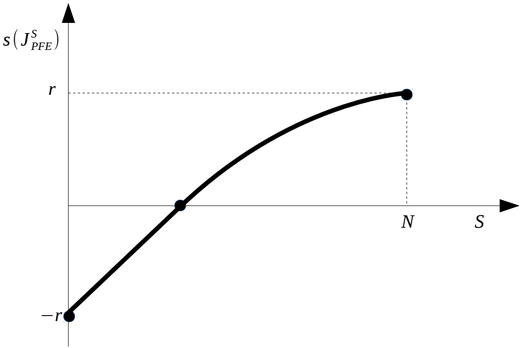
As J_{PFE}^S is essentially nonnegative, its spectral abscissa $s(J_{\mathrm{PFE}}^S)$ is an eigenvalue. Eigenvalues of J_{PFE}^S depend continuously on S (Theorem A.2). By Lemma 8.4, $s(J_{\mathrm{PFE}}^0) < 0$ and $s(J_{\mathrm{PFE}}^N) > 0$, so by the Intermediate Value Theorem, there exists at least one point $S^c \in (0, N)$ such that $s(J_{\mathrm{PFE}}^{S^c}) = 0$

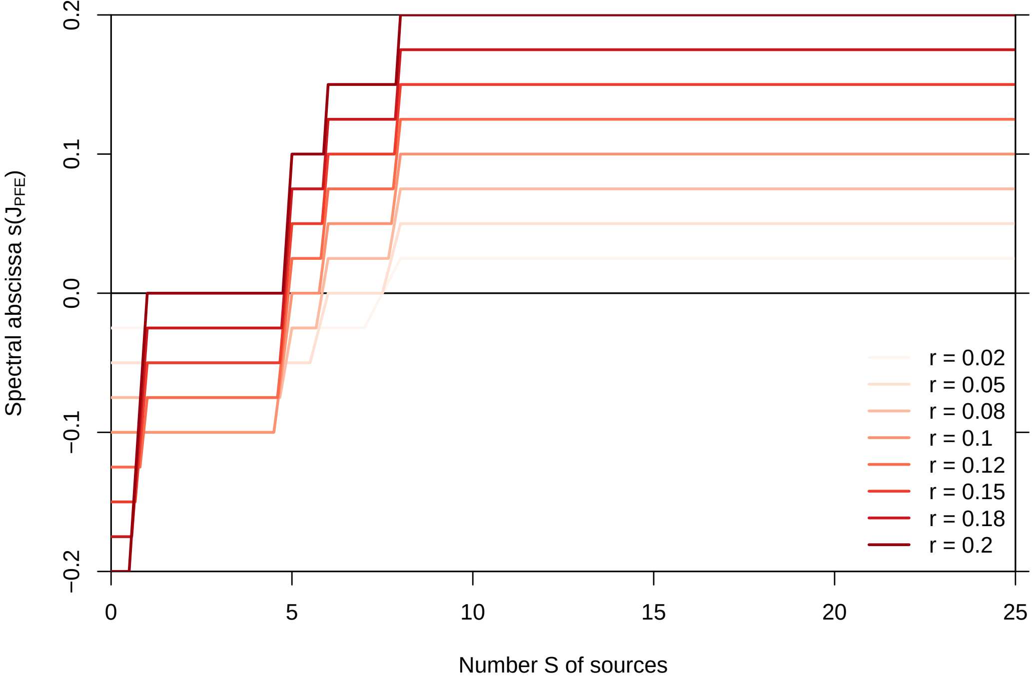
In the case where $\mathcal{M}$ is irreducible, $s(J_{\mathrm{PFE}}^S)$ is increasing by Proposition 8.6 and as a consequence, S^c is unique. In the case where $\mathcal{M}$ is reducible, $s(J_{\mathrm{PFE}}^S)$ is nondecreasing, therefore there exists an interval $\mathcal{S}_{int}$, possibly reduced to a single point, such that $s(J_{\mathrm{PFE}}^S) = 0$ for all $S \in \mathcal{S}_{int}$

The usual criteria for local asymptotic stability and instability of equilibria then imply the first part of Theorem 8.9 for $S < S^c$ and $S > S^c$ (irreducible case) or $S < \min(\mathcal{S}_{int})$ and $S > \max(\mathcal{S}_{int})$ (reducible case)

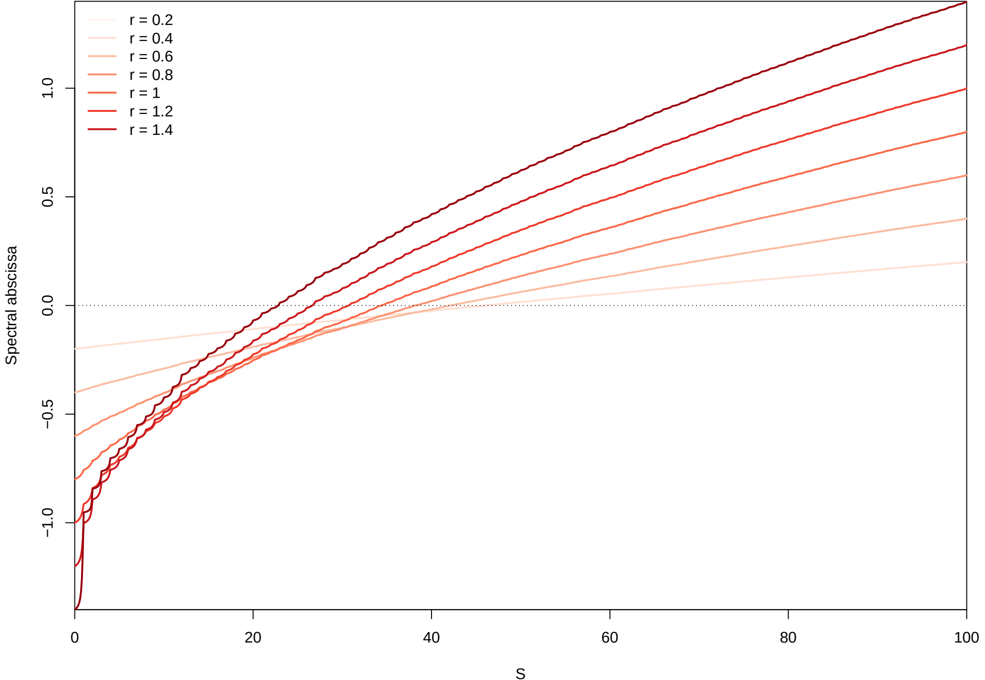
- $\mathcal{M}$ reducible: $\exists \mathcal{S}_{int} \subset (0, N)$ s.t. PFE LAS if $S < \min(\mathcal{S}_{int})$ and PFE unstable if $S > \max(\mathcal{S}_{int})$
- $\mathcal{M}$ irreducible: $\exists S^c \in (0, N)$ s.t. PFE LAS if $S < S^c$ and PFE unstable if $S > S^c$

