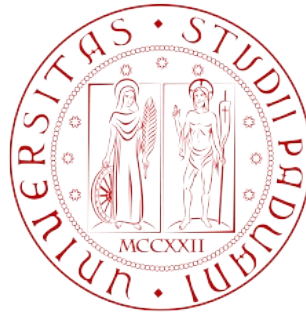


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COEXISTENCE OF MANY SPECIES IN RANDOM ECOSYSTEMS

by CARLOS A. SERVÁN, et al. (2018)

FRANCESCO FONTANA

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April 29 , 2022

1) INTRODUCTION

- *Basic concepts and goals*
- *Stability & Feasibility*
- *Food web example*

2) DISTRIBUTION

- *First intuition*
- *Some simulations*
- *Adding correlation*

3) STRUCTURE ADDITION

- *Some types of structure*
- *Simulations with structure*

4) ROLE OF MEAN ($\neq 0$)

- *Multivariate normal distribution*
- *Adding structure*

5) CONCLUSIONS

- *Discussion*
- *Related application & future work*
- *Summary*

❖ *BACKUP SLIDES*

Starting from Generalized Lotka-Volterra (GLV) population dynamics:

$$\frac{dX_i(t)}{dt} = X_i(t) \left(r_i + \sum_j A_{ij} X_j(t) \right) \quad i \in [1, 2, \dots, n] \quad [1]$$

n : # of different species

X_i : i -esim species abundance

r_i : i -esim growth rate

A_{ij} : interaction matrix of species

PROBLEMS:

- difficult to manage with a lot of species \rightarrow parameters fine tuning
- we observe only a portions (*pruned by dynamics*) instead of the entire species' pool



DIFFERENT PERSPECTIVE

What is the probability that ***all*** the species in a community coexist?

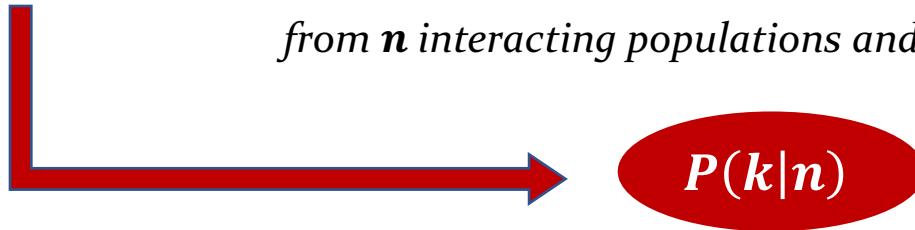
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Probability of finding k species (out of n) after the dynamic evolution

BASIC CONCEPTS & GOALS



GOAL: *Finding the probability to have k species, after that the dynamic has evolved, starting from n interacting populations and **random** parameters.*



We need two important feature:

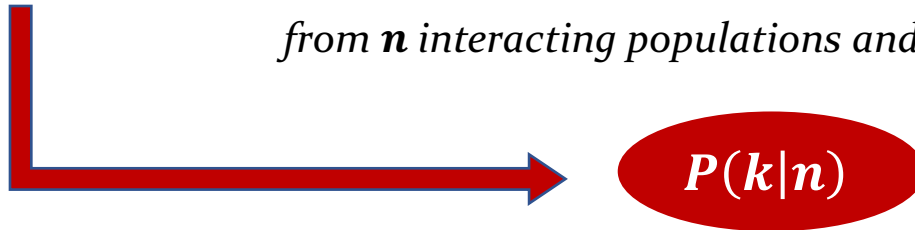
COEXISTANCE

STABILITY

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Dynamic evolution = *species pruning*

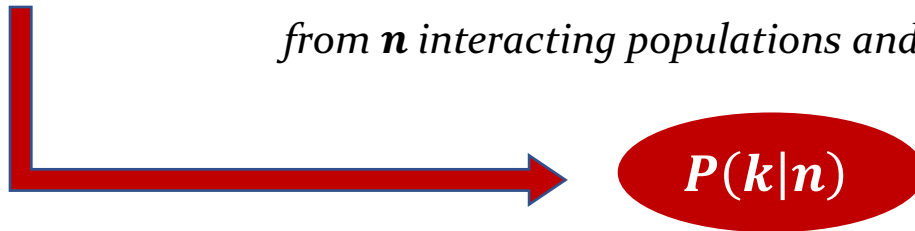


Stationary solution (*Equilibria*)

BASIC CONCEPTS & GOALS



GOAL: *Finding the probability to have k species*, after that the dynamic has evolved, starting from n interacting populations and **random** parameters.



