# Properties of large Lotka Volterra systems with random interactions 

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joint work with
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Lotka-Volterra systems of coupled differential equations

Equilibrium and stability

Feasibility

Extensions

## Lotka-Volterra systems of coupled differential equations

A popular model to describe the dynamics of interacting species in foodwebs is given by a system of Lotka-Volterra equations:

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\frac{d x_{k}(t)}{d t}=x_{k}\left(r_{k}-x_{k}+(B \boldsymbol{x})_{k}\right), \quad k \in[n], \quad \boldsymbol{x}=\left(x_{k}\right) .
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1. if $\left.\boldsymbol{x}\right|_{t=0}>0$ then for all $t>0, \boldsymbol{x}(t)>0$.
2. if $B=0$ (no interactions), we recover the logistic equation

$$
\frac{d x_{k}(t)}{d t}=x_{k}\left(r_{k}-x_{k}\right)
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## Questions

- Existence of an equilibrium $\boldsymbol{x}^{*}=\left(x_{k}^{*}\right)$ such that

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- Feasibility of this equilibrium: $x_{k}^{*}>0$ for all $k \in[n]$
- Species extinction $x_{k}^{*}=0 \quad$ for some $k \in[n]$ ? In the latter case, we have

$$
\begin{cases}\text { surviving species if } & x_{k}^{*}>0 \\ \text { vanishing species if } & x_{k}^{*}=0\end{cases}
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## Assumption 1: A random model for the interaction matrix $B$

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No maths $=$ no understanding $\quad P$. Rossberg, in Food webs and biodiversity (Wiley)

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- The elliptic model: encodes the natural correlation between $B_{k \ell}$ and $B_{\ell k}$ but limited because of a unique single trend

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- Sparse models: encodes the fact that a species only interacts with $d \ll n$ other species.


## Assumption 2: $n \rightarrow \infty$

This assuption is relevant

- to model large foodwebs with many species
- to take advantage of self-averaging properties of large random matrices
- and leverage on random matrix theory

We need to normalize accordingly the interaction matrix so that (for instance)

$$
\|B\|=\left\|B_{n}\right\|=\mathcal{O}(1)
$$

as $n \rightarrow \infty$.

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## Equilibrium and global stability

Theorem (Takeuchi \& Adachi 1980)
Consider the LV system

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If there exists a diagonal positive matrix $W$ such that

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W(-I+B)+\left(-I+B^{T}\right) W<0 \quad \text { (negative definite) }
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then if $\left.\boldsymbol{x}\right|_{t=0}>0$, system (1) has a unique non negative stable equilibrium:

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## Remark on uniqueness

- if $\left.\boldsymbol{x}\right|_{t=0}>0$ then $\boldsymbol{x}^{*}$ is the unique solution of the Linear Complementarity Problem (LCP):

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- if $\left.x_{1}\right|_{t=0}=0$, just consider the subsystem where $x_{1}$ 's interactions are erased in matrix $B$.


## Equilibrium and global stability: i.i.d. model

Corollary I (RMT - i.i.d. case)
Assume that $B_{k \ell}=\frac{A_{k \ell}}{\alpha \sqrt{n}}$ where $\left\{\begin{array}{l}A_{k \ell} \text { i.i.d. }, \\ \mathbb{E} A_{k \ell}=0, \\ \mathbb{E} A_{k \ell}^{2}=1\end{array}+\mathbb{E}\left|A_{k \ell}\right|^{4}<\infty\right.$.

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Well-known that $\lambda_{\max }\left(\frac{A+A^{T}}{\sqrt{2} \sqrt{n}}\right) \xrightarrow[n \rightarrow \infty]{\text { a.s. }} 2$ - we conclude easily.

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- The choice $W=I$ might not be optimal.


## Equilibrium and global stability: elliptic model I

Let $A=\left(A_{i j}\right)$ a $n \times n$ matrix. Assume that

- The $\left(A_{i i}\right)$ are i.i.d $\mathcal{N}(0,1)$, the $\left(A_{i j}, A_{j i}\right)$ are i.i.d. $\mathcal{N}_{2}\left(0,\binom{1, \rho}{\rho, 1}\right)$
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Figure: Centered elliptical model $(\mu=0)$ for various correlations $\rho$. Notice that $\rho=0$ represents the model with i.i.d. entries.

Equilibrium and global stability: elliptic model II
Consider the model

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## Equilibrium and global stability: elliptic model II

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Figure: Elliptic model with $\mu=2$. The outlier is very close to $\mu$.

Equilibrium and global stability: elliptic model III
Corollary II (RMT - elliptic case)
Consider the following set of admissible parameters:

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\begin{aligned}
\mathcal{A}=\{(\rho, \alpha, \mu) \in(-1,1) \times(0, \infty) \times \mathbb{R} & , \\
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Figure: Representation of the set of admissible parameters $\mathcal{A}$ by a heat map. The $x$-axis corresponds to $\rho$, the $y$-axis to $\sigma$ and the intensity of the color $\mu$.