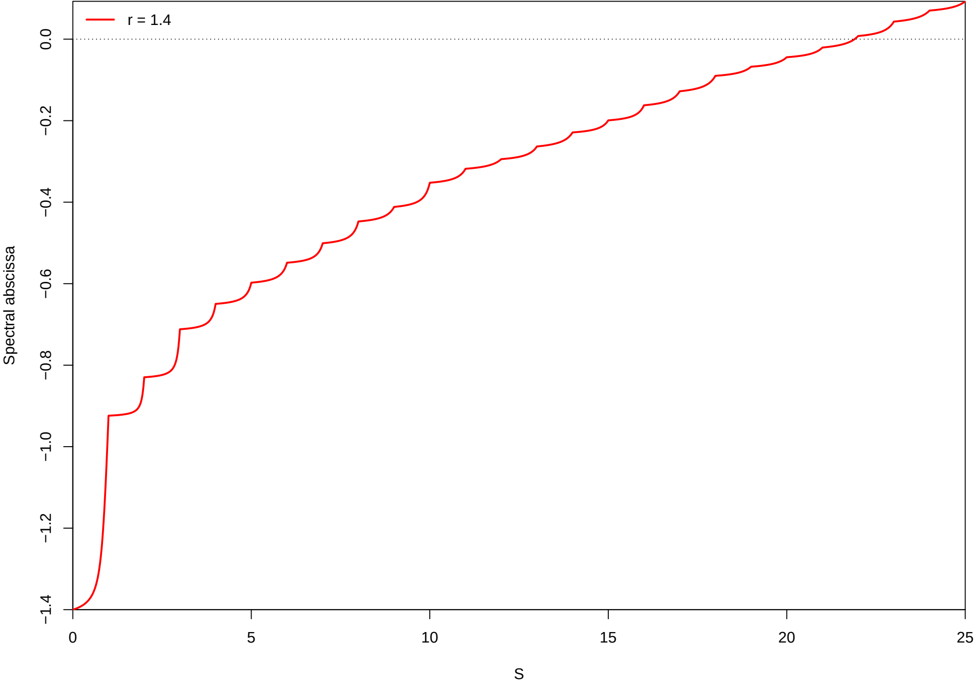






Spectral abscissa s(J_PFE)
Number S of sources
0.2
0.1
0.0
−0.1
−0.2
0
5
10
15
20
25
r = 0.02
r = 0.05
r = 0.08
r = 0.1
r = 0.12
r = 0.15
r = 0.18
r = 0.2


r = 0.2
r = 0.4
r = 0.6
r = 0.8
r = 1
r = 1.2
r = 1.4
Spectral abscissa
1.0
0.5
0.0
−0.5
−1.0
0
20
40
60
80
100
S


r = 1.4
Spectral abscissa
0.0
−0.2
−0.4
−0.6
−0.8
−1.0
−1.2
−1.4
0
5
10
15
20
25
S

As indicated by [?], perturbation of the diagonal leads to convex changes in the spectral abscissa on each sub-interval

We have a reproduction number when $\mathcal{M}$ irreducible

Proposition 8.7

Suppose $\mathcal{M}$ irreducible. Define the basic reproduction number

$$\mathcal{R}_0 = \rho\left(\left(\mathcal{M}_s + \mathcal{M}_{st}(\mathcal{D}_t - \mathcal{M}_t)^{-1}\mathcal{M}_{ts}\right)^{-1}\mathcal{D}_s\right) \tag{7}$$

where $\mathcal{M}_s, \mathcal{M}_t, \mathcal{M}_{st}, \mathcal{M}_{ts}$ are defined as in (2), $\mathcal{D}_s = \mathrm{diag}(r_1, \ldots, r_S)$ *and* $\mathcal{D}_t = \mathrm{diag}(r_{S+1}, \ldots, r_N)$. *Then*

$$s(J^S_{PFE}) < 0 \iff \mathcal{R}_0 < 1 \text{ and } s(J^S_{PFE}) > 0 \iff \mathcal{R}_0 > 1 \tag{8}$$

Proof of Proposition 8.7

Write (3) as

$$J^S_{\mathrm{PFE}} = \mathcal{M} + \tilde{\mathcal{D}}_s - \tilde{D}_t$$

where $\tilde{\mathcal{D}}_s = \mathcal{D}_s \oplus \mathbf{0}_{N-S\times N-S}$ and $\tilde{\mathcal{D}}_t = \mathbf{0}_{S\times S} \oplus \mathcal{D}_t$. Let $-\alpha$ be the spectral abscissa of $\mathcal{M} + \tilde{\mathcal{D}}_s - \tilde{\mathcal{D}}_t$. From Proposition 8.3(2), there is a vector $\mathbf{v} \gg \mathbf{0}$ such that

$$(\mathcal{M} + \tilde{\mathcal{D}}_s - \tilde{\mathcal{D}}_t)\mathbf{v} = -\alpha\mathbf{v}$$

