

An iterative approach for studying the Lotka-Volterra equilibrium in high dimensional regime

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joint work with W. Hachem, J. Najim

Marne la Vallée - november 2023



Outline

Introduction : A problem from theoretical ecology

Lotka-Volterra system of coupled differential equations

Elliptic matrices

Approximate Message Passing

Elements of proof

Lotka-Volterra system of coupled differential equations

Motivation In order to study the behavior of species coexistence within large ecosystems we will have to describe the dynamics of these interacting species and try to answer some questions:

- ▶ How many species survive at the equilibrium ?
- ▶ What are the statistical properties of these surviving species ?

Model A popular model used in this setting is given by a system of Lotka-Volterra equations:

$$\boxed{\frac{dx_i(t)}{dt} = x_i \left(r_i - x_i + \left(\frac{1}{\alpha} B\mathbf{x} \right)_i \right)} \quad i \in [n], \quad \mathbf{x} = (x_i).$$

Here $(B\mathbf{x})_i = \sum_{\ell} B_{i\ell}x_{\ell}$.

- ▶ n is the **number of species** in a given food-web,
- ▶ $x_i = x_i(t)$ is the **abundance** (=population) of species i at time t ,
- ▶ r_i is the **intrinsic growth rate** of species i ,
- ▶ $B = (B_{ij})$ where B_{ij} is the **interaction** between species j and species i .
- ▶ α an extra parameter representing the **interaction strength**.

To simplify the study we will put $r_i = 1 \quad \forall i \in [n]$.

Equilibrium in Lotka-Volterra system

- **Model** We model the dynamics using Lotka-Volterra's system of differential equations.

$$\frac{dx_i}{dt} = x_i \left(1 - x_i + \left(\frac{B}{\alpha} \mathbf{x} \right)_i \right), \quad i = 1, \dots, n$$

- **Goal** We are interested in studying the properties of the equilibrium vector of abundances $\mathbf{x}^* \in \mathbb{R}_+^n$, i.e. the vector \mathbf{x}^* that satisfies

$$\begin{aligned} \frac{dx}{dt} \Big|_{\mathbf{x}=\mathbf{x}^*} &= 0 \\ x_i^* \left(1 - x_i^* + \left(\frac{B}{\alpha} \mathbf{x}^* \right)_i \right) &= 0 \end{aligned}$$

► Questions

1. Can we describe the statistical properties of the equilibrium ?
2. In particular, what is the proportion of surviving species at the equilibrium ?

$$\frac{\#\{i : x_i^* > 0\}}{n}$$

Main assumption: a random model for the interaction matrix B

- ▶ The study of large Lotka-Volterra systems makes it **very difficult to calibrate** the model and **estimate** matrix B .
- ▶ An alternative is to consider **random matrices** [May72], the statistical properties of which encode some real properties of the food-web.

Some random models

- ▶ **The Wigner model, (real) Ginibre model:** poor adequation to reality but a good benchmark to explore the mathematical tractability.
- ▶ **The elliptic model:** encodes the natural correlation between $B_{k\ell}$ and $B_{\ell k}$.
- ▶ **Sparse models:** encodes the fact that a species only interacts with $d \ll n$ other species.
- ▶ **Variance profiles, non-centered matrices,** etc: of interest but harder to analyze.

Elliptic matrices

- ▶ A matrix B is $n \times n$ random, ρ -Elliptic if

$$\begin{pmatrix} B_{ij} \\ B_{ji} \end{pmatrix} \sim \mathcal{N}_2 \left(\mathbf{0}, \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix} \right) \quad \text{for } i < j.$$

And, all the elements of $\{B_{ii}, i \in [n]\} \cup \{(B_{ij}, B_{ji}), i < j\}$ are independent.

Elliptic matrices I

We plot the eigenvalues $Sp_{\mathbb{C}}(B)$ for elliptic matrices B with $\rho = 0.6 > 0$ and $\rho = -0.3 < 0$.

