Properties of large dynamic Lotka Volterra systems equilibria for theoretical ecology

Master thesis presentation

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September 15, 2022

A bit of history [Bacaër, 2011]

- **1750s :** *Leonhard Euler* human population as a geometric series
- **1798 :** *Thomas Robert Malthus* 'the power of population is indefinitely greater than the power in the earth to produce subsistence for man'
- **1838 :** *Pierre-François Verhulst* logistic growth
- **1920 :** *Alfred James Lotka* biological systems dynamics exhibit oscillations

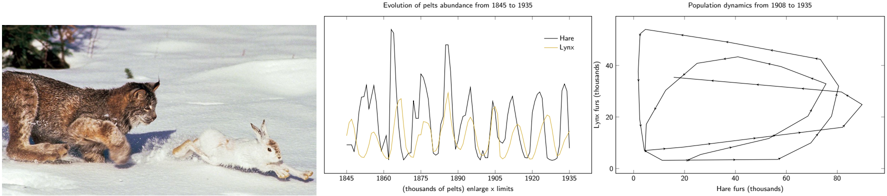


Figure: A Canadian lynx chasing a snowshoe hare (left). Illustration of the cyclical model for lynx and snowhare collected pelts based on hunting data from 1845 to 1935 (middle) and of the population dynamics over a time window from 1908 to 1935 (right).

The Lotka-Volterra for a community of species

Lotka Volterra system is about understanding abundances dynamics for N species having interactions. For each $k \in [\![1, N]\!]$,

$$\frac{\partial x_k}{\partial t} = x_k \left(r_k - x_k + [\Gamma_N \cdot \vec{x}]_k \right) = x_k \left(r_k - [(I_N - \Gamma_N) \cdot \vec{x}]_k \right)$$

$\vec{x}$ abundances vector
$x_k = x_k(t)$ abundance of species k
r_k natural growth rate of species k
Γ_N $N \times N$ interaction matrix

Non-invasibility assumption:

$$\forall k \in [\![1, N]\!], \left(\frac{1}{x_k} \frac{\partial x_k}{\partial t} \right)_{x_k \to 0^+} \leq 0 \iff \forall k \in [\![1, N]\!], \ r_k - [(I_N - \Gamma_N) \cdot \vec{x}^\star]_k \leq 0$$

[Law and Morton, 1996, 'Condition for invasion by a new specie'].

From Lotka-Volterra to RMT

After R. M. May ideas in 1972, we started using random matrices to model interactions matrix.

$\Gamma_{10} =$

	0.17	0.54	-0.97	-1.4	-1.72	-1.47	0.54	-0.25	-0.25	0.74
	1.02	0.44	0.13	0.85	-0.6	-0.45	0.97	0.21	-1.63	-0.14
	0.56	1.36	-1	-1.2	-0.71	-0.64	0.18	1.12	-0.59	0.18
	-1.05	-0.63	-0.03	0	0.95	-0.06	0.39	1.72	1.35	-0.62
	-0.44	0.49	0.84	0.14	-0.69	0.76	-0.26	-0.28	1.22	0.83
	-0.02	-0.79	-0.43	-1.79	-1.92	-1.28	-0.16	-0.66	-0.76	0.38
	0.54	0.98	0.76	0.02	1.32	-0.36	-1.48	-0.66	0.05	-0.75
	-0.46	-0.13	0.56	-0.64	-1.47	-1.48	1.5	-0.66	0.14	-0.58
	-1.52	1.09	1.62	-0.91	0.85	0.12	-1.73	-1.39	-1.25	-0.23
	0.3	0.8	0.2	-0.5	0.33	-0.53	-0.19	0.58	1.86	0.96

Figure: Example of a 10×10 random matrix to represent the interactions within a community of species.

The i.i.d. model

We use the the i.i.d. model of interactions and we study a LV system where $r = \mathbb{1}_N$ and $\Gamma_N = \frac{X_N}{\alpha\sqrt{N}}$, X_N being fulfilled with centered entries of unit variance.