We need two important feature:

COEXISTENCE



Caused by what?
Any impact due to the structure?



We'll see later on...

STABILITY



Dynamic evolution = *species pruning*



Stationary solution (*Equilibria*)

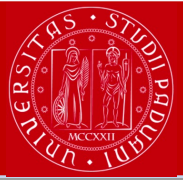
STABILITY & FEASIBILITY



Stationary solution of GLV [1]: $x_i^* (r_i + \sum_j A_{ij} x_j) = 0$ for $i \in [1, 2, \dots, n]$ [2]

$$\Rightarrow \mathbf{x}^* = -A^{-1} \mathbf{r} \quad [3]$$

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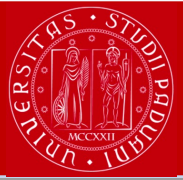
Equilibrium stability



Lyapunov stability:
diagonally stable interaction matrix A

DEFINITION: A generic matrix A is *Lyapunov diagonally stable* (**LDS**) if there exists a positive diagonal matrix D such that $(DA + A^T D)$ is negative definite.

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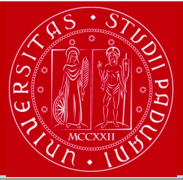
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Assuming interaction matrix A negative defined $\Rightarrow D$ could be the identity matrix \mathbb{I}_n

$$D = \mathbb{I}_n \quad \Rightarrow \quad \text{eigenvalues } (A + A^T) < 0$$

Why
LDS ?

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Why
LDS ?

LDS imply that \exists **globally attractive** fixed point

Non-invasible solution



GOAL: Distribution of non-invasible fixed point?

FEASIBILITY

DEFINITION: A system is feasible if all abundances at equilibrium are positive

$$\Rightarrow x_i^* > 0, \forall i$$

STABILITY & FEASIBILITY how are related to COEXISTENCE?

- ❖ **Feasibility** is necessary
- ❖ **Stability**, if added, completes the hypothesis to study **coexistence**

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Given these conditions, it's possible to find an
analytical solution for $P(k|n)$!

FOOD WEB EXAMPLE

Considering the GLV system of equations [1], the dynamic evolves with:

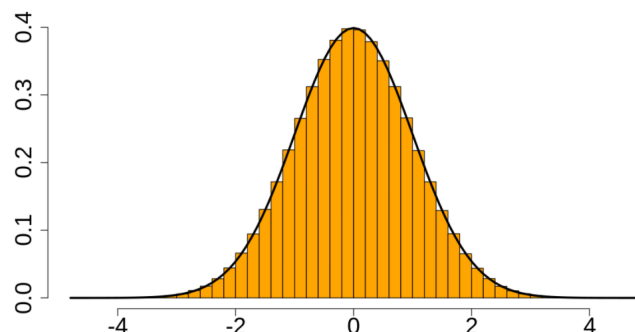
- ✓ $r_i > 0 \rightarrow$ grow in isolation (*producers*)
- ✓ $r_i < 0 \rightarrow$ grow with interactions (*consumers*)
- ✓ **Random** interactions A_{ij}

$r_i, A_{ij} (j \neq i)$
Simmetric $\mathcal{N}(0, 1)$

A_{ii} (diagonal)
 $\mathcal{N}(0, 1) + d$

$d < 0$
(LDS)

Simmetric Gaussian Distribution



Example: matrix $A_{(5 \times 5)}$ with $d = -5$

-4,550	-0,265	-0,546	-1,028	-0,685
-0,882	-4,419	-0,753	1,939	1,078
1,540	0,133	-4,531	0,137	2,646
0,301	-0,332	0,796	-5,374	1,440
-0,298	1,109	2,137	-0,253	-4,389



Easy Model \rightarrow UNCOUPLED LOGISTIC EQUATION

- Suppose that species *do not interact with each other* \rightarrow A off-diagonal terms = 0
- For LDS $\rightarrow A_{ii} < 0, \forall i$.
- If p_i is the probability that $r_i > 0$, and the stationary solution is [3] ($x_i^* = -A^{-1} r_i$)

DISTRIBUTION – FIRST INTUITION

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$$P_{NI} = \prod_{i \in \{S\}_k} p_i \prod_{i \notin \{S\}_k} (1 - p_i)$$

Probability to have a *non-invasible solution* x^* with **k positive components**

If r_i distribution is symmetric

$$\rightarrow p_i = \frac{1}{2} \Rightarrow P_{NI} = \frac{1}{2^n}$$

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$$\Rightarrow P(k|n) = \binom{n}{k} p^k (1 - p)^{n-k} = \binom{n}{k} \frac{1}{2^n}$$

... but is *Binomial* also when species interact??