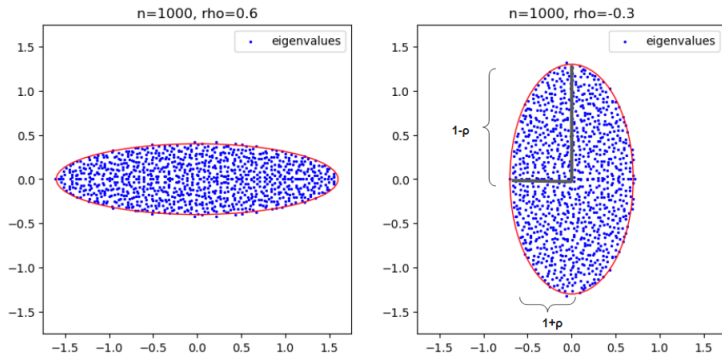


Figure: These type of matrices are called elliptic because the spectrum's boundary has an elliptic shape. [Nau12]

Elliptic matrices II

We plot the eigenvalues $Sp_{\mathbb{C}}(B)$ for elliptic matrices B with $\rho = 1$ and $\rho = 0$.

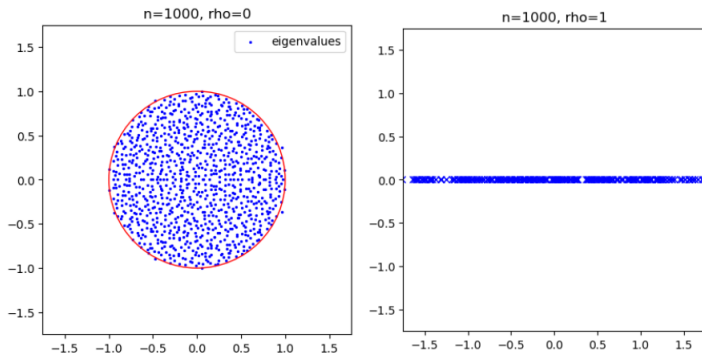


Figure: In the left: $\rho = 0$, i.e. **i.i.d.** entries. In the right: $\rho = 1$, i.e. **symmetric** matrix $B_{ij} = B_{ji}$.

Elliptic matrices III

We plot the histogram of the eigenvalues $Sp_{\mathbb{C}}(B) \subset \mathbb{R}$ of a symmetric matrix B (i.e. $\rho = 1$).

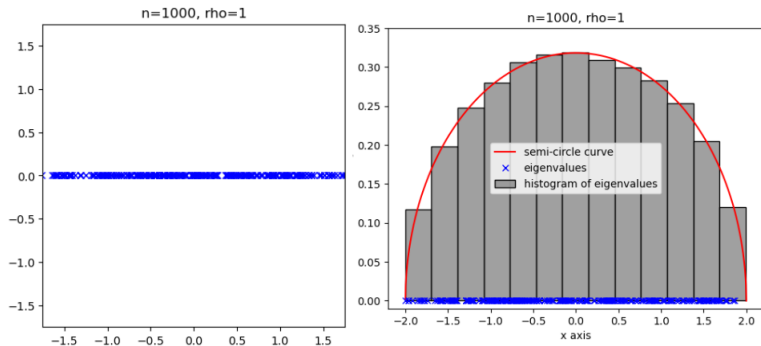


Figure: In the left: the eigenvalues of a symmetric matrix . In the right: distribution of these eigenvalues.

If B is a “Wigner” matrix then

$$\lambda_{\max} \left(\frac{1}{\sqrt{n}} B \right) \xrightarrow{n \rightarrow \infty} 2.$$

Considered random matrix model

In our case we will consider a normalized ρ -elliptic model.

$$B = \frac{A}{\sqrt{n}}$$

where $A_{ij} \sim \mathcal{N}(0, 1)$ and (A_{ij}, A_{ji}) are correlated with coefficient $\rho \in [-1, 1]$.

The Lotka-Volterra system writes

$$\frac{dx_i(t)}{dt} = x_i \left(1 - x_i + \left(\frac{A}{\alpha\sqrt{n}} \mathbf{x} \right)_i \right) \quad i \in [n], \quad \mathbf{x} = (x_i).$$

And the equilibrium writes

$$\boxed{x_i^* \left(1 - x_i^* + \left(\frac{A}{\alpha\sqrt{n}} \mathbf{x}^* \right)_i \right) = 0} \quad i \in [n], \quad \mathbf{x}^* = (x_i^*).$$