For each $k \in [\![1, N]\!]$,

$$\frac{\partial x_k}{\partial t} = x_k \left(1 - \left[\left(I_N - \frac{X_N}{\alpha\sqrt{N}} \right) \cdot \vec{x} \right]_k \right)$$

> X_N $N \times N$ non hermitian random matrix
> $1/\alpha$ the interaction strength

Objective:
$\Longrightarrow$ analyze the properties of this system of coupled equations depending on the interaction strength values (in non hermitian context)

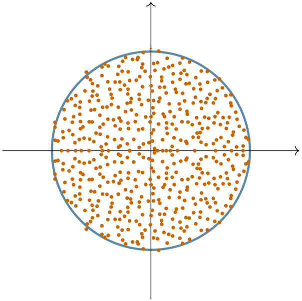


Figure: Uniform distribution of Γ_N eigenvalues in the disk for a non hermitian random matrix of size 500×500. In blue, the circle of radius equals to the entries standard deviation, $1/\alpha$.

Different nature of interactions

	+	0	−
+	mutualism *bees and flowers*		
0	commensalism *small fishes hidden on sharks*	neutralism	
−	parasitism *caterpillars on oak or pine trees*	amensalism *humans and Earth*	competition *for food, shelter, partner or sunlight*

Table: Different kind of species interactions that can be found in nature.

Properties of interest

An equilibrium point is defined as:

$$\forall k \quad \frac{\partial {x_k}^\star}{\partial t} = 0$$
$$\iff \forall k \quad {x_k}^\star \left(1 - \left[\left(I_N - \frac{X_N}{\alpha\sqrt{N}}\right) \cdot \vec{x}^\star\right]_k\right) = 0$$

Then, for each k, either ${x_k}^\star = 0$ or $1 - \left[\left(I_N - \frac{X_N}{\alpha\sqrt{N}}\right) \cdot \vec{x}^\star\right]_k = 0$

We investigate the possible equilibria points of the LV system and some of their properties:

- existence and uniqueness
- non negativity, and even more feasibility (strict positivity)
- stability, and even more global stability

The Linear Complementarity Problem

The Linear complementarity Problem is to find out solutions $x, y \in \mathbb{R}^N$ such that

$$
\begin{aligned}
& y = Ax + r \geq 0, \\
& x \geq 0, \\
& y^T \cdot x = 0
\end{aligned}
$$

for A a $N \times N$ matrix and $r \in \mathbb{R}^N$. We denote this system LCP(A, r).
Finding an equilibrium point to the LV system is equivalent to solve the LCP$(I_N - \Gamma_N, -\mathbb{1}_N)$:

$$
\begin{aligned}
& (I_N - \Gamma_N) \cdot \vec{x}^\star - \mathbb{1}_N \geq 0, \\
& \vec{x}^\star \geq 0, \\
& ((I_N - \Gamma_N)\,\vec{x}^\star - \mathbb{1}_N)^T \cdot \vec{x}^\star = 0
\end{aligned}
$$

$\Longrightarrow$ Focus on **existence and uniqueness** of solution(s) to this LCP, **feasibility** and **global stability**, that we will analyze according to the values of the interaction strength.

Existence and uniqueness of the solution

Definition

Principal minors are the determinant of principal submatrices obtained when striking out a same set of rows and columns.

Definition

A is a *P-matrix* if all its principal minors are strictly positive.

Theorem (Murty)

[Murty, 1972, Theorem 4.2] $LCP(A, r)$ has a unique solution for each $r \in \mathbb{R}^N$ if and only if A is a P-matrix.

$\implies$ Focus on the P-property.

However, [Rohn and Rex, 1996, Theorem 3.4] shows that the problem is NP-hard for a general real matrix.

Jiri Rohn's algorithm

Nevertheless [Rohn, 2012] proposes an algorithm which might converge quickly in some favourable cases, or alternatively which explore exhaustively the principal minors.

During the internship I translated the initial matlab program into python.

We conjecture a phase transition for the P-property, in the non hermitian setting, at $\frac{1}{\alpha} = 1$.