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Since there is the symmetry hypothesis:

$(D_k A D_k)$	\rightarrow	same distribution of A
$D_k \mathbf{r}$	\rightarrow	same distribution of \mathbf{r}

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$P(k|n)$ is the same as before

SOME SIMULATIONS

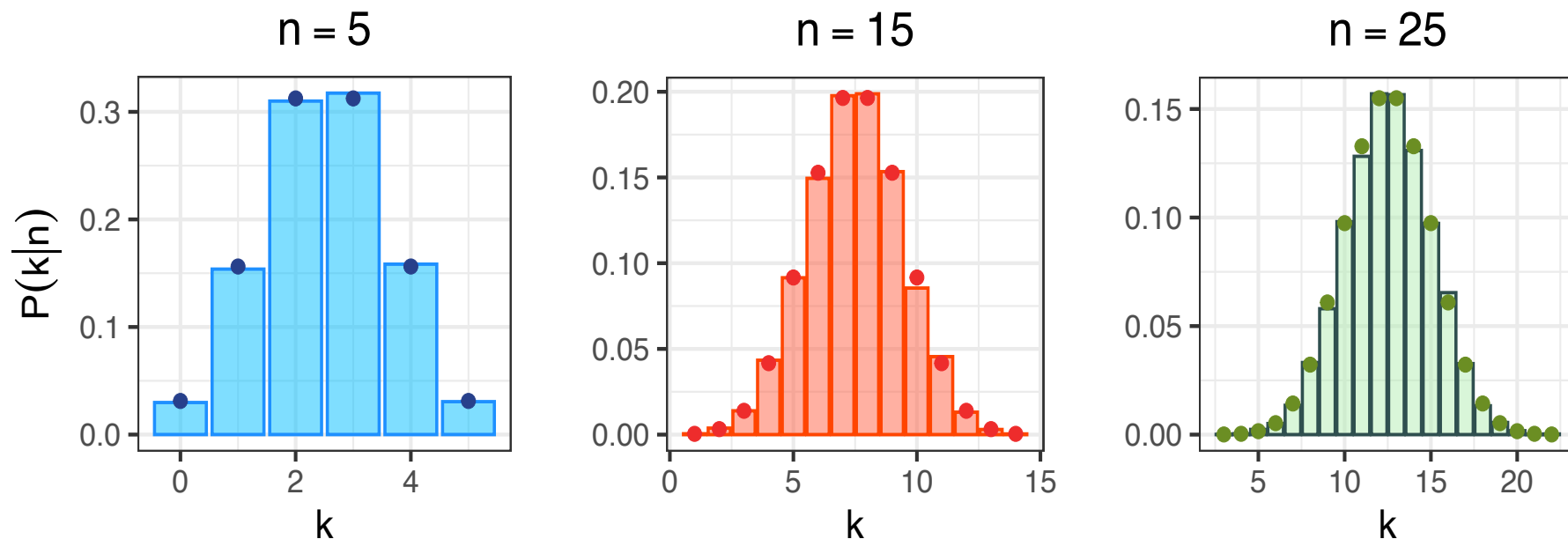


FIGURE 1: Simulations of the number of coexisting species k with 10000 iterations, for systems with different initial value n of species.
The dots are the expected values given by the Binomial distribution