System of equations for the equilibrium

If \mathbf{x}^* is an equilibrium of the system

$$\frac{dx_i(t)}{dt} = x_i \left(1 - x_i + \left(\frac{A}{\alpha\sqrt{n}} \mathbf{x} \right)_i \right), \quad i \in [n],$$

Then

- ▶ $\mathbf{x}^* \geq 0$
- ▶ $x_i^* \left(1 - x_i^* + \left(\frac{A}{\alpha\sqrt{n}} \mathbf{x}^* \right)_i \right) = 0$

Stable equilibrium

$$\begin{cases} \mathbf{x}^* & \geq 0, \\ \left(I - \frac{A}{\alpha\sqrt{n}} \right) \mathbf{x}^* - \mathbf{1} & \geq 0, \\ x_i^* \left(\left[\left(I - \frac{A}{\alpha\sqrt{n}} \right) \mathbf{x}^* \right]_i - 1 \right) & = 0. \end{cases}$$

- ▶ **Stability condition** [Tak96]: Lyapunov stability condition or non-invasibility condition.
- ▶ **Sufficient condition for the existence, uniqueness and stability of the equilibrium** : $\boxed{\alpha > \sqrt{2(1 + \rho)}}$ [CEFN22].

Statistical properties on the equilibrium

Let A be a ρ -elliptic matrix and consider the LV system.

$$\frac{dx_i(t)}{dt} = x_i \left(1 - x_i + \frac{1}{\alpha} (B\mathbf{x})_i \right) \quad \text{where} \quad B = \frac{A}{\sqrt{n}}.$$

and assume that $\alpha > \sqrt{2(1+\rho)}$.

Theorem (G., Hachem, Najim, 2023)

- There exists a (random) **unique stable equilibrium** \mathbf{x}_n^* : $\boxed{\mathbf{x}_n(t) \xrightarrow[t \rightarrow \infty]{} \mathbf{x}_n^*}$ and

$$\text{(a.s.)} \quad \mu^{\mathbf{x}^*} \triangleq \frac{1}{n} \sum_{i \in [n]} \delta_{\mathbf{x}_i^*} \xrightarrow[n \rightarrow \infty]{weak, L^2} \mathcal{L} \left((1 + \rho\gamma/\delta^2) (\sigma\bar{Z} + 1)_+ \right)$$

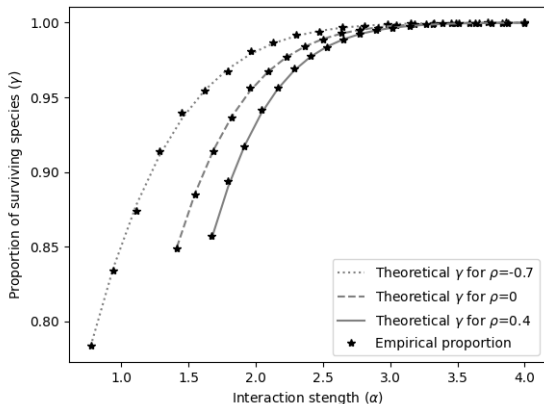
- where $(\delta, \sigma, \gamma) \in (0, \infty)^3$ is the unique triple solution of **the fixed point equations**

$$\begin{aligned} \alpha &= \delta + \rho \frac{\gamma}{\delta}, \\ \sigma^2 &= \frac{1}{\delta^2} \mathbb{E} (\sigma\bar{Z} + 1)_+^2, \quad \bar{Z} \sim \mathcal{N}(0, 1), \\ \gamma &= \mathbb{P} [\sigma\bar{Z} + 1 > 0]. \end{aligned}$$

- Similar results were obtained by [\[Bun17\]](#) and [\[Gal18\]](#) using statistical physics methods such as “Replica trick”.

Proportion of surviving species

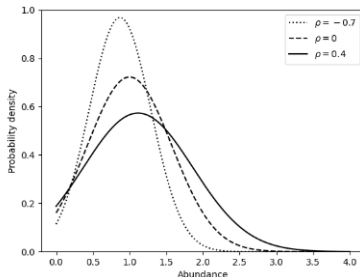
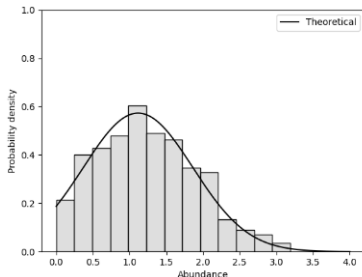
- **Theoretical values:** We solve the **fixed point equations** for (δ, σ, γ) for different values of α . We plot $\gamma = \gamma(\alpha)$.
- **Experimental values:** (Monte-Carlo) we solve the **Equilibrium system** associated to the Lotka-Volterra equations for 500 samples of random matrices A . (using Lemke solver in python).



