Sign Pattern Matrices in Population Biology

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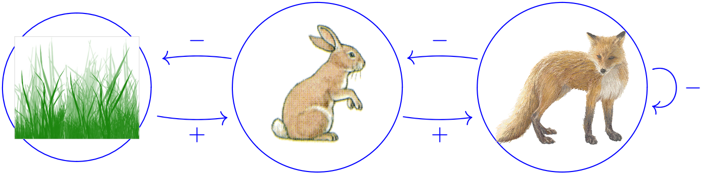
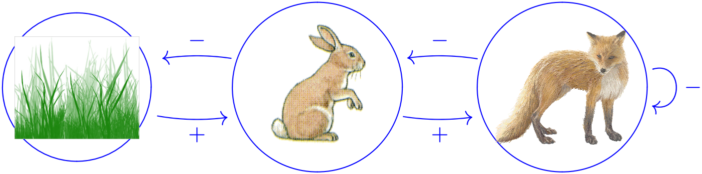
Dynamical system for Grass-Rabbit-Fox



Let G, R, F denote a measure of the grass, rabbit, fox population in a closed region

Given positive initial conditions, $a, ..., h > 0$, populations change with time as the ODE dynamical system :

$$\begin{aligned} \frac{dG}{dt} &= aG - bRG \\ \frac{dR}{dt} &= cR - dRF + eRG \\ \frac{dF}{dt} &= fF - gF^2 + hRF \end{aligned}$$



For certain parameter values, there exists a unique equilibrium with all populations positive G^*, R^*, F^*

Stability is governed by the linearized community matrix

$$A = \begin{bmatrix} 0 & -bG^* & 0 \\ eR^* & 0 & -dR* \\ 0 & hF* & -gF* \end{bmatrix}$$

The characteristic polynomial of the matrix A is

$$p_A(z) = z^3 + gF^* z^2 + (beG^* R^* + dhR^* F^*)z + begG^* R^* F^*$$

Routh-Hurwitz conditions imply that this polynomial has all eigenvalues with negative real parts

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Thus A is a (negative) stable matrix for all parameter values

So the grass-rabbit-fox positive equilibrium is locally stable for all magnitudes of interactions

For any magnitudes of the parameters (provided that G^*, R^*, F^* exist) this community matrix has sign pattern $\mathcal{S}$ given by

$$\mathcal{S} = \begin{bmatrix} 0 & - & 0 \\ + & 0 & - \\ 0 & + & - \end{bmatrix}$$

and this is stable for all matrix realizations

Sign pattern of community matrix with entries $\in \{+, -, 0\}$

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$$\mathcal{S} = \begin{bmatrix} 0 & - & 0 \\ + & 0 & - \\ 0 & + & - \end{bmatrix}$$

and this is stable for all matrix realizations

This sign pattern $\mathcal{S}$ is called sign stable, $\mathcal{S}$ requires stability

If $\mathcal{S}$ has some matrix realization that is stable, then S is potentially stable, $\mathcal{S}$ allows stability
Example: Superpattern of $\mathcal{S}$ with 2,2 entry $+$

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Digraph $D(\mathcal{S})$

Associated with the $n \times n$ sign pattern $\mathcal{S} = [s_{ij}]$ is a signed digraph $D(\mathcal{S})$ with $s_{ij} \in \{+, -, 0\}$

- vertex set $\{1, ..., n\}$
- arc set $\{(i, j) : s_{ij} \neq 0\}$
- signed arc $(i, j) = s_{ij}$

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$\mathcal{S}$ is a tree sign pattern if $D(\mathcal{S})$ is strongly connected and has no k-cycles for $k \geq 3$
i.e. has only 2-cycles and loops:
examples are path sign patterns, star sign patterns
(the G, R, F system)

Conditions for potential or sign stability are often stated in terms of this signed digraph

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Sign patterns

- Samuelson (1947) considered qualitative problems in economics involving sign patterns
- Quirk (1968) and Quirk and Maybee (1969) studied these from a matrix/digraph point of view and wrote:
  "*Specification of necessary and sufficient conditions for potential stability remains an unsolved problem*"
  Apart from a few special cases, this remains true today