ADDING CORRELATION

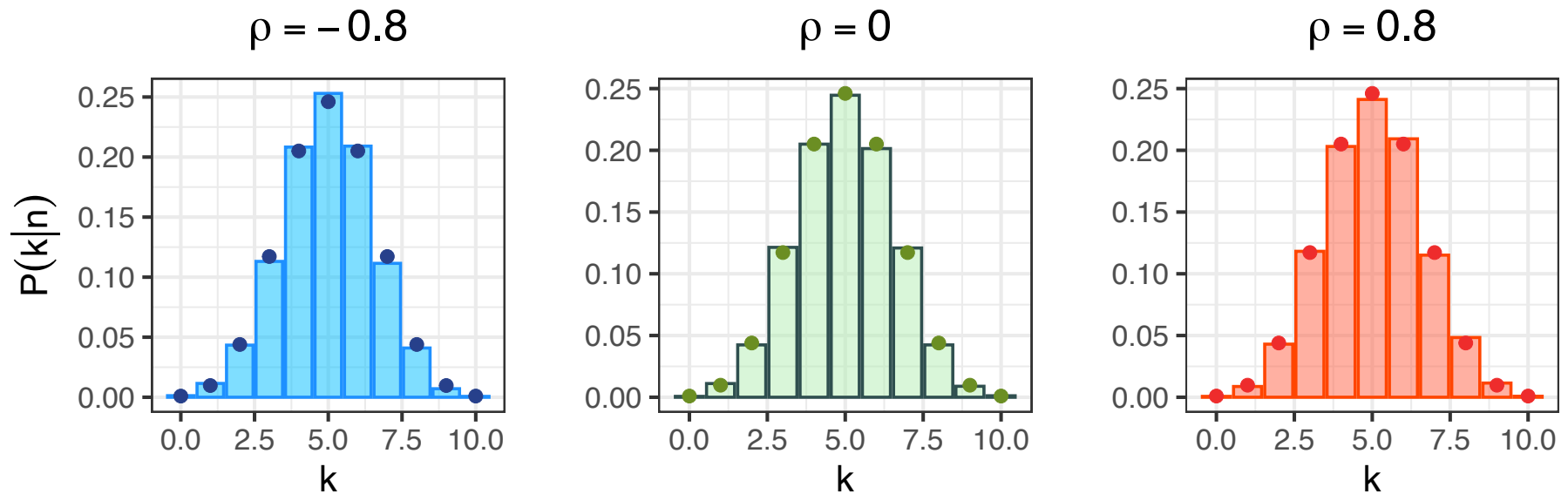
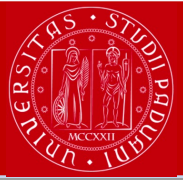


FIGURE 2: Simulations of the number of coexisting species k with 10000 iterations, for systems with $n = 10$ starting species, for different value of correlation ρ .

- G : adjacency matrix of an undirected graph (structure)
- $M = G \circ A \leftrightarrow$ Hadamard (entry-wise) product
- $D(G \circ A)D = G \circ (DAD)$ for D diagonal
- Recalling: $D_k = (-1)^{\delta_{ik}} \delta_{ij} \rightarrow D_k A D_k$ has the same distribution of A
 $\rightarrow D_k r$ has the same distribution of r
- Distribution of M remains invariant to $D_k M D_k$