In other words,

$$\alpha\mathbf{v} = (\tilde{\mathcal{D}}_t - \mathcal{M})\mathbf{v} - \tilde{\mathcal{D}}_s\mathbf{v}$$

Proof of Proposition 8.7 (cont'd)

By the assumption of irreducibility of $\mathcal{M}$, it follows from Proposition 8.3(4) that $\tilde{\mathcal{D}}_t - \mathcal{M}$ is an irreducible nonsingular M-matrix and $(\tilde{\mathcal{D}}_t - \mathcal{M})^{-1} \gg \mathbf{0}$

Then

$$\alpha \left(\tilde{\mathcal{D}}_t - \mathcal{M}\right)^{-1} \mathbf{v} = \mathbf{v} - \left(\tilde{\mathcal{D}}_t - \mathcal{M}\right)^{-1} \tilde{\mathcal{D}}_s \mathbf{v}$$

with the matrix $(\tilde{\mathcal{D}}_t - \mathcal{M})^{-1}\tilde{\mathcal{D}}_s > \mathbf{0}$

As a consequence, from the Perron-Frobenius Theorem A.5, the spectral radius of $(\tilde{\mathcal{D}}_t - \mathcal{M})^{-1}\tilde{\mathcal{D}}_s$ is an eigenvalue and is associated to a nonnegative eigenvector

Proof of Proposition 8.7 (cont'd)

Let $\mathbf{u}$ be such an eigenvector, normalised so that $\mathbf{u}^T\mathbf{v} = 1$. Then

$$\alpha \mathbf{u}^T \left(\tilde{\mathcal{D}}_t - \mathcal{M}\right)^{-1} \mathbf{v} = \mathbf{u}^T \mathbf{v} \left(1 - \rho\left\{\left(\tilde{\mathcal{D}}_t - \mathcal{M}\right)^{-1} \tilde{\mathcal{D}}_s\right\}\right)$$

Thus

$$\alpha > 0 \iff \rho\left\{\left(\tilde{\mathcal{D}}_t - \mathcal{M}\right)^{-1} \tilde{\mathcal{D}}_s\right\} < 1$$

and

$$\alpha < 0 \iff \rho\left\{\left(\tilde{\mathcal{D}}_t - \mathcal{M}\right)^{-1} \tilde{\mathcal{D}}_s\right\} > 1$$

Proof of Proposition 8.7 (cont'd)

From the structure of $\tilde{\mathcal{D}}_s$, the spectral radius of $(\tilde{\mathcal{D}}_t - \mathcal{M})^{-1}\tilde{\mathcal{D}}_s$ is the spectral radius of

$$\left(\tilde{\mathcal{D}}_t - \mathcal{M}\right)^{-1}_{[11]} \mathcal{D}_s$$

where $(\tilde{\mathcal{D}}_t - \mathcal{M})^{-1}_{[11]}$ is the (1,1) block in $(\tilde{\mathcal{D}}_t - \mathcal{M})^{-1}$

Writing $\mathcal{M}$ as (2), we have by the formula for the inverse of a 2×2 block matrix that

$$\left(\tilde{\mathcal{D}}_t - \mathcal{M}\right)^{-1}_{[11]} = (-\mathcal{M}_s - \mathcal{M}_{st}(\mathcal{D}_t - \mathcal{M}_t)^{-1}\mathcal{M}_{ts})^{-1}$$

Proof of Proposition 8.7 (cont'd)

Clearly,

$$
\begin{aligned}
&\rho\left((-\mathcal{M}_s - \mathcal{M}_{st}(\mathcal{D}_t - \mathcal{M}_t)^{-1}\mathcal{M}_{ts})^{-1}\mathcal{D}_s\right) \\
&\qquad = \rho\left((\mathcal{M}_s + \mathcal{M}_{st}(\mathcal{D}_t - \mathcal{M}_t)^{-1}\mathcal{M}_{ts})^{-1}\mathcal{D}_s\right)
\end{aligned}
$$

giving the result

So..

we are done!

.. Are we? The result is only local, can we go further?

System (1) is cooperative

Jacobian of (1):

$$J(\mathbf{P}_s, \mathbf{P}_t) = \begin{pmatrix} \mathbf{G}_s'(\mathbf{P}_s)\mathbf{P}_s + \mathbf{G}_s(\mathbf{P}_s) + \mathcal{M}_s & \mathcal{M}_{st} \\ \mathcal{M}_{ts} & -\mathcal{D}_t + \mathcal{M}_t \end{pmatrix} \tag{9}$$

where

$$\mathbf{G}_s'(\mathbf{P}_s) = \operatorname{diag}\left(-\frac{r_1}{K_1}, \ldots, -\frac{r_S}{K_s}\right)$$

Thus

$$J(\mathbf{P}_s, \mathbf{P}_t) = \mathcal{M} + \big((\mathbf{G}_s'(\mathbf{P}_s)\mathbf{P}_s + \mathbf{G}_s(\mathbf{P}_s)) \oplus -\mathcal{D}_t\big)$$

with $\mathbf{G}_s'(\mathbf{P}_s)\mathbf{P}_s + \mathbf{G}_s(\mathbf{P}_s)$ and $-\mathcal{D}_t$ diagonal

$\implies$ system (1) is cooperative

A theorem of Hirsch

So, to move forward, we would like to apply the following result

Theorem 8.8 (Th. 6.1 in Hirsch (1984) – BAMS 11(1))

Let $\mathbf{F}$ be a C^1 vector field in $\mathbb{R}^n$ with flow ϕ preserving $\mathbb{R}^n_+$ for $t > 0$ and strongly monotone in $\mathbb{R}^n_+$. Suppose that the origin is an equilibrium and all trajectories in $\mathbb{R}^n_+$ are bounded. Suppose the matrix-valued map $D\mathbf{F} : \mathbb{R}^n_+ \to \mathbb{R}^{n\times n}$ is strictly antimonotone, i.e.,

$$\mathbf{x} > \mathbf{y} \implies D\mathbf{F}(\mathbf{x}) < D\mathbf{F}(\mathbf{y})$$

Then either all trajectories in $\mathbb{R}^n_+$ go to the origin, or there exists a unique equilibrium $\mathbf{P}^\star \in \mathrm{Int}\mathbb{R}^n_+$ and all trajectories in $\mathbb{R}^n_+ \setminus \{\mathbf{0}\}$ limit to $\mathbf{P}^\star$

OK, nice, but..