Distribution of surviving species

We fix $\alpha = 2$.

- **Theoretical values:** We plot the theoretical **truncated gaussian density function** for the adequate values of (δ, σ, γ) .
- **Experimental values:** We plot the following empirical conditional distribution $\mathcal{L}(x_i^* \mid x_i^* > 0)$.



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Fixed point equation

Elliptic Approximate Message Passing

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A fixed point equation

- ▶ We want to study the solution \mathbf{x}^* of the following system

$$\begin{cases} \mathbf{x}^* & \geq 0, \\ \left(I - \frac{A}{\alpha\sqrt{n}}\right) \mathbf{x}^* - \mathbf{1} & \geq 0, \\ x_i^* \left(\left[\left(I - \frac{A}{\alpha\sqrt{n}}\right) \mathbf{x}^*\right]_i - 1 \right) & = 0. \end{cases} \quad (1)$$

- ▶ To use an iterative scheme we need a fixed point equation. Consider the following equation of $\mathbf{z} \in \mathbb{R}^n$.

$$\boxed{\mathbf{z} = \frac{A}{\alpha\sqrt{n}} \mathbf{z}^+ + \mathbf{1}} \quad (2)$$

- ▶ If \mathbf{z} is a solution to (2) then \mathbf{z}^+ is a solution to (1).

- ▶ Write $\mathbf{z} = \mathbf{z}^+ - \mathbf{z}^-$, then

$$\mathbf{z}^- = \left(I - \frac{A}{\alpha\sqrt{n}}\right) \mathbf{z}^+ - \mathbf{1}$$

- ▶ **Question:** We want an iterative algorithm $(\mathbf{u}^k)_k$ to solve (2) while tracking

$$\boxed{\mu^{\mathbf{u}^k} \triangleq \frac{1}{n} \sum_{i=1}^n \delta_{u_i}}$$

- ▶ An obvious algorithm $\mathbf{z}^{k+1} = \frac{A}{\alpha\sqrt{n}} (\mathbf{z}^k)^+ + \mathbf{1}$ does not have this property.

Elliptic Approximate Message Passing

► **Notation** Given $f : \mathbb{R}^2 \rightarrow \mathbb{R}$ denote by $\langle f'(\mathbf{u}, \mathbf{v}) \rangle = \frac{1}{n} \sum_{i=1}^n \frac{\partial f}{\partial u}(u_i, v_i)$.

Assumptions

► \mathbf{u}^0 independent from A and \mathbf{a} a constant parameter vector.

► $\mu^{\mathbf{u}^0} \xrightarrow[n \rightarrow \infty]{} \mathcal{L}(\bar{\mathbf{u}})$

Theorem (G., Hachem, Najim, 2023)

The AMP recursion for a ρ -elliptic matrix A is defined as

$$\mathbf{u}^{k+1} = \frac{A}{\sqrt{n}} f_k(\mathbf{u}^k, \mathbf{a}) - \rho \langle f'_k(\mathbf{u}^k, \mathbf{a}) \rangle f_{k-1}(\mathbf{u}^{k-1}, \mathbf{a})$$

Then (a.s)

$$\mu^{\mathbf{u}^1, \dots, \mathbf{u}^k} = \frac{1}{n} \sum_{i=1}^n \delta_{(u_i^1, \dots, u_i^k)} \xrightarrow[n \rightarrow \infty]{weak, L^2} (Z_1, \dots, Z_k) \sim \mathcal{N}_k(\mathbf{0}, \Gamma^k)$$

where Γ^k is defined recursively (**State Evolution Equations**).

Remark

Note that this result is well known in the case of symmetric matrices ($\rho = 1$) and it is due to [BM11].