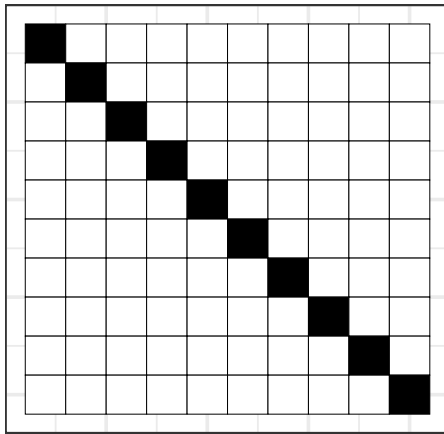


ADDING NETWORK STRUCTURE DOES NOT CHANGE THE
OVERALL PROBABILITY DISTRIBUTION

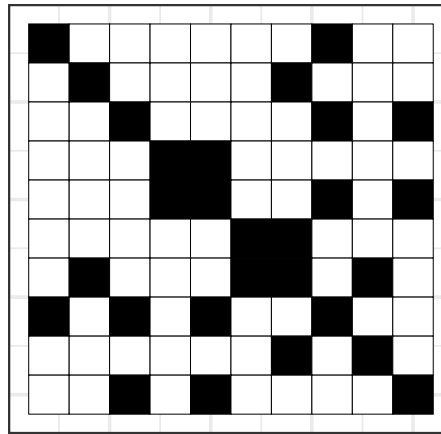
SOME TYPES OF STRUCTURE



Fixed matrix



Power law



2 blocks

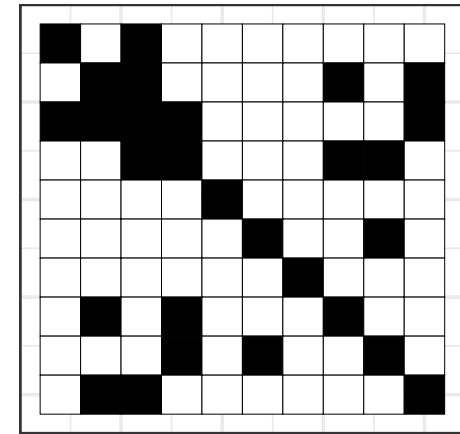


FIGURE 3: *Examples of 3 types of symmetric interaction matrix.
Position of non-zero coefficients.*

SIMULATIONS WITH STRUCTURE

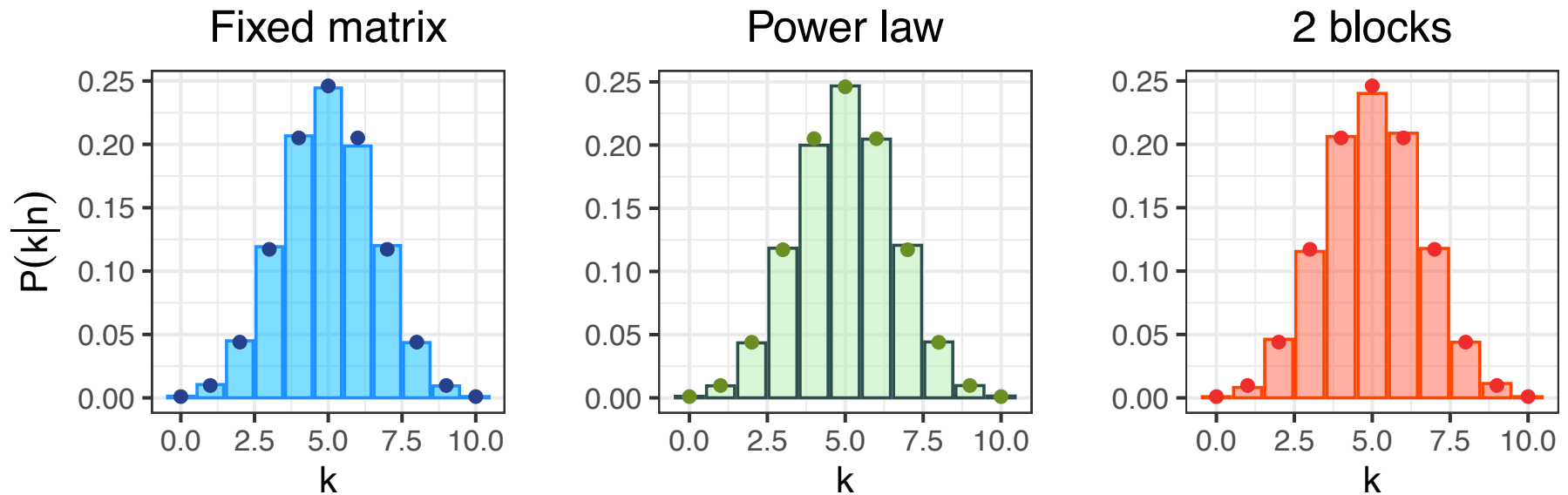
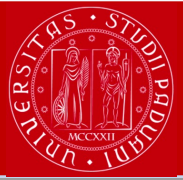


FIGURE 4: Simulations of the number of coexisting species k with 10000 iterations, for systems with $n = 10$ starting species, for different types of interaction matrix.

ROLE OF MEAN ($\neq 0$)

Now, we'll introduce *INTERACTING COMPETITORS*, so that:

- $A_{ij} < 0, \forall i, j$
- $r_i \sim \mathcal{N}(\gamma, 1)$ with $\gamma \neq 0$

In particular for the interaction matrix A :

$A_{ij} = \mu = \frac{\hat{\mu}}{n} < 0$	←	INTER-SPECIFIC INTERACTION (<i>COMPETITIVE</i>)
$A_{ii} = d_i = \alpha < 0$	←	INTRA-SPECIFIC INTERACTION

Since, we want to keep **LDS** condition:
 $\alpha < \mu < 0$



Values used in the simulations:
 $(\mu = -0.5; \alpha = -1)$

ROLE OF MEAN ($\neq 0$)