Take

$$\mathbf{P}_1 = (0, \ldots, 0, \star, \ldots, \star) \text{ and } \mathbf{P}_2 = (0, \ldots, 0, \star, \ldots, \star)$$

have their first S entries zero, i.e., $\mathbf{P}_1 = (\mathbf{0}_s, \mathbf{P}_t^1)$ and $\mathbf{P}_2 = (\mathbf{0}_s, \mathbf{P}_t^2)$; assume $\mathbf{P}_1 > \mathbf{P}_2$, i.e., $\mathbf{P}_t^1 > \mathbf{P}_t^2$

Then

$$\begin{aligned} J(\mathbf{0}_s, \mathbf{P}_t^1) &= \mathcal{M} + \left((\mathbf{G}_s'(\mathbf{0}_s)\mathbf{0}_s + \mathbf{G}_s(\mathbf{0}_s)) \oplus -\mathcal{D}_t \right) \\ &= \mathcal{M} + (\mathcal{D}_s \oplus -\mathcal{D}_t) \\ &= J(\mathbf{0}_s, \mathbf{P}_t^2) \end{aligned}$$

i.e.,

$$J^S_{\mathbf{P}_1} = J^S_{\mathbf{P}_2}$$

$\implies$ (1) is not strictly antimonotone

(non) lasciate ogne sperenza, voi ch'intrate

Except for strict antimonotonicity of $\mathbf{F}$, all hypotheses of [Hirsch (1984) – Th. 6.1] are satisfied:

- in the case $\mathcal{M}$ irreducible, (1) is strongly monotone (by [Hirsch (1984) – Th. 1.7])
- the origin is an equilibrium
- all solutions of (1) are bounded in $\mathbb{R}_+^N$ (not shown here, but not hard)

$\implies$ by other results (*e.g.*, Hirsch *ibid*), there exists $\mathbf{P}^* \gg \mathbf{0}$

What is the use of strict antimonotonicity in the proof of [Hirsch (1984) – Th. 6.1]? ..
To show uniqueness of $\mathbf{P}^*$

More precisely: let $\mathbf{z} \in (\mathbf{0}, \mathbf{P}^*)$, where $\mathbf{P}^* \gg \mathbf{0}$ is a nontrivial equilibrium

Strict antimonotonicity $\implies$ $\mathbf{F}(\mathbf{z}) > \mathbf{0}$, and we can then proceed with the remainder of the proof of [Hirsch (1984) – Th. 6.1]

Let us show that we indeed have $\mathbf{F}(\mathbf{z}) > \mathbf{0}$ for (1), despite the lack of strict antimonotonicity

As in [Hirsch (1984) – Th. 6.1]: for $i = 1, \ldots, N$, let

$$
\begin{aligned}
g_i : [0,1] &\to \mathbb{R} \\
s &\mapsto F_i(s\mathbf{P}^*)
\end{aligned}
$$

Then $g_i(0) = g_i(1) = 0$ for $i = 1, \ldots, N$ and, for $i = S+1, \ldots, N$ (sinks),

$$g_i(s) = -r_i s P_i^* + \sum_{j=1}^{N} m_{ij} s P_j^* = \left(r_i P_i^* + \sum_{j=1}^{N} m_{ij} P_j^* \right) s = 0$$

However, for $i = 1, \ldots, S$ (sources),

$$g_i(s) = r_i \left(1 - \frac{s P_i^*}{K_i} \right) s P_i^* + \sum_{j=1}^{N} m_{ij} s P_j^*$$

Ha!

$$g_i''(s) = -\frac{2 r_i P_i^{*2}}{K} < 0, \quad i = 1, \ldots, S$$

$\implies$ for $i = 1, \ldots, S$, $g_i(s) > 0$ when $s \in (0,1)$
$\implies$ when $S > 0$, $\mathbf{F}(\mathbf{z}) > \mathbf{0}$, $\forall \mathbf{z} \in (\mathbf{0}, \mathbf{P}^*)$

And we can then carry on with the remainder of the proof of [Hirsch (1984) – Th. 6.1]

To finish, the case $S = 0$ is easy:

$$\left(\sum_{i=1}^{N} P_i\right)' = -\sum_{i=1}^{N} r_i P_i < 0$$

since at least one of the $P_i(0) > 0$

$\implies \left(\sum_{i=1}^{N} P_i\right) \to 0 \implies \lim_{t\to\infty} P_i(t) = 0$ for $i = 1, \ldots, N$

Et hop! $\square$

To conclude (mathematically)

Theorem 8.9

There exists a critical interval $\mathcal{S}_{int} \subset (0, N) \subset \mathbb{R}$ *s.t.*

- $S < \min(\mathcal{S}_{int}) \implies$ *PFE LAS*
- $S > \max(\mathcal{S}_{int}) \implies$ *PFE instable*