## Open question

## Statistical properties of the equilibrium

Consider the i.i.d. model and $\alpha>\sqrt{2}$. The equilibrium $\boldsymbol{x}^{*}$ is the solution of the LCP problem

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- For fixed $\alpha$, is it possible to asymptotically estimate the number of vanishing/surviving species?
-     + other statistical properties of equilibrium $\boldsymbol{x}^{*}$ ?
- Yes, using statistical physics techniques, but no mathematical proof so far.


## Reference

- Ecological communities with Lotka-Volterra dynamics, G. Bunin, Phys. Rev. E (2017)

Lotka-Volterra systems of coupled differential equations

## Equilibrium and stability

Feasibility
A puzzling result by Mazza et al.
A logarithmic correction implies feasibility Elements of proof

[^1]Feasible equilibrium: a simple linear equation

- Recall the LV system

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- Such an equilibrium should satisfy

$$
r_{k}-x_{k}^{*}+\left(B \boldsymbol{x}^{*}\right)_{k}=0 \quad \Leftrightarrow \quad \boldsymbol{x}^{*}=\boldsymbol{r}+B \boldsymbol{x}^{*}, \quad \boldsymbol{x}^{*}>0
$$

## Feasible equilibrium: a simple linear equation

- Recall the LV system

$$
\dot{x}_{k}=x_{k}\left(r_{k}-x_{k}+(B \boldsymbol{x})_{k}\right) .
$$

- We investigate the case where there exists a positive equilibrium

$$
\boldsymbol{x}^{*}>0 \quad \Leftrightarrow \quad x_{k}^{*}>0 \quad \forall k \in[n] .
$$

- In theoretical ecology it is called a feasible equilibrium and is of interest because all species survive.
- Such an equilibrium should satisfy

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r_{k}-x_{k}^{*}+\left(B \boldsymbol{x}^{*}\right)_{k}=0 \quad \Leftrightarrow \quad \boldsymbol{x}^{*}=\boldsymbol{r}+B \boldsymbol{x}^{*}, \quad \boldsymbol{x}^{*}>0
$$

- If matrix $I-B$ is invertible, then

$$
\boldsymbol{x}^{*}=(I-B)^{-1} \boldsymbol{r} .
$$

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B=\frac{A}{\alpha \sqrt{n}}, \quad \alpha>4
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## References

- "The feasibility of equilibria in large ecosystems: A primary but neglected concept in the complexity-stability debate",
Dougoud, Vikenbosch, Rohr, Bersier, Mazza, PLoS Comput. Biology, 2018
- "A chaos hypothesis for some large systems of random equations". Geman and Hwang, 1982.


## Elements of proof

Theorem (Geman, Hwang)

- Let $M$ fixed, $\boldsymbol{\alpha}>4$ and $\boldsymbol{x}^{*}=\mathbf{1}+\frac{A}{\alpha \sqrt{n}} \boldsymbol{x}^{*}$


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## Corollary

- If $\boldsymbol{\alpha}>4$ fixed, the probability to obtain a positive solution goes to zero:

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\mathbb{P}\left\{\inf _{k \in[n]} x_{k}^{*}>0\right\} \leq \mathbb{P}\left\{\inf _{k \in[M]} x_{k}^{*}>0\right\} \sim \prod_{k \in[M]} \mathbb{P}\left\{x_{k}^{*}>0\right\} \xrightarrow[M \rightarrow \infty]{ } 0
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## Conclusion

- Feasible solutions for $\boldsymbol{x}^{*}=\mathbf{1}+\frac{A}{\boldsymbol{\alpha} \sqrt{N}} \boldsymbol{x}^{*}$ are eventually extremely rare.


## Lotka-Volterra systems of coupled differential equations

## Equilibrium and stability

Feasibility
A puzzling result by Mazza et al
A logarithmic correction implies feasibility
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## Extensions

## Feasibility of the solution

## Consider the system

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## References

- Positive solutions for large random linear systems, Bizeul-N., Proc AMS, 2021


## Phase transition (gaussian case)

Homogeneous case, Gaussian entries


- We plot the frequency of positive solutions over 10000 trials for the system

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- A phase transition occurs at the critical value $\kappa=\sqrt{2}$.