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The AMP recursion for a ρ -elliptic matrix A is defined as

$$\mathbf{u}^{k+1} = \frac{\textcolor{red}{A}}{\sqrt{n}} f_k(\mathbf{u}^k, \mathbf{a}) - \textcolor{red}{\rho} \langle f'_k(\mathbf{u}^k, \mathbf{a}) \rangle f_{k-1}(\mathbf{u}^{k-1}, \mathbf{a})$$

Then (a.s)

$$\mu^{\mathbf{u}^k} = \frac{1}{n} \sum_{i=1}^n \delta_{u_i^k} \xrightarrow[n \rightarrow \infty]{weak, L^2} Z_k \sim \mathcal{N}(\mathbf{0}, \textcolor{red}{\sigma}_k^2)$$

where $\textcolor{red}{\sigma}_{k+1}^2 = \mathbb{E} \left[(f_k(Z_k))^2 \right]$ and $Z_k \sim \mathcal{N}(0, \textcolor{red}{\sigma}_k^2)$.

Remark

Note that this result is well known in the case of symmetric matrices ($\textcolor{red}{\rho} = 1$) and it is due to [\[BM11\]](#).

Design of an AMP algorithm to solve the FP equation

- ▶ We want to solve the fixed point equation $z = \frac{A}{\alpha\sqrt{n}}z_+ + \mathbf{1}$ using AMP.
- ▶ We need to calibrate the functions f_k and the parameter \mathbf{a} ([AHMN23]) in the following recursion equation

$$\mathbf{u}^{k+1} = \frac{A}{\sqrt{n}}f_k(\mathbf{u}^k + \mathbf{a}) - \rho\langle f'_k(\mathbf{u}^k, \mathbf{a}) \rangle f_{k-1}(\mathbf{u}^{k-1}, \mathbf{a})$$

- ▶ Given α we determine δ and γ and we set $f_k(x, \mathbf{a}) = \frac{(x+\mathbf{a})_+}{\delta}$. \mathbf{a} will be calibrated later. Then

$$\mathbf{u}^{k+1} = \frac{A}{\delta\sqrt{n}}(\mathbf{u}^k + \mathbf{a})_+ - \rho \frac{\langle \mathbf{1}_{\mathbf{u}^k + \mathbf{a} > 0} \rangle}{\delta^2}(\mathbf{u}^{k-1} + \mathbf{a})_+$$

- ▶ **Fact 1** $\langle \mathbf{1}_{\mathbf{u}^k + \mathbf{a} > 0} \rangle \approx \gamma$ for k large.

- ▶ Set $\xi^k = \mathbf{u}^k + \mathbf{a}$, then we get

$$\xi^{k+1} = \frac{A}{\delta\sqrt{n}}\xi_+^k - \rho \frac{\gamma}{\delta^2}\xi_+^{k-1} + \mathbf{a} + \epsilon$$

- ▶ **Fact 2** $\xi^{k+1} \approx \xi^k \approx \xi^{k-1}$ when k is large. Set $\mathbf{a} = 1 + \rho \frac{\gamma}{\delta^2} = \frac{\alpha}{\delta}$. Then after massaging the previous equation.

$$\xi_+ - \frac{\xi_-}{1 + \rho \frac{\gamma}{\delta^2}} = \frac{A}{\alpha\sqrt{n}}\xi_+ + \mathbf{1} + \epsilon \Rightarrow \boxed{z \triangleq \xi_+ - \frac{\xi_-}{1 + \rho \frac{\gamma}{\delta^2}}} \text{ satisfies the FPE.}$$

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Idea of the proof I

- Let $\mathbf{u}^{k+1} = \frac{A}{\sqrt{n}} f_k(\mathbf{u}^k, \mathbf{a}) - \rho \langle f'_k(\mathbf{u}^k, \mathbf{a}) \rangle f_{k-1}(\mathbf{u}^{k-1}, \mathbf{a})$, we want to prove that

$$(a.s) \quad \mu^{\mathbf{u}^1, \dots, \mathbf{u}^k} = \frac{1}{n} \sum_{i=1}^n \delta_{(\mathbf{u}_i^1, \dots, \mathbf{u}_i^k)} \xrightarrow[n \rightarrow \infty]{weak, L^2} (Z_1, \dots, Z_k) \sim \mathcal{N}_k(\mathbf{0}, \Gamma^k)$$

- We prove this theorem by **induction on k** , i.e. we suppose that we know the behavior of the probability measure $\mu^{\mathbf{u}^1, \dots, \mathbf{u}^k}$ and we want to study $\mu^{\mathbf{u}^1, \dots, \mathbf{u}^k, \mathbf{u}^{k+1}}$.