Additionally, if the patch digraph is strongly connected, then

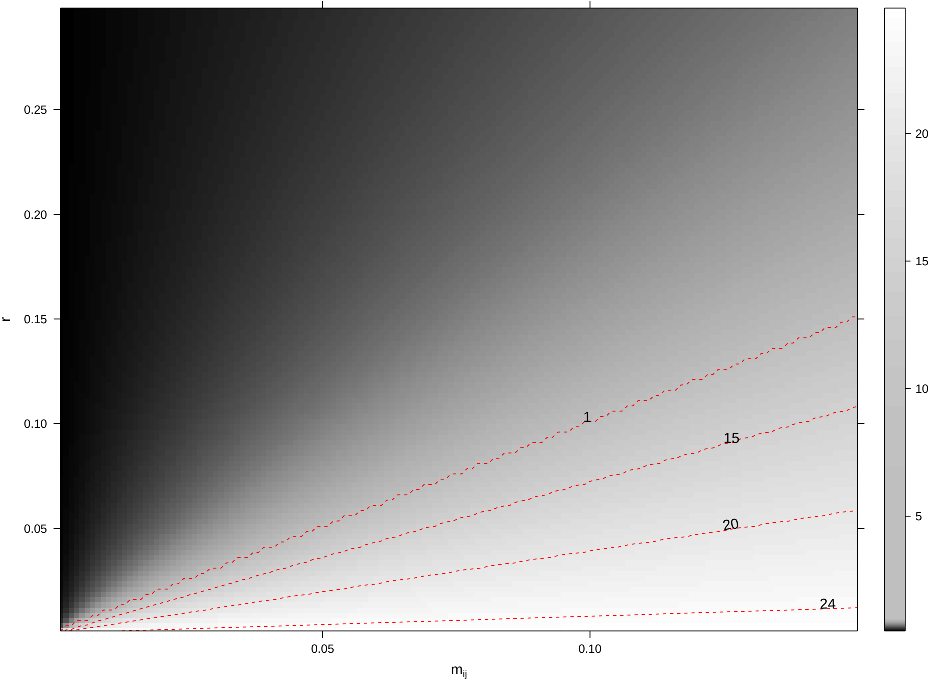
- $\mathcal{S}_{int}$ *is reduced to a point* S^c
- $S < S^c \implies$ *PFE GAS*
- $S > S^c \implies \exists! \mathbf{P}^* \gg \mathbf{0}$ *GAS for* $\mathbb{R}_+^N \setminus \{\mathbf{0}\}$

In the 2 figures that follow:

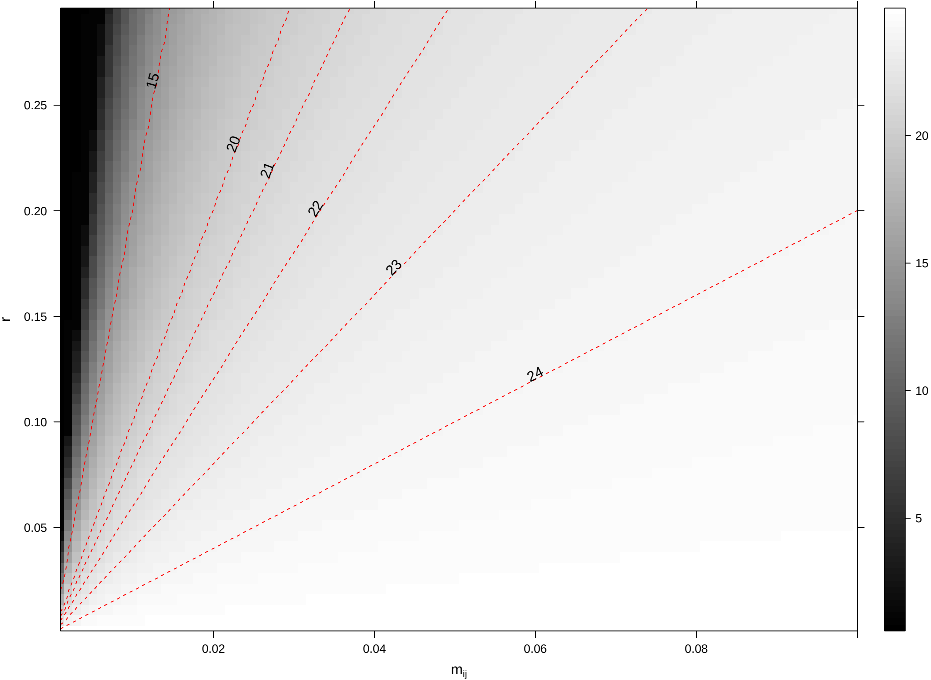
- $N = 50$
- $r = r_i, \forall i = 1, \ldots, N$
- $m_{ij} = m, \forall i, j = 1, \ldots, N$ s.t. $m_{ij} > 0$
- plot is value of S^c as a function of m and r

Figure 1: ring of patches

Figure 2: complete digraph



r
0.25
0.20
0.15
0.10
0.05
0.05
0.10
m_{ij}
1
15
20
24
20
15
10
5



r
0.25
0.20
0.15
0.10
0.05
0.02
0.04
0.06
0.08
m_{ij}
15
20
21
22
23
24
20
15
10
5

Case of complete homogeneous movement

Proposition 8.10

Suppose that the movement digraph is complete and that $m_{ij} = m$ *for* $i, j = 1, \ldots, N$, $i \neq j$

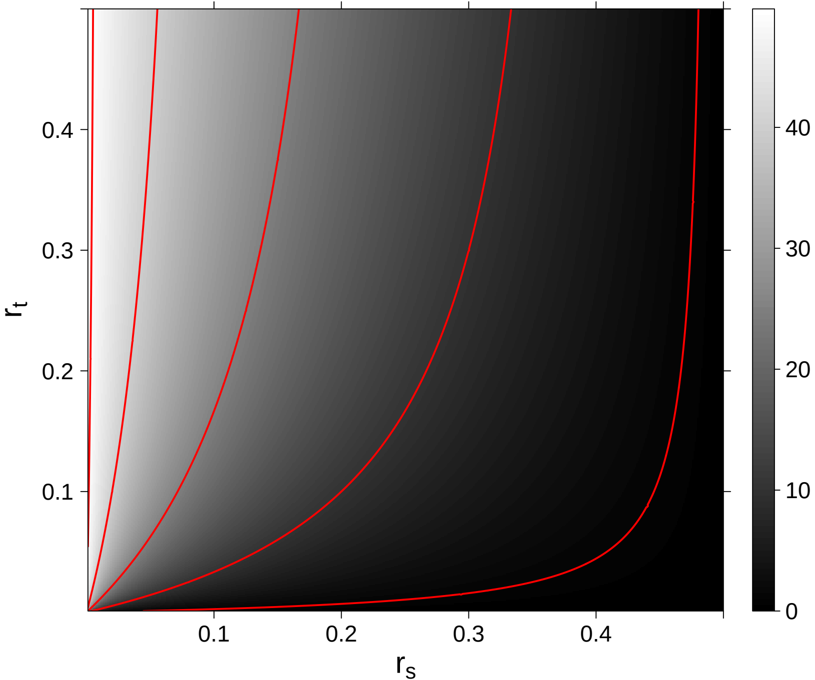
Suppose that $S \in \{1, \ldots, N-1\}$, *that for* $i = 1, \ldots, S$, $r_i = r_s$ *and that for* $i = S+1, \ldots, N$, $r_i = r_t$