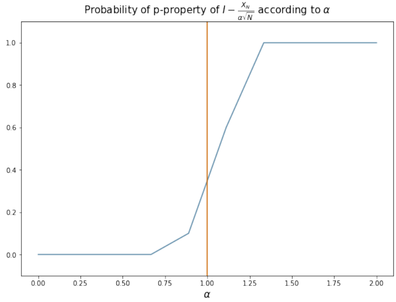


Figure: Simulation of the probability of being a P-Matrix based on Rohn's algorithm. Phase transition at $\alpha = 1$. For each value $\alpha \in (0, 2]$ the value of the curve corresponds to a Montecarlo simulation over 10 iterations for $\Gamma_N = \frac{X_N}{\alpha\sqrt{N}}$ of size 15×15.

Elements for the proof

Conjecture:
Let $\frac{X_N}{\alpha\sqrt{N}}$ be a normalized random matrix, centered with unit variance and bounded fourth moments. For all $\varepsilon > 0$ we consider $\left(\frac{1}{\beta} + \varepsilon\right) I_N - \frac{X_N}{\alpha\sqrt{N}}$, and we conjecture that

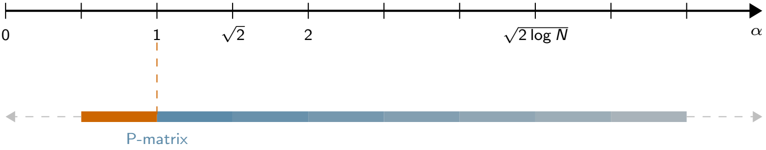
- if $\frac{1}{\beta} < \frac{1}{\alpha}$, then $\left(\frac{1}{\beta} + \varepsilon\right) I_N - \frac{X_N}{\alpha\sqrt{N}}$ is not a P-matrix
- if $\frac{1}{\beta} > \frac{1}{\alpha}$, then $\left(\frac{1}{\beta} + \varepsilon\right) I_N - \frac{X_N}{\alpha\sqrt{N}}$ is a P-matrix

- P-matrix $\implies$ positive real eigenvalues, [Cottle et al., 2009, Theorem 3.3.4]
- $\forall \lambda_k \in \mathbb{R}$, $\frac{1}{\beta} + \varepsilon - \frac{\lambda_k\left(\frac{X_N}{\sqrt{N}}\right)}{\alpha}$ should be positive
- $\lambda_k\left(\frac{X_N}{\sqrt{N}}\right)$ belongs to $[-1, 1]$ (circular law) a.s. for N large

$$\frac{1}{\beta} + \varepsilon - \frac{\lambda_k\left(\frac{X_N}{\sqrt{N}}\right)}{\alpha} > 0, \forall \lambda_k \in \mathbb{R}$$
$$\iff \frac{1}{\beta} + \varepsilon > \frac{1}{\alpha}$$

Thus
$\frac{1}{\beta} + \varepsilon < \frac{1}{\alpha} \implies \left(\frac{1}{\beta} + \varepsilon\right) I_N - \frac{X_N}{\alpha\sqrt{N}}$ is not a P-matrix.

Phase transition phenomena in the LCP$\left(I_N - \frac{X_N}{\alpha\sqrt{N}}, -\mathbb{1}_N\right)$ depending on α



Proof

Conjecture

Feasibility

Feasibility: $\forall k \in [\![1, N]\!], {x_k}^\star > 0 \iff \vec{x}^\star = (I_N - \Gamma_N)^{-1} \cdot \mathbb{1}_N$

The analyze of LCP$(I_N - \Gamma_N, -\mathbb{1}_N)$ from the perspective of linear algebra shows evidence of a phase transition phenomenon for feasibility of the LV model equilibrium at $\frac{1}{\alpha} = \frac{1}{\sqrt{2 \log N}}$, [Bizeul and Najim, 2021, Theorem 1.1].