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  "*Specification of necessary and sufficient conditions for potential stability remains an unsolved problem*"
  Apart from a few special cases, this remains true today
- Sign stability was characterized by Jeffries et al (1977) and they gave an algorithm to test whether or not a sign pattern is sign stable
- Since the 1970s researchers have derived many results about sign patterns and applied some to dynamical systems e.g. economics, food webs

Stability of a dynamical system

Assume a general ODE dynamical system is at an equilibrium $x^* \in \mathbb{R}^n$

Considering small perturbations and linearizing about x^* the time evolution is governed by

$$\frac{dx(t)}{dt} = Ax(t)$$

for some $n \times n$ Jacobian community matrix A

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To investigate this and other possibilities, we introduce two sets determined by the eigenvalues of A

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The refined inertia of matrix $A \in \mathbb{R}^{n\times n}$ is the 4-tuple of nonnegative integers summing to n

$ri(A) = (n_+, n_-, n_0, 2n_p)$, where (counting multiplicities):

n_+ is the number of eigenvalues with positive real part

n_- is the number of eigenvalues with negative real part

n_0 is the number of zero eigenvalues

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Note that the inertia of A is $(n_+, n_-, n_0 + 2n_p)$

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The refined inertia of $\mathcal{S}$ is $\{ri(A) : A$ is a realization of $\mathcal{S}\}$

If $(0, n, 0, 0) \in ri(\mathcal{S})$ then $\mathcal{S}$ is potentially stable

If $\{(0, n, 0, 0)\} = ri(\mathcal{S})$ then $\mathcal{S}$ is sign stable

Sets of refined inertias

Bodine et al. (2012) For $n \geq 3$, define the set of refined inertias

$$\mathbb{H}_n = \{(0,n,0,0),(0,n-2,0,2),(2,n-2,0,0)\}$$

The set $\mathbb{H}_n$ includes two pure imaginary eigenvalues that cross over into the positive half plane, and signal the possibility of Hopf bifurcation leading to an oscillatory solution

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Berliner et al. (2017) For $n \geq 2$, define the set of inertias

$$\mathbb{S}_n = \{(0,n,0),(0,n-1,1),(1,n-1,0)\}$$

The set $\mathbb{S}_n$ includes one zero eigenvalue that crosses to positive, and signals the possibility of a saddle node bifurcation

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Goodwin model

The Goodwin model for a regulatory mechanism in cellular physiology is formulated as a system of 3 ODEs

$$\frac{dM}{dt} = \frac{V}{K + P^m} - aM \qquad \frac{dE}{dt} = bM - cE \qquad \frac{dP}{dt} = dE - \frac{eP}{k + P}$$

M, E, P represent the concentrations of messenger RNA, the enzyme and the product of the reaction of the enzyme and a substrate, other letters are positive parameters, with Hill constant m

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Linearizing about an equilibrium (with $P > 0$ at its equilibrium value)

$$A = \begin{bmatrix} -a & 0 & -\frac{VmP^{m-1}}{(K+P^m)^2} \\ b & -c & 0 \\ 0 & d & -\frac{ek}{(k+P)^2} \end{bmatrix}$$

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Sign patterns with a full diagonal

Bodine et al (2012)

Theorem

Let $\mathcal{S}_n$ be an $n \times n$ sign pattern with all its diagonal entries nonzero. If $\mathcal{S}_n$ allows refined inertia $(n_+, n_-, n_0, 2n_p)$ then it allows refined inertias $(n_+ + n_0 + 2n_p, n_-, 0, 0)$ and $(n_+, n_- + n_0 + 2n_p, 0, 0)$

If A is a realization of $\mathcal{S}_n$ with $\mathrm{ri}(A) = (n_+, n_-, n_0, 2n_p)$, then by continuity $A \pm \varepsilon I_n$ are also realizations of $\mathcal{S}_n$ with $\mathrm{ri}(n_+ + n_0 + 2n_p, n_-, 0, 0)$ and $\mathrm{ri}(n_+, n_- + n_0 + 2n_p, 0, 0)$, resp.