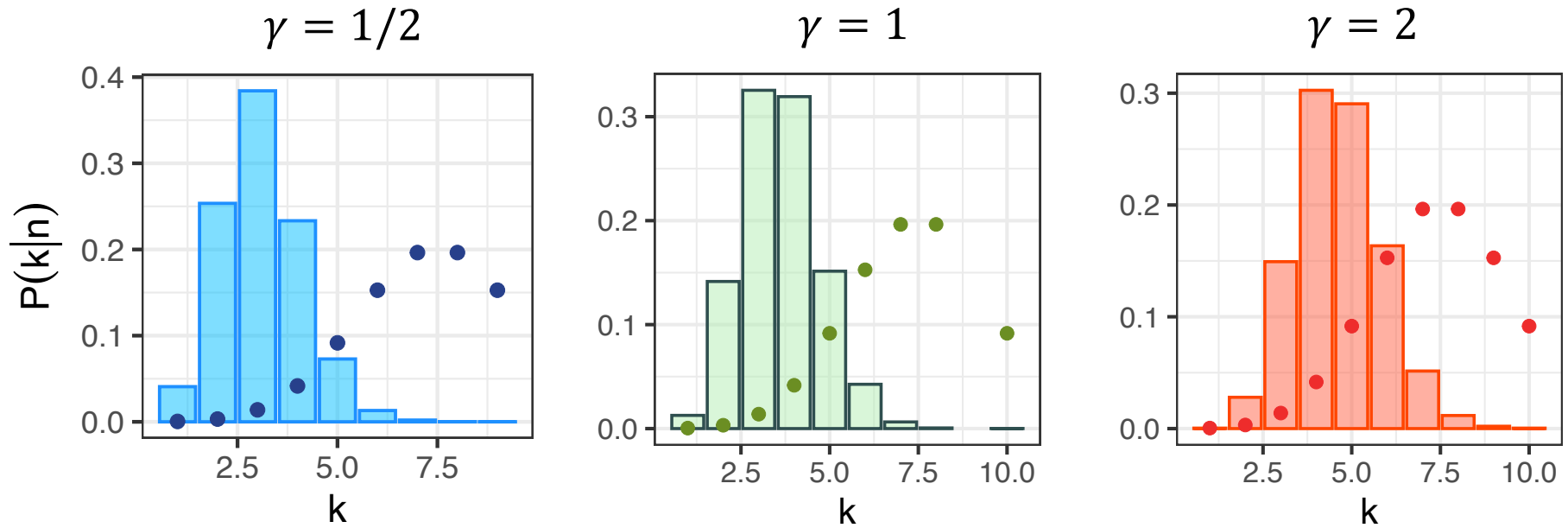
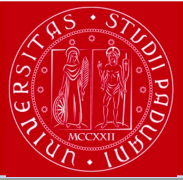


FIGURE 4: Simulations of the number of coexisting species k with 10000 iterations, for systems with $n = 15$ starting species, for different values of γ

ROLE OF MEAN ($\neq 0$)