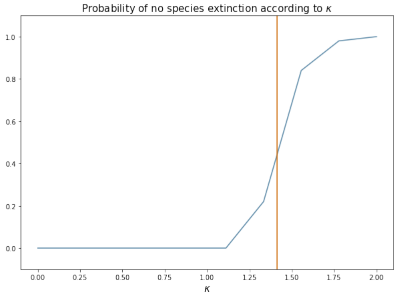
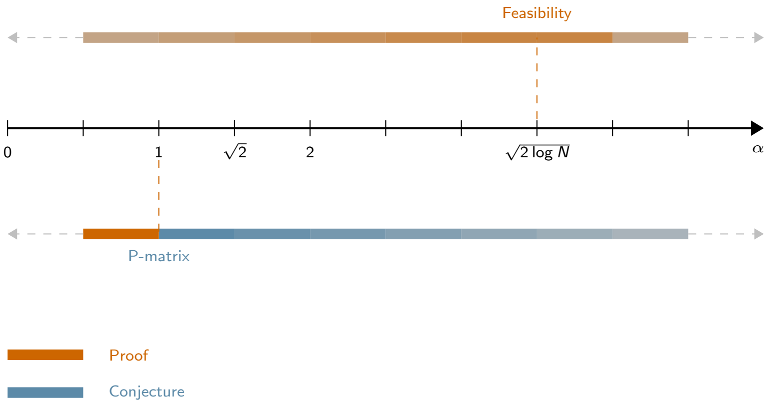


Figure: Simulation of the probability of no species extinction. Phase transition at $\kappa = \sqrt{2}$. For each value $\kappa \in (0, 2]$ the value of the curve corresponds to a Montecarlo simulation over 50 iterations for $\Gamma_N = \frac{X_N}{\kappa \sqrt{N \log N}}$ of size 500×500.

Phase transition phenomena in the LCP$\left(I_N - \frac{X_N}{\alpha\sqrt{N}}, -\mathbb{1}_N\right)$ depending on α



Global stability

Definition

A is Volterra Lyapunov stable means there exists a D positive definite diagonal matrix such that, $DA + A^{\star}D$ is symmetric negative definite.

Theorem (Takeuchi & Adachi)

[Takeuchi, 1996, Theorem 3.2.1] The Lotka Volterra system $\dot{x}_k = x_k \left(r_k - \sum_{l=1}^{N} A_{k,l} x_l \right)$ *for* $k \in [\![1, N]\!]$ *has a non negative and globally stable equilibrium point* $x^{\star}$ *for each* $r \in \mathbb{R}^N$ *if* $-A$ *is Volterra Lyapunov stable.*

Theorem (Takeuchi, Adachi and Tokumaru)

[Takeuchi et al., 1978, Theorem 2] and [Takeuchi, 1996, Lemma 3.2.1] If $-A$ *is Volterra Lyaunov stable, then* A *is a P-matrix and the real parts of its eigenvalues are positive.*

$\implies$ The P-property is weaker than the Volterra Lyapunov stability.

Non hermitian case $\Gamma_N = \frac{X_N}{\alpha\sqrt{N}}$

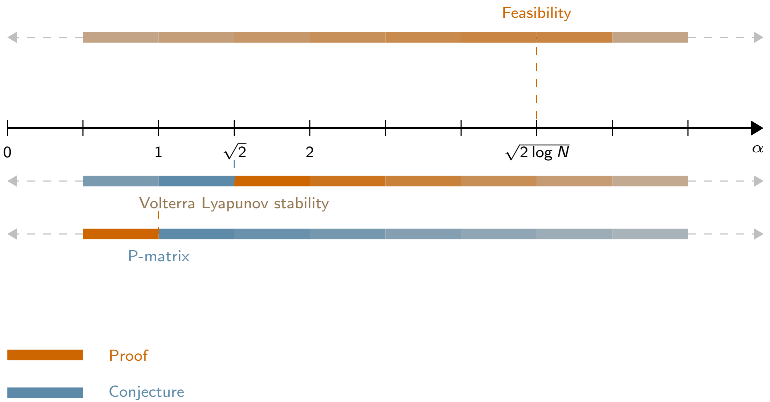
We check the Volterra Lyapunov stability condition for the positive definite diagonal matrix $D = I$.