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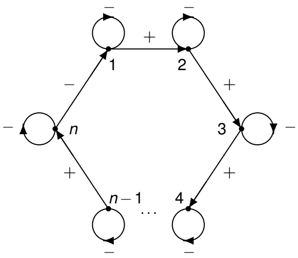
Corollary

An $n \times n$ sign pattern with all entries on its diagonal negative allows $\mathbb{H}_n$ if and only if it allows refined inertia $(0, n-2, 0, 2)$

For $n \geq 3$, let sign pattern $\mathcal{K}_n = -\mathcal{I}_n + \mathcal{C}_n$ where

$\mathcal{I}_n$ has each diagonal entry equal to + and all other entries 0

$\mathcal{C}_n = [c_{ij}]$ is the sign pattern of a negative *n*-cycle matrix with $c_{12}, c_{23}, \cdots, c_{n-1,n} = +, c_{n1} = -$ and all other entries 0



Negative diagonal plus negative n-cycle

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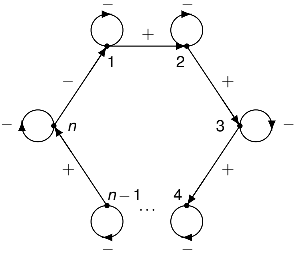

Sign pattern of linearized Goodwin model is equivalent to $\mathcal{K}_3$

$\mathcal{K}_n = -\mathcal{I}_n + \mathcal{C}_n$

- $\mathcal{K}_n$ allows $\mathbb{H}_n$ for all $n \geq 3$
  The set of eigenvalues of a realization C_n of $\mathcal{C}_n$ consists of a positive scalar multiple of the n^{th} roots of -1, so C_n has a unique pair of complex conjugate eigenvalues with maximum real part $\alpha > 0$. Matrix $-\alpha I_n + C_n$ has refined inertia $(0, n-2, 0, 2)$, then apply the Corollary

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- $\mathcal{K}_n$ requires $\mathbb{H}_n$ for $3 \leq n \leq 6$
- For $n = 3$, if $\mathcal{K}_3$ allows $\mathbb{H}_3$ then it requires $\mathbb{H}_3$
  In this case any realization A has trace$(A) < 0$, det$(A) < 0$, so has at least one negative eigenvalue and the product of the other two eigenvalues is positive
  Thus (0,3,0,0), (0,1,0,2), (2,1,0,0) are the only possible refined inertias

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Oscillations occur in the linearized Goodwin model, and are found in the nonlinear Goodwin model due to Hopf bifurcation

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Infectious disease model

Consider a constant population that is divided into three disjoint classes with $S(t), I(t), R(t)$ denoting the fractions of the population that are *S*usceptible to, *I*nfectious with, *R*ecovered from a disease

β is the constant contact rate
γ is the constant recovery rate

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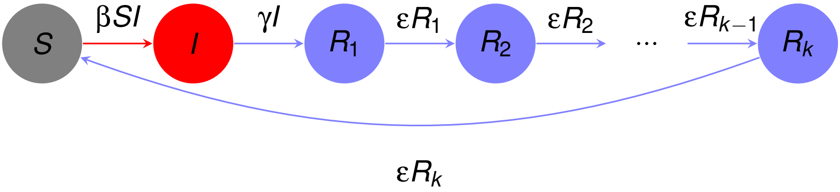
Assume that the disease confers temporary immunity on recovery (e.g. influenza, COVID-19?)