Then

$$S^c = \frac{mNr_t - r_s r_t}{m(r_s + r_t)} \tag{10}$$

If $r_s = r_t = r$, then

$$S^c = \frac{N}{2} - \frac{r}{2m} \tag{11}$$



0.4
0.3
0.2
0.1
r_t
0.1
0.2
0.3
0.4
r_s
40
30
20
10
0

Proof of Prop 8.10 uses equitable partitions

Section 9.3 in *Algebraic Graph Theory*, Godsil & Royle (2013)

An **equitable partition** π splits a graph X into **cells** $\mathcal{C}_i$, $i = 1, \ldots, r$, s.t. for a vertex u in cell $\mathcal{C}_i$, the number of neighbours in cell $\mathcal{C}_j$ is a constant b_{ij} that does not depend on u

$\iff$ the subgraph of X induced by each cell is regular [vertices have same degree] and edges joining two distinct cells form a semiregular bipartite graph [vertices have same degree in each bipartite component]

The digraph with the r cells of π as vertices and the b_{ij} arcs from the i^{th} to the j^{th} cell of π is the **quotient** X/π of X on π. The adjacency matrix of X/π is $A(X/\pi) = [b_{ij}]$

Characterising an equitable partition

Lemma 8.11 (A friendly characterisation)

X graph, $A(X)$ its adjacency matrix, π a partition of $V(X)$ with characteristic matrix P. Then

$$\pi \text{ equitable} \iff \text{column space of } P \text{ is } A\text{-invariant}$$

Write

$$J^S_{\mathrm{PFE}} = \begin{pmatrix} m\mathbb{J} - Nm\mathbb{I} + r_s\mathbb{I} & m\mathbb{J} \\ m\mathbb{J} & m\mathbb{J} - Nm\mathbb{I} - r_t\mathbb{I} \end{pmatrix} \tag{12}$$

with $\mathbb{J}$ matrix of all 1's

Consider (12) as the adjacency matrix of a digraph $\mathcal{G}$

Suppose partition π splits $\mathcal{G}$ in two cells, $\{S_i\}_{i=1,\ldots,S}$ (sources) and $\{T_i\}_{i=S+1,\ldots,N}$ (sinks)

The characteristic matrix of π is the $N \times 2$-matrix

$$C = \begin{pmatrix} \mathbb{1}_S & \mathbf{0}_S \\ \mathbf{0}_{N-S} & \mathbb{1}_{N-S} \end{pmatrix}$$

We have

$$J^S_{\mathrm{PFE}}\mathbb{1} = J^S_{\mathrm{PFE}}\begin{pmatrix}\mathbb{1}_S \\ \mathbb{1}_{N-S}\end{pmatrix} = \begin{pmatrix}r_s\mathbb{1}_S \\ -r_t\mathbb{1}_{N-S}\end{pmatrix}$$

Thus the column space of C is J^S_{PFE}-invariant $\implies$ π is equitable

Properties of equitable partitions

Lemma 8.12

π equitable partition of graph X with characteristic matrix P, and $B = A(X/\pi)$. Then $AP = PB$ and $B = (P^T P)^{-1} P^T AP$

Theorem 8.13

π equitable partition of graph $X \implies$ characteristic polynomial of $A(X/\pi)$ divides characteristic polynomial of $A(X)$

$\implies$ the quotient matrix B^S_{PFE} satisfies

$$B^S_{\mathrm{PFE}} = (C^T C)^{-1} C^T J^S_{\mathrm{PFE}} C$$

$$\implies B^S_{\mathrm{PFE}} = \begin{pmatrix} mS - mN + r_s & m(N-S) \\ mS & -(mS + r_s) \end{pmatrix}$$

And $\sigma(B^S_{\mathrm{PFE}}) \subset \sigma(J^S_{\mathrm{PFE}})$

B^S_{PFE} essentially nonnegative (and clearly irreducible)

$$\implies \exists ! \mathbf{v}_p \gg \mathbf{0} \text{ s.t. } B^S_{\mathrm{PFE}} \mathbf{v}_p = \lambda_p \mathbf{v}_p = s(B^S_{\mathrm{PFE}}) \mathbf{v}_p$$

Then $J^S_{\mathrm{PFE}} C = C B^S_{\mathrm{PFE}}$

So

$$J^S_{\mathrm{PFE}} C \mathbf{v}_p = C B^S_{\mathrm{PFE}} \mathbf{v}_p = \lambda_p C \mathbf{v}_p$$

and $C\mathbf{v}_p$ is an eigenvector of J^S_{PFE} that is also $\gg \mathbf{0}$

As the only eigenvector $\gg \mathbf{0}$ of J^S_{PFE} corresponds to $s(J^S_{\mathrm{PFE}})$, we have $s(J^S_{\mathrm{PFE}}) = s(B^S_{\mathrm{PFE}})$

To compute S^c, recall S^c is value of S where PFE loses stability

Consider B^S_{PFE}. We have $\mathrm{tr}(B^S_{\mathrm{PFE}}) = -mN + r_s - r_t$ and

$$\det(B^S_{\mathrm{PFE}}) = -mS(r_s + r_t) - r_s r_t + mNr_t$$

One shows easily that $\det(\cdot)$ gouverns stability

$$\implies S^c = \frac{mNr_t - r_s r_t}{m(r_s + r_t)}$$

$\square$

Position of the problem

A metapopulation of sources and sinks with explicit movement

The movement matrix

Local analysis of the model

Global behaviour

An interesting special case

Mathematical w.l.o.g. $\neq$ numerical w.l.o.g.