$$\begin{aligned} &(-I + \Gamma_N) + (-I + \Gamma_N)^\star < 0 \\ \iff & -2I + \Gamma_N + \Gamma_N^\star < 0 \\ \iff & \lambda_{\max}\left(\Gamma_N + \Gamma_N^\star\right) < 2 \end{aligned}$$

- $[\Gamma_N + \Gamma_N^\star]_{i,j} = \frac{X_{N\,i,j} + X_{N\,j,i}}{\alpha\sqrt{N}} = [\Gamma_N + \Gamma_N^\star]_{j,i} \implies$ Wigner matrix
- then, $\lambda_{\max}\left(\Gamma_N + \Gamma_N^\star\right) \xrightarrow[N\to\infty]{a.s.} 2\frac{\sqrt{2}}{\alpha}$

$$\begin{aligned} & -I + \Gamma_N \text{ Volterra Lyapunov stable a.s. for } N \text{ large for matrix } I \\ \iff & \lambda_{\max}\left(\Gamma_N + \Gamma_N^\star\right) < 2 \\ \iff & \frac{1}{\alpha} < \frac{1}{\sqrt{2}} \quad \text{a.s. for } N \text{ large} \end{aligned}$$

Phase transition phenomena in the LCP $\left(I_N - \frac{X_N}{\alpha\sqrt{N}}, -\mathbb{1}_N\right)$ depending on α



From the P-property to regularity of an interval matrix

Definition

A *matrix interval* $[\underline{B}, \overline{B}] = \{B \in \mathbb{R}^{m \times n}; \underline{B} \leq B \leq \overline{B}\}$ is regular if it contains no singular matrix, otherwise it is singular.

Theorem

[Rump, 2003, Theorem 2.1] If $A - I$ and $A + I$ are non singular then the following properties are equivalent

- *A is a P-matrix*
- $\left[(A-I)^{-1}(A+I) - I, (A-I)^{-1}(A+I) + I\right]$ *is regular*
- $\max_{x \in \{\pm 1\}^n} \rho^{\mathbb{R}}\left((A+I)^{-1}(A-I)D_x\right) < 1$

Spectral characterization of the P-matrix problem

- [Rump, 2003, Theorem 2.1] gives a spectral characterization of the P-property.

$$I_N - \Gamma_N \text{ P-matrix}$$
$$\iff \left[-2{\Gamma_N}^{-1}, -2{\Gamma_N}^{-1} + 2I_N\right] \text{ is regular}$$

- matrices in this interval have the form: $-2{\Gamma_N}^{-1} + \Delta$, Δ being a diagonal matrix with entries in $[0, 2]$

We need to explore the matrix interval to prove either

- the existence of a singular matrix in the interval

or

- the fact that all matrices in the interval are non singular

Then, it is 'easier' to show the singularity of an interval rather than its regularity.

Spectrum of random matrices

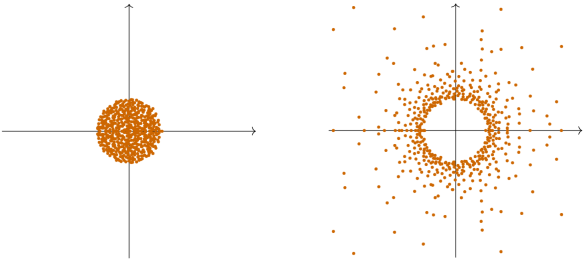


Figure: Eigenvalues in the complex plan for a normalized random matrix (500×500) on the left and its inverse on the right.

- Random matrices have their spectrum uniformly distributed in a circle [Girko, 1985, Main result],
- Eigenvalues of the inverse are the inverse of eigenvalues
  $\implies$ in the RMT context, they are spread outside the circle

To go further, we need to explore the spectrum of ${\Gamma_N}^{-1}$ under a positive diagonal deformation.