This can be modeled by splitting $R(t)$ into a chain of recovered classes $R_1, R_2, \ldots, R_k$ with the waiting time in each subclass assumed exponentially distributed with mean waiting time $1/\varepsilon$

The $S, I, R_1, R_2, \ldots, R_k, S$ model is described schematically by



Dynamical system for the infectious disease model

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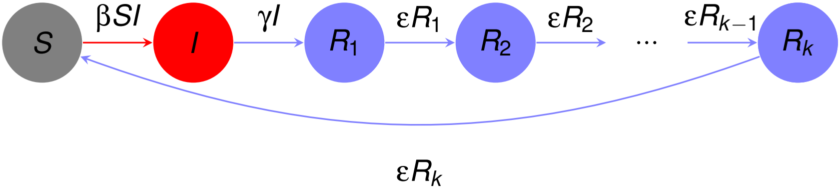

The differential equations governing the evolution of disease with $S = 1 - I - R_1 - \cdots - R_k$ are:

$$\frac{dI}{dt} = \beta S I - \gamma I$$

$$\frac{dR_1}{dt} = \gamma I - \varepsilon R_1$$

$$\frac{dR_i}{dt} = \varepsilon R_{i-1} - \varepsilon R_i, \quad i = 2, \ldots, k$$

This system has a disease free equilibrium with $S = 1$ and other variables zero

Equilibria

This system has a disease free equilibrium with $S = 1$ and other variables zero

Here $\mathcal{R}_0 = \frac{\beta}{\gamma}$ is the basic reproduction number

If $\mathcal{R}_0 < 1$ then this is the only equilibrium
and the disease dies out

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If $\mathcal{R}_0 > 1$ there is also an endemic (positive) equilibrium with

$$S^* = \frac{1}{\mathcal{R}_0}, \quad I^* = (1 - \frac{1}{\mathcal{R}_0})/(1 + \frac{n\,\gamma}{\varepsilon}), \quad R_i^* = \frac{\gamma I^*}{\varepsilon}$$

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To find out about linear stability of this endemic equilibrium, consider the Jacobian matrix at this equilibrium

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Magnitudes matter

Take for example 3 recovered classes ($k = 3$)

$$A = \begin{bmatrix} -\beta I^* & -\beta I^* & -\beta I^* & -\beta I^* \\ \gamma & -\varepsilon & 0 & 0 \\ 0 & \varepsilon & -\varepsilon & 0 \\ 0 & 0 & \varepsilon & -\varepsilon \end{bmatrix}$$

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$k = 2$: S, I, R_1, R_2, S: The leading 3×3 subpattern allows $\mathbb{H}_3$ but the magnitude structure restricts its refined inertia to (0,3,0,0): stable

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$k = 3$: S, I, R_1, R_2, R_3, S: Here $\mathcal{S}^r$ allows $\mathbb{H}_4$ and for some parameter values this model exhibits periodic solutions arising from a Hopf bifurcation

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Parasitoid wasp ovipositing into the body of an aphid

[en.wikipedia.org]

$$\frac{dH}{dt} = rH - \frac{HP}{1+T_h H}$$

$$\frac{dP}{dt} = \frac{HP}{1+T_h H} - (d+e)P + fQ$$

$$\frac{dQ}{dt} = eP - (f+s)Q$$

H, P = host, parasitoid density in patch
Q = density of parasitoid in transit
r = rate of H growth in absence of P
d, s = death rate of P, Q
e, f = emigration rate of P, Q
T_h = handling time (Type II functional response) of parasitoids, measures the limit of hosts that the parasitoids can parasitise

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If $\alpha T_h < 1$ with $\alpha = d + \frac{es}{f+s}$ then $\exists$ positive equilibrium H^*, P^*, Q^*

Linearizing about this positive equilibrium and using the equilibrium conditions gives the Jacobian matrix

$$A = \begin{bmatrix} \alpha r T_h & -\alpha & 0 \\ r(1-\alpha T_h) & \alpha-(d+e) & f \\ 0 & e & -(f+s) \end{bmatrix}$$

with tree sign pattern

$$\mathcal{S} = \begin{bmatrix} + & - & 0 \\ + & - & + \\ 0 & + & - \end{bmatrix}$$

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$$\mathcal{S} = \begin{bmatrix} + & - & 0 \\ + & - & + \\ 0 & + & - \end{bmatrix}$$

This sign pattern allows both $\mathbb{S}_3$ and $\mathbb{H}_3$, so depending on the parameter values, the host parasitoid system may have a saddle node or a Hopf bifurcation

By continuity we just need to show that $\mathcal{S}$ allows inertia (0,2,1) and refined inertia (0,1,0,2)