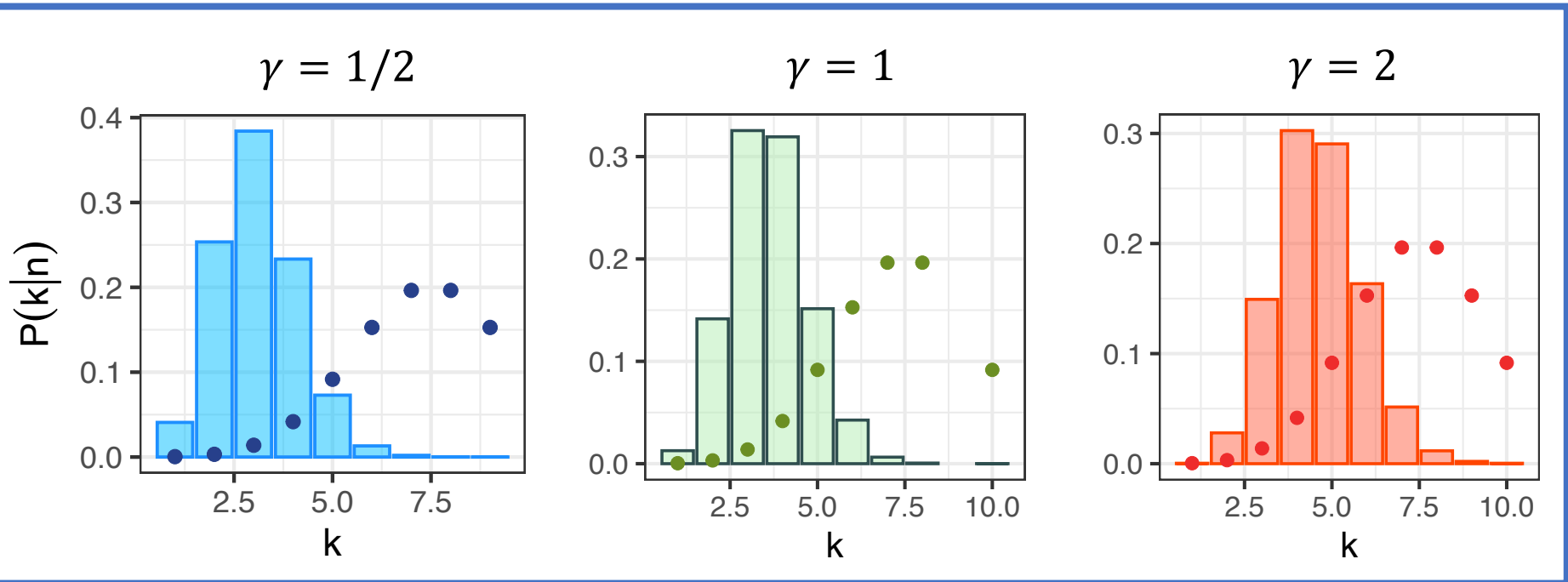
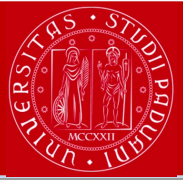
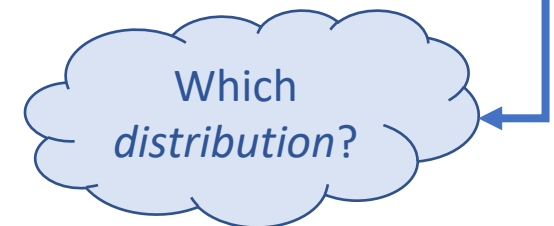


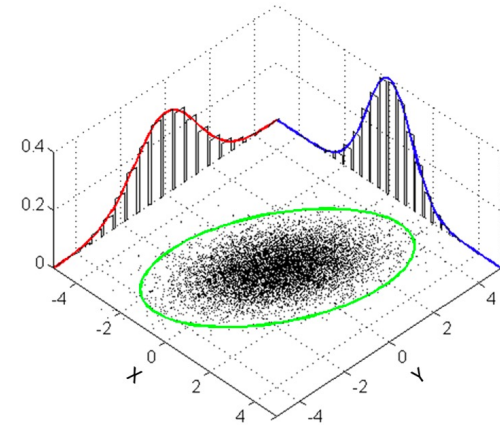
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MULTIVARIATE NORMAL DISTRIBUTION



Since $r_i \sim \mathcal{N}(\gamma, 1)$ with $\gamma \neq 0$. \Rightarrow solution $x^* = -A^{-1} r$ follow a ***multivariate normal distribution***



MULTIVARIATE NORMAL DISTRIBUTION



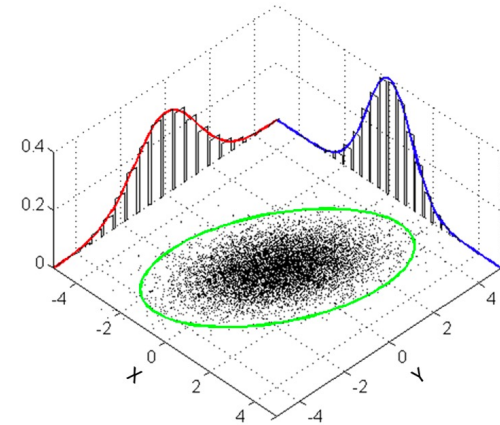
Since $r_i \sim \mathcal{N}(\gamma, 1)$ with $\gamma \neq 0$. \Rightarrow solution $x^* = -A^{-1} r$ follow a
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$P(k|n)$ can be written as double integral (**BAD BEAST**)



COMPUTED NUMERICALLY

⌈ with many approximations: **saddle-point** [for $n \gg 1$],
Hubbard-Stratonovich, FFT, Stirling,... ⌋



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