Γ_N and ${\Gamma_N}^{-1}$

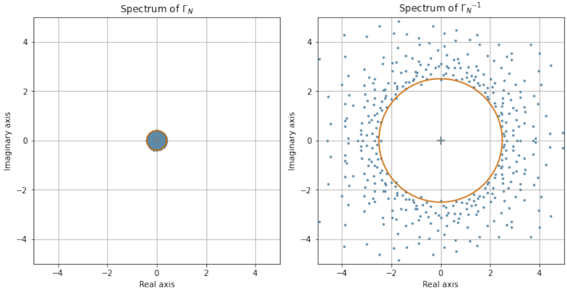


Figure: Spectrum of the 500 × 500 random matrix Γ_N and ${\Gamma_N}^{-1}$ fulfilled with Gaussian entries with $\mu = 0, \sigma = 1$ normalized by $\alpha\sqrt{N}$ where $\alpha = \frac{1}{0.4}$. The radius for Γ_N is the standard deviation that is $\frac{1}{\alpha} = 0.4$ and the one for ${\Gamma_N}^{-1}$ is its inverse.

Spectrum of $\Gamma_N^{-1} + \delta I$

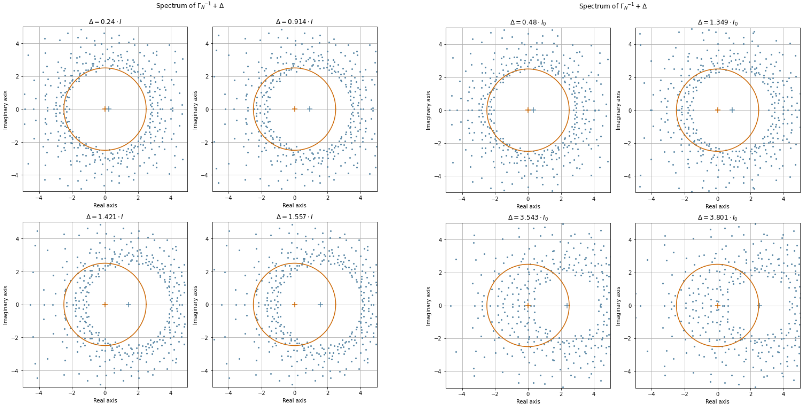


Figure: Evolution of the spectrum for a 500×500 random matrix inverse ${\Gamma_N}^{-1}$ perturbed by $\delta \cdot I$ with $\delta \in [0, 4]$ (left) and its sparse version with a third of zeros (right). $\Gamma_N = \frac{X_N}{\alpha\sqrt{N}}$ where $\alpha = \frac{1}{0.4}$. In orange, the circle of radius equals to the inverse of the standard deviation, that is to say α in this case. In blue, the eigenvalues of ${\Gamma_N}^{-1} + \delta I$.

Spectrum of $\Gamma_N^{-1} + \Delta$

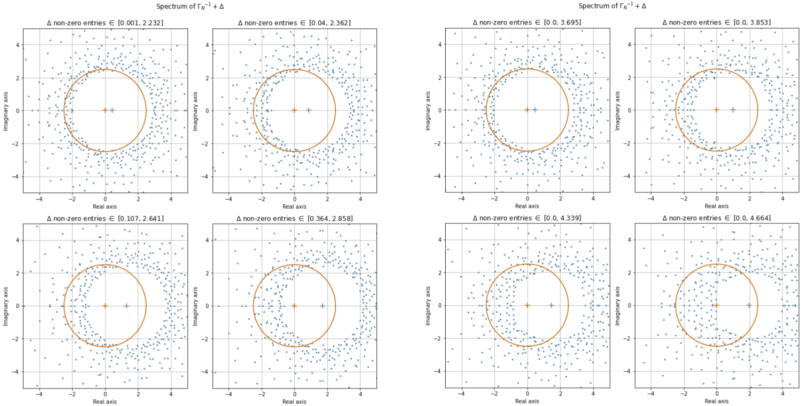


Figure: Evolution of the spectrum for a 500×500 random matrix inverse ${\Gamma_N}^{-1}$ perturbed by a diagonal Δ with distinct entries in $[0, 4]$ (left) and its sparse version with a third of zeros (right). $\Gamma_N = \frac{X_N}{\alpha\sqrt{N}}$ where $\alpha = \frac{1}{0.4}$. In orange, the circle of radius equals to the inverse of the standard deviation, that is to say α in this case. In blue, the eigenvalues of ${\Gamma_N}^{-1} + \Delta$.