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- Notice that all the iterates \mathbf{u}^k depend on A and thus are correlated.

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- Notice that all the iterates \mathbf{u}^k depend on A and thus are correlated.
Idea Express \mathbf{u}^{k+1} as follows

$$\mathbf{u}^{k+1} = \mathcal{F}(\mathbf{u}^1, \dots, \mathbf{u}^k) + \text{independent term.}$$

Idea of the proof II

Our main contribution can be summarized in the two following propositions.

Proposition

We can prove the following structural expression:

$$\mathbf{u}^{k+1} = \sum_{i=1}^k \alpha_i \mathbf{u}^i + \left(A - \rho P_k A^\top \right) P_k^\perp \mathbf{q}^k + o_{n \rightarrow \infty}(1),$$

where $\mathbf{q}^k = f_k(\mathbf{u}^k, \mathbf{a})$ and P_k is the $n \times n$ projection matrix on the space $\text{Vect}(\mathbf{q}^1, \dots, \mathbf{q}^k)$. And $P_k^\perp = I - P_k$.

Proposition

We have to following equality in law

$$\left(A - \rho P_k A^\top \right) P_k^\perp \stackrel{\mathcal{L}}{=} \Big|_{\mathbf{u}^1, \dots, \mathbf{u}^k} \left(\tilde{A} - \rho P_k \tilde{A}^\top \right) P_k^\perp,$$

Where $\tilde{A} \stackrel{\mathcal{L}}{=} A$ and \tilde{A} is independent of the past $\{\mathbf{u}^1, \dots, \mathbf{u}^k\}$.

- Core element of Bolthausen's conditioning technique [Bol14], it was historically proved (for ex. in [FVRS21]) in the case of a symmetric matrix ($\rho = 1$).

Consequence

Finally, we write

$$\mathbf{u}^{k+1} \stackrel{\mathcal{L}}{=} \Big|_{\mathbf{u}^1, \dots, \mathbf{u}^k} \sum_{i=1}^k \alpha_i \mathbf{u}^i + \left(\tilde{A} - \rho P_k \tilde{A}^\top \right) P_k^\perp \mathbf{q}^k + o_{n \rightarrow \infty}(1).$$

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Existence of a stable equilibrium

Theorem (Takeuchi and Adachi (1980))

*If there exists a positive diagonal matrix Δ such that $\Delta M + M^\top \Delta$ is positive definite, then there exists a **unique** and **stable** equilibrium of the Lotka-Volterra system.*

Lemma

Let A an elliptic matrix with coefficient ρ and $\alpha > \sqrt{2(1+\rho)}$, then

$\left(I - \frac{A}{\alpha\sqrt{n}}\right) + \left(I - \frac{A}{\alpha\sqrt{n}}\right)^\top$ is a.s. positive definite.

Proof.

Let $\Delta = I$,

$$\left(I - \frac{A}{\alpha\sqrt{n}}\right) + \left(I - \frac{A}{\alpha\sqrt{n}}\right)^\top = 2I - \frac{A + A^\top}{\alpha\sqrt{n}}$$



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A is ρ -elliptic $\Rightarrow A_{ij} + A_{ji} \sim \mathcal{N}(0, 2(1+\rho))$



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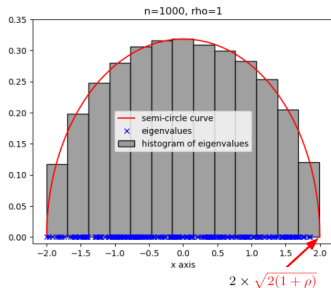
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$$2I - \frac{A + A^\top}{\alpha\sqrt{n}}$$
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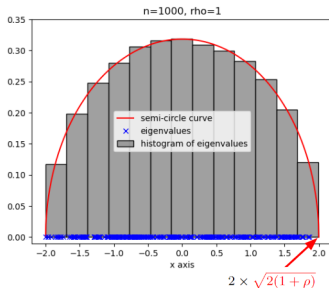
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$\left(I - \frac{A}{\alpha\sqrt{n}}\right) + \left(I - \frac{A}{\alpha\sqrt{n}}\right)^\top$ is a.s. positive definite.