- inertia (0,2,1) for $\mathcal{S}$ to allow $\mathbb{S}_3$

$$\begin{bmatrix} 1 & -1 & 0 \\ 2 & -3 & 1 \\ 0 & 2 & -2 \end{bmatrix}$$

has eigenvalues $0, -2 \pm \sqrt{3}$
Berliner et al. (2018)

Numerical examples

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- refined inertia (0,1,0,2) for $\mathcal{S}$ to allow $\mathbb{H}_3$

$$\begin{bmatrix} 0.01 & -1 & 0 \\ 1 & -0.1 & 1 \\ 0 & 1 & -11.03128 \end{bmatrix}$$

  has eigenvalues approx. $\pm 0.995i, -11.121$
  Culos et al. (2016)

Zero handling time

If $T_h = 0$ i.e. the handling time is zero, then the system becomes a Lotka-Volterra System
The linearized matrix becomes

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Using the Routh-Hurwitz conditions, this matrix is stable for all parameters $r, d, s, f, e > 0$

So the Type II functional response of the parasitoids is responsible for the instability
If the handling time is small, then the system is locally stable, but higher handling time can lead to "extremely complicated dynamics"

An *n*-patch predator prey system with only the predators moving between patches feeding on the prey, the prey grow linearly, die due to predation, with a linear Lotka-Volterra type functional response:

For $i = 1...n$, the ODE model is:

$$\frac{dP_i}{dt} = P_i(a_i b_i R_i - C_i - E_{ii}) + \sum_{j \neq i} E_{ij} P_j$$

$$\frac{dR_i}{dt} = R_i(r_i - a_i P_i)$$

P_i, R_i are population levels of predator, prey in patch i

r_i = per capita growth rate of prey in patch i

a_i = rate at which predator catches prey in patch i

b_i = measure of foraging for P_i

C_i = mortality rate for P_i

E_{ij} = predator emigration/immigration rates between patches

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Predator prey n-patch model with linear prey growth

An n-patch predator prey system with only the predators moving between patches feeding on the prey, the prey grow linearly, die due to predation, with a linear Lotka-Volterra type functional response:

For $i = 1...n$, the ODE model is:

$$\frac{dP_i}{dt} = P_i(a_i b_i R_i - C_i - E_{ii}) + \sum_{j \neq i} E_{ij} P_j$$
$$\frac{dR_i}{dt} = R_i(r_i - a_i P_i)$$

P_i, R_i are population levels of predator, prey in patch i

r_i = per capita growth rate of prey in patch i

a_i = rate at which predator catches prey in patch i

b_i = measure of foraging for P_i

C_i = mortality rate for P_i

E_{ij} = predator emigration/immigration rates between patches

At equilibrium:

$P_i^* = r_i / a_i = d_i, \;\; R_i^* = (C_i + E_{ii} - \sum_{j \neq i} E_{ij} P_j^* / P_i^*) / a_i b_i$ assume > 0

Linearizing around this equilibrium and taking a positive diagonal similarity gives

$$J = \begin{bmatrix} B & C \\ I & 0 \end{bmatrix}$$

where $B = [b_{ij}]$ has $b_{ii} = -\frac{1}{d_i} \sum_{j \neq i} E_{ij} d_j, b_{ij} = E_{ij}, i \neq j$
and C is a diagonal matrix with i^{th} diagonal entry $-a_i b_i r_i R_i^*$

Note that J has a fixed sign pattern and is nonsingular

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If μ is an eigenvalue of J then taking a Schur complement μ is a root of the quadratic

$$det(\mu^2 I - \mu B - C) = 0$$

This is the quadratic eigenvalue problem (QEP)
see Tisseur, Meerbergen (2001)for a review of QEP

Two patches, Holt 1984

For two patches:

$$J = \begin{bmatrix} -E_{12}d_2/d_1 & E_{12} & -a_1 b_1 r_1 R_1^* & 0 \\ E_{21} & -E_{21} d_1/d_2 & 0 & -a_2 b_2 r_2 R_2^* \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \end{bmatrix}$$