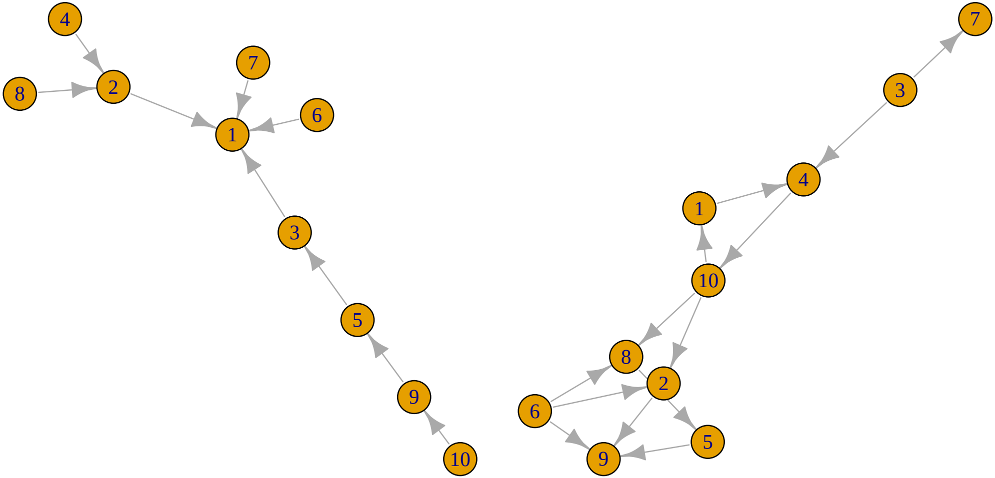
Ordering of vertices is important

To show mathematical results, we have assumed (without loss of generality) that sources came first

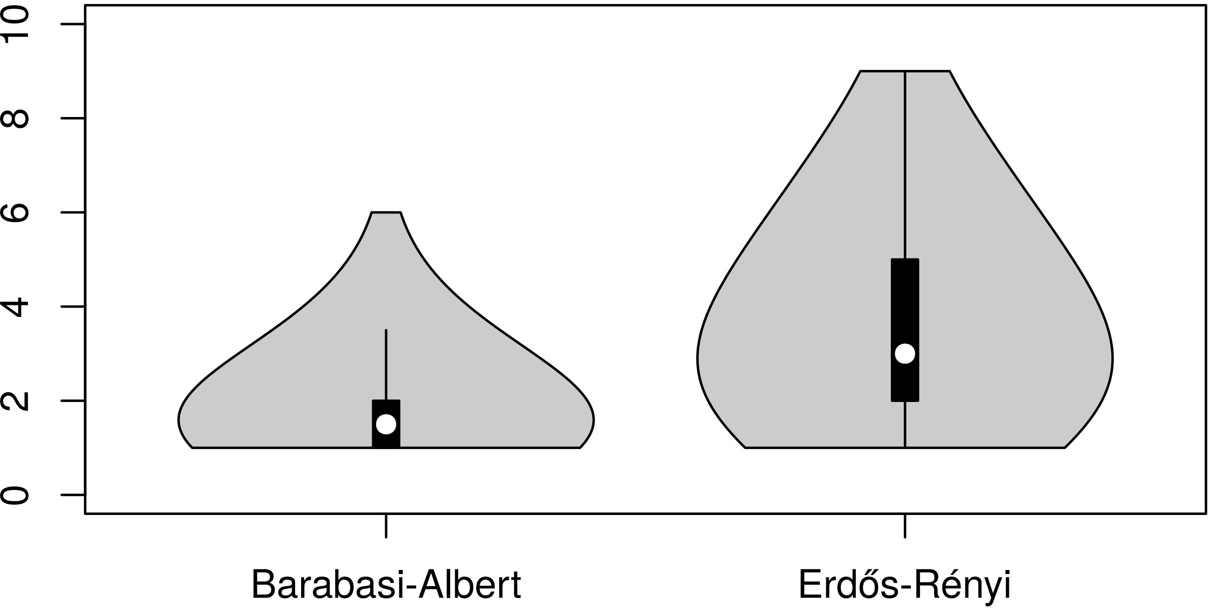
When digraph is complete, no problem

When digraph not complete, not that clear

Digraphs for investigation of effect of vertex order



Consider $10! = 3{,}628{,}800$ vertex permutations on each graph



0
2
4
6
8
10
Barabasi-Albert
Erdős-Rényi

Appendix – Used results

[?]

Theorem A.1 ([?, Problem 1.2.P8])

Let $A \in \mathcal{M}_n$ and $\lambda \in \mathbb{C}$ be given. Suppose that the eigenvalues of A are $\lambda_1, \ldots, \lambda_n$. Explain why $p_{A+\lambda\mathbb{I}}(t) = p_A(t-\lambda)$ and deduce from this identity that the eigenvalues of $A + \lambda\mathbb{I}$ are $\lambda_1 + \lambda, \ldots, \lambda_n + \lambda$

Theorem A.2 ([?, Theorem 2.4.9.2])

Let an infinite sequence $A_1, A_2, \ldots \in \mathcal{M}_n$ *be given and suppose that* $\lim_{k\to\infty} A_k = A$ *(entrywise convergence)*

Let $\lambda(A) = [\lambda_1(A) \cdots \lambda_n(A)]^T$ *and* $\lambda(A_k) = [\lambda_1(A_k) \cdots \lambda_n(A_k)]^T$ *be given presentations of the eigenvalues of* A *and* A_k*, respectively, for* $k = 1, 2, \ldots$. *Let* $S_n = \{\pi : \pi \text{ is a permutation of } \{1, 2, \ldots, n\}\}$. *Then for each given* $\varepsilon > 0$ *there exists a positive integer* $N = N(\varepsilon)$ *such that*

$$\min_{\pi \in S_n} \max_{i=1,\ldots,n} \left\{ \left| \lambda_{\pi(i)}(A_k) - \lambda_i(A) \right| \right\} \leq \varepsilon \text{ for all } k \geq N$$

[?]