Proof.

Let $\Delta = I$,

$$\begin{aligned} 2I - \frac{A + A^\top}{\alpha\sqrt{n}} \\ \lambda_{\max} \left(\frac{A + A^\top}{\sqrt{n}} \right) &\xrightarrow{n \rightarrow \infty} 2 \times \sqrt{2(1+\rho)} \\ \lambda_{\min} \left(2I - \frac{A + A^\top}{\alpha\sqrt{n}} \right) &= 2 - \frac{1}{\alpha} \lambda_{\max} \left(\frac{A + A^\top}{\sqrt{n}} \right) \\ &\approx 2 - \frac{2\sqrt{2(1+\rho)}}{\alpha} \end{aligned}$$



□

Existence of a stable equilibrium

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Lemma

Let A an elliptic matrix with coefficient ρ and $\alpha > \sqrt{2(1+\rho)}$, then

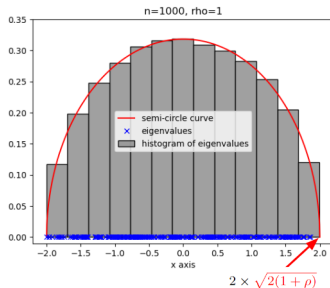
$\left(I - \frac{A}{\alpha\sqrt{n}}\right) + \left(I - \frac{A}{\alpha\sqrt{n}}\right)^\top$ is a.s. positive definite.

Proof.

Let $\Delta = I$,

$$\lambda_{\min} \left(2I - \frac{A + A^\top}{\alpha\sqrt{n}} \right) \approx 2 - \frac{2\sqrt{2(1+\rho)}}{\alpha} > 0$$

$\alpha > \sqrt{2(1+\rho)}$



Proportion of surviving species

Given $\alpha > \sqrt{2(1+\rho)}$, we have $\mu^{x_n^*} \xrightarrow{n \rightarrow \infty} \pi := \mathcal{L} \left((1 + \rho\gamma/\delta^2) (\sigma\bar{Z} + \bar{r})_+ \right)$ i.e.

$$\forall \varphi \in \mathcal{C}_b \quad \frac{1}{n} \sum_{i=1}^n \varphi(x_i^*) \xrightarrow{n \rightarrow \infty} \mathbb{E} \left[\varphi \left((1 + \rho\gamma/\delta^2) (\sigma\bar{Z} + \bar{r})_+ \right) \right]$$

In particular, the proportion of surviving species can be accessed via $\varphi(x) = \mathbf{1}_{x>0}$.

$$\frac{\#\{i : x_i^* > 0\}}{n} \xrightarrow{n \rightarrow \infty} \mathbb{P} [\sigma\bar{Z} + r > 0] = \gamma.$$

Elliptic Approximate Message Passing

Theorem (G., Hachem, Najim, 2023)

The AMP recursion for a ρ -**elliptic matrix** A is defined as

$$\mathbf{u}^{k+1} = \frac{A}{\sqrt{n}} f_k(\mathbf{u}^k, \mathbf{a}) - \rho \langle f'_k(\mathbf{u}^k, \mathbf{a}) \rangle f_{k-1}(\mathbf{u}^{k-1}, \mathbf{a})$$

Then

$$(a.s) \quad \mu^{\mathbf{u}^1, \dots, \mathbf{u}^k} = \frac{1}{n} \sum_{i=1}^n \delta_{(u_i^1, \dots, u_i^k)} \xrightarrow[N \rightarrow \infty]{weak, L^2} (Z_1, \dots, Z_k) \sim \mathcal{N}_k(\mathbf{0}, \Gamma^k)$$

where Γ^k is defined recursively (**State Evolution Equations**).

State Evolution Equations

The $k \times k$ covariance matrices Γ^k are recursively defined as follows

$$\Gamma_{ij}^k = \mathbb{E}[f_{i-1}(Z_{i-1}) f_{j-1}(Z_{j-1})] \text{ where } (Z_1, \dots, Z_k) \sim \mathcal{N}_{k-1}(\mathbf{0}, \Gamma^{k-1}).$$

In particular

$$\mathbb{E}[Z_{k+1}^2] = \mathbb{E}[(f_k(Z_k))^2]$$