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But B has a zero eigenvalue and a negative eigenvalue
When $\lambda = 0$, $\mu^2 = c$, so $\pm i\sqrt{c}$ are eigenvalues of J
When $\lambda < 0$, the real parts of μ are negative

In this case the predator prey system is semi-stable

With more general C in the two-patch case, B can be diagonally symmetrized, so J has the same eigenvalues as

$$H = \begin{bmatrix} F & G \\ -G & 0 \end{bmatrix}$$

where $det(F) = 0, f_{ii} < 0, f_{12} = f_{21} = \sqrt{E_{12}E_{21}}$, G is diagonal

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Using Bendixson's Theorem:

$\mathcal{R}e$ (an eigenvalue of H) $\leq$ max eigenvalue of $\frac{H+H^T}{2}$

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Holt used Routh Hurwitz conditions, Angeli et al. (2014) used the second additive compound matrix to prove that if $a_1 b_1 r_1 R_1^* \neq a_2 b_2 r_2 R_2^*$ the predator prey system is linearly stable showing the stabilizing effect of predator movement

No periodic solutions occur for this predator-prey system rather there is coexistence for this two-patch case

For $n \geq 3$ matrix J is not diagonally symmetrizable, so use M-matrix theory

$$J = \begin{bmatrix} B & C \\ I & 0 \end{bmatrix}$$

Matrix B is singular with a positive right nullvector $x = [d_1, d_2, ..., d_n]^T$ and $-B$ has the Z sign pattern
$-B$ is a singular M-matrix since $(-B + \varepsilon I)x = \varepsilon x > 0$ for $\varepsilon > 0$
see e.g. Berman, Plemmons (1994, Chapter 6), Horn, Johnson (1991, Section 2.5)

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Theorem

If $-B$ is a singular M-matrix and C is a diagonal matrix with all $c_{ii} < 0$, then J is semi-stable.

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Idea of Proof:

With X a diagonal matrix with $x_{ii} = \sqrt{a_i b_i r_i R_i^*}$, J is diagonally similar to

$$K = \begin{bmatrix} B & -X \\ X & 0 \end{bmatrix}$$

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Letting $\bigoplus$ denote the direct sum:

$$K^T(Y \bigoplus Y) + (Y \bigoplus Y)K = B^T Y + YB \bigoplus 0$$

since X and Y are diagonal

Thus $K^T(Y \oplus Y) + (Y \oplus Y)K$ is negative semi-definite and so J is semi-stable, Horn, Johnson (1991, Lemma 2.4.5)
No Hopf bifurcation occurs in this n-group predator prey model

Suppose A is an order n real matrix with $m \geq n$ nonzero entries $a_{i_1 j_1}, a_{i_2 j_2}, \ldots, a_{i_m j_m}$

Let X denote the matrix obtained from A by replacing $a_{i_k j_k}$ with the variable x_k for $k = 1, \ldots, m$

The characteristic polynomial of X is

$p_X(z) = z^n + p_1 z^{n-1} + \cdots + p_{n-1} z + p_n$ with $p_i = p_i(x_1, x_2, \ldots, x_m)$

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Let $J = J_X$ be the $n \times m$ Jacobian matrix with (i,j) entry equal to $\frac{\partial p_i}{\partial x_j}$ for $1 \leq i \leq n$ and $1 \leq j \leq m$, and $J_{X=A}$ denote the Jacobian matrix evaluated at $x_k = a_{i_k j_k}$ for $1 \leq k \leq m$

If J has rank n then A allows a Jacobian of full rank

This Jacobian and the Implicit Function Theorem are used to prove the following result

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Berliner et al. (2020) based on Cavers et al. (2013)

Theorem

Let $\mathcal{A}_n$ be a sign pattern of order n with a matrix realization A having $i(A) = (0, n-1, 1)$ or $ri(A) = (0, n-2, 0, 2)$ and A allows a Jacobian of full rank
Then $\mathcal{A}_n$ and any superpattern allows $\mathbb{S}_n$ or $\mathbb{H}_n$ resp.

This leads to superpatterns that indicate bifurcations of biological dynamical systems?