Let $A \in \mathcal{M}_n(\mathbb{C})$. Denote $N = \{1, \ldots, n\}$. For $i \in N$, define

$$r_i(A) = \sum_{j \in N \setminus \{i\}} |a_{ij}|$$

to be the ith deleted row sums of A. Assume that $r_i(A) = 0$ if $n = 1$. Let

$$\Gamma_i(A) = \{z \in \mathbb{C} \mid |z - a_{ii}| \leq r_i(A)\} \qquad i \in N$$

be the ith **Gershgorin disk** of A and

$$\Gamma(A) = \bigcup_{i \in N} \Gamma_i(A)$$

be the **Gershgorin set** of A. Γ_i and Γ are closed and bounded in $\mathbb{C}$. $\Gamma_i(A)$ is a disk centred at a_{ii} and with radius $r_i(A)$, $i \in N$.

Theorem A.3 (Gershgorin, 1931)

For all $A \in \mathcal{M}_n(\mathbb{C})$ and for all $\lambda \in \sigma(A)$, there exists $k \in \mathbb{N}$ such that

$$|\lambda - a_{kk}| \leq r_k(A)$$

i.e., $\lambda \in \Gamma_k(A)$ and thus $\lambda \in \Gamma(A)$. Since this is true for all λ, we have

$$\sigma(A) \subseteq \Gamma(A)$$

Remark A.4

This also works with deleted column sums; indeed, just consider A^T in this case. However, this typically gives different disks

[?]

Theorem A.5 (Perron-Frobenius [?, Theorem 4.2.1])

$A \geq 0$ be irreducible. Then $\rho(A)$ is a simple positive eigenvalue of A and there exists a positive eigenvector $\mathbf{x}$ associated to $\rho(A)$. No other nonnegative vector is associated with any other eigenvalue of A

Definition A.6

A matrix is of class Z_n if it is in $\mathcal{M}_n(\mathbb{R})$ and such that $a_{i,j} \leq 0$, $i \neq j$, $i,j = 1, \ldots, n$

$$Z_n = \{A \in \mathcal{M}_n : a_{i,j} \leq 0, i \neq j\}$$

We also say that $A \in Z_n$ has the **Z-sign pattern**

Theorem A.7 ([?, Theorem 5.1.1])

Let $A \in Z_n$. TFAE and define matrices of class K (or nonsingular M-matrix)

1. *There is a nonnegative vector x such that $Ax > 0$*
2. *There is a positive vector x such that $Ax > 0$*
3. *There is a diagonal matrix $\text{diag}(D) > 0$ such that the entries in $AD = [w_{ik}]$ are such that*
$$w_{ii} > \sum_{k \neq i} |w_{ik}| \forall i$$
4. *For any $B \in Z_n$ such that $A \geq A$, then B is nonsingular*
5. *Every real eigenvalue of any principal submatrix of A is positive.*
6. *All principal minors of A are positive*

Theorem A.7 ([?, Theorem 5.1.1] (continued))

7. *For all* $k = 1, \ldots, n$*, the sum of all principal minors is positive*
8. *Every real eigenvalue of* A *is positive*
9. *There exists a matrix* $C \geq 0$ *and a number* $k > \rho(A)$ *such that* $A = k\mathbb{I} - C$
10. *There exists a splitting* $A = P - Q$ *of the matrix* A *such that* $P^{-1} \geq 0$*,* $Q \geq 0$*, and* $\rho(P^{-1}Q < 1)$
11. A *is nonsingular and* $A^{-1} \geq 0$
12.
13.
14.
15.
16.
17.
18. *The real part of any eigenvalue of* A *is positive*

Theorem A.8 ([?, Theorem 5.2.1])

Let $A \in Z_n$. TFAE and define matrices of class K_0

1. $A + \varepsilon \mathbb{I} \in K$ *for all* $\varepsilon > 0$
2. *Every real eigenvalue of a principal submatrix of A is nonnegative*
3. *All principal minors of A are nonnegative*
4. *The sum of all principal minors of order $k = 1, \ldots, n$ is nonnegative*
5. *Every real eigenvaue of A is nonegative*
6. *There exists $C \geq 0$ and $k \geq \rho(C)$ such that $A = k\mathbb{I} - C$*
7. *Every eigenvalue of A has nonnegative real part*

Theorem A.9 ([**?**, Theorem 5.2.10])

Let $A \in Z$ be irreducible. TFAE

1. $\exists \mathbf{x} > \mathbf{0}$ *s.t.* $A\mathbf{x} > 0$
2. $\exists \mathbf{x} > \mathbf{0}$ *s.t.* $A\mathbf{x} \geq \mathbf{0}$ *and* $A\mathbf{x} \neq \mathbf{0}$
3. $A \in K$
4. $A^{-1} > 0$

[?]

Theorem A.10 ([?, Corollary 4.3.2])

Let A be quasi-positive. Then $s(A) \in \sigma(A)$ and $\exists \mathbf{v} > \mathbf{0}$ such that $A\mathbf{v} = s(A)\mathbf{v}$. Moreover, $Re\,\lambda < s(A)$ for all $\lambda \in \sigma(A) \setminus \{s(A)\}$. If, in addition, A is irreducible, then

1. *$s(A)$ has algebraic multiplicity 1*
2. *$\mathbf{v} \gg \mathbf{0}$ and any eigenvector $\mathbf{w} > \mathbf{0}$ of A is a positive multiple of $\mathbf{v}$*
3. *If B is a matrix satisfying $B > A$, then $S(B) > s(A)$*
4. *If $s(A) < 0$ then $-A^{-1} \gg \mathbf{0}$*