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## Important facts

Gaussian extreme values

- Let $\left(Z_{k}\right)_{k \in[n]}$ i.i.d. $\mathcal{N}(0,1)$ random variables, Denote by

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\check{M}_{n}=\min _{k \in[n]} Z_{k}
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Existence of the resolvent

- Recall that

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\rho\left(\frac{A}{\sqrt{n}}\right) \xrightarrow[n \rightarrow \infty]{\text { a.s. }} 1 \quad \text { and } \quad\left\|\frac{A}{\sqrt{n}}\right\| \xrightarrow[n \rightarrow \infty]{\text { a.s. }} 2 .
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As a consequence, if $\boldsymbol{\alpha}>1$ then $\left(I-\frac{A}{\alpha \sqrt{n}}\right)$ is eventually invertible and

$$
\boldsymbol{x}^{*}=\left(I-\frac{A}{\boldsymbol{\alpha} \sqrt{n}}\right)^{-1} \mathbf{1}
$$

is well-defined.

## A heuristics for the critical scaling

1. Unfold the resolvent.

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Crux of proof: to handle the remaining term $R_{k}$

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Recall that the feasible solution $\boldsymbol{x}^{*}=\left(x_{k}^{*}\right)$ writes

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$\Rightarrow$ The main effort is to prove that $A \mapsto \widetilde{R}_{k}(A)$ is $K$-Lipschitz.

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- Let $\varphi: \mathbb{R}^{+} \rightarrow[0,1]$ a smooth cut-off function



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- Notice that

$$
\begin{aligned}
& \mathbb{P}\left(\max _{k \in[n]} R_{k} \neq \max _{k \in[N]} \tilde{R}_{k}\right) \\
& \quad \leq \mathbb{P}\left(\exists k_{0}, R_{k_{0}} \neq \tilde{R}_{k_{0}}\right)=\mathbb{P}(\|A / \sqrt{n}\| \geq 2+\eta) \xrightarrow[n \rightarrow \infty]{ } 0
\end{aligned}
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## A truncated version of the remainder term

- Let $\varphi: \mathbb{R}^{+} \rightarrow[0,1]$ a smooth cut-off function

- Recall that $\left\|\frac{A}{\sqrt{n}}\right\| \frac{\text { a.s. }}{n \rightarrow \infty} 2, \quad$ consider $\tilde{R}_{k}=\varphi\left(\left\|\frac{A}{\sqrt{n}}\right\|\right) R_{k}$
- Notice that

$$
\begin{aligned}
& \mathbb{P}\left(\max _{k \in[n]} R_{k} \neq \max _{k \in[N]} \tilde{R}_{k}\right) \\
& \quad \leq \mathbb{P}\left(\exists k_{0}, R_{k_{0}} \neq \tilde{R}_{k_{0}}\right)=\mathbb{P}(\|A / \sqrt{n}\| \geq 2+\eta) \xrightarrow[n \rightarrow \infty]{ } 0
\end{aligned}
$$

- No asymptotic loss when replacing $R_{k}$ by $\widetilde{R}_{k}$.


## Proof of sub-gaussianity of $\tilde{R}_{k}$ : concentration

- We first prove that $A \mapsto \tilde{R}_{k}(A)$ is $K$-lipschitz:

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- We then proceed by density to complete the proof of the Lipschitz property.

Lotka-Volterra systems of coupled differential equations

## Equilibrium and stability

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Extensions
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## Sparse interactions

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## References

- Explorability and the origin of network sparsity in living systems, by Busiello et al. Scientific reports, 2017.
- Feasibility of sparse large Lotka-Volterra ecosystems, by Akjouj and N., 2021.

More on the block matrix structure assumption
The block matrix structure

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Example where $m=4$
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Open question

- Possible to relax this block structure assumption? Simulations suggest yes.

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## Feasibility for the elliptical model

## Theorem (Clenet, El Ferchichi, N.)

Consider the model

$$
B(\boldsymbol{\alpha})=\frac{A}{\boldsymbol{\alpha} \sqrt{n}}+\frac{\mu}{n} \mathbf{1 1}^{T}
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and assume that $\mu<1$. Then the same phase transition as before occurs.

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Let $\boldsymbol{r}$ is $N \times 1$ deterministic. We are interested in the equation

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\boldsymbol{x}=\boldsymbol{r}+\frac{A}{\boldsymbol{\alpha} \sqrt{N}} \boldsymbol{x} \quad \text { where } \quad\left\{\begin{array}{l}
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## Non-homogeneous case II



- In the non-homogeneous case, there is a transition buffer

$$
\frac{\boldsymbol{\alpha}_{N}}{\boldsymbol{\alpha}_{N}^{*}} \in\left[\frac{\sigma_{\boldsymbol{r}}(n)}{\boldsymbol{r}_{\max }(n)}, \frac{\sigma_{\boldsymbol{r}}(n)}{\boldsymbol{r}_{\min }(n)}\right]
$$

and not a sharp transition at $\frac{\boldsymbol{\alpha}_{N}}{\boldsymbol{\alpha}_{N}^{*}} \sim 1$.

Thank you for your attention!


[^0]:    No maths $=$ no understanding $\quad P$. Rossberg, in Food webs and biodiversity (Wiley)

[^1]:    Extensions