- Lotka Volterra equations play a key role in mathematical modeling for ecology, biology or chemistry
- Using random matrices theory in such context allows to alleviate the difficulty to observe real interactions within large ecosystem (with high number of species)
- Working on the phase transition phenomena according to some parameters values help understanding species dynamics subject to abiotic factors
- Random Matrix Theory may help to analyze the P-property of $I_N - \Gamma_N$

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Thank You !

Appendix

Wigner matrices, [Bai and Yin, 1988]

W_N ($N \times N$) symmetric random matrix with i.i.d. entries such that:

- $\mathbb{E}\left[W_{N i<j}\right] = 0$,
- extra diagonal variance $\mathbb{V}\left(W_{N i<j}\right) = \sigma^2$,
- finite fourth moment
- $\lambda_{\max}\left(\frac{W_N}{\sqrt{N}}\right) \xrightarrow[N\to\infty]{a.s.} 2\sigma$
- $\lambda_{\min}\left(\frac{W_N}{\sqrt{N}}\right) \xrightarrow[N\to\infty]{a.s.} -2\sigma$

Distribution of normalized Wigner eigenvalues follows semi circular distribution $\frac{\sqrt{(4\sigma^2-\lambda^2)_+}}{2\pi\sigma} d\lambda$

$$\left\|\frac{W_N}{\sqrt{N}}\right\| = \sqrt{\lambda_{\max}\left(\frac{1}{N} W_N W_N^\star\right)} = \left|\lambda_{\max}\left(\frac{W_N}{\sqrt{N}}\right)\right| \vee \left|\lambda_{\min}\left(\frac{W_N}{\sqrt{N}}\right)\right| \xrightarrow[N\to\infty]{a.s.} 2\sigma$$

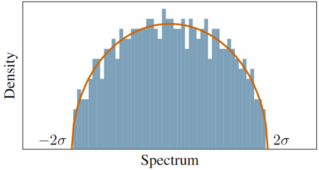

Figure: Eigenvalues histogram of a normalized Wigner matrix of size 500×500 fulfilled with gaussian entries (centered with variance equals to σ^2). In orange, the density of the semi circular law.

Jiri Rohn's algorithm

Consider the interval $[A_c \pm \Delta]$

- A_c singular $\implies [A_c \pm \Delta]$ is singular
- $|A_C x| \leq \Delta |x|$ has a non zero solution $x \iff [A_c \pm \Delta]$ is singular, [Rex and Rohn, 1998, Theorem 2.1 from Oettli and Prager]
- steepest determinant descent, [Rohn, 1989]
- $[A_c \pm \Delta]$ is singular $\iff$ the linear programming problem $(\star)$ is unbounded for some $z \in \{\pm 1\}^n$.
  $(\star) = \max\{z^T \cdot x; (A_c - \Delta D_z) \cdot x \leq 0, (A_c + \Delta D_z) \cdot x \geq 0, D_z \cdot x \geq 0\}$,
  [Jansson and Rohn, 1999, Theorem 4.3]
- $\rho(|{A_C}^{-1}|\Delta) < 1 \implies [A_C \pm \Delta]$ is regular, [Rex and Rohn, 1998, Corollary 3.2 from Beeck]
- [Rex and Rohn, 1998, Sections 4 and 5],
  - $\lambda_{\max}(\Delta^T \Delta) < \lambda_{\min}({A_c}^T A_c) \implies [A_C \pm \Delta]$ is regular
  - $\lambda_{\max}({A_c}^T A_c) \leq \lambda_{\min}(\Delta^T \Delta) \implies [A_C \pm \Delta]$ is singular
  - ${A_c}^T A_c - \|\Delta^T \Delta\| I$ positive definite $\implies [A_C \pm \Delta]$ is regular
  - $\Delta^T \Delta - {A_c}^T A_c$ positive definite $\implies [A_C \pm \Delta]$ is singular
- Loop on $\{\pm 1\}^n$ to identify the possible singular matrix which should have a specific form described in [Rohn, 1993, theorem 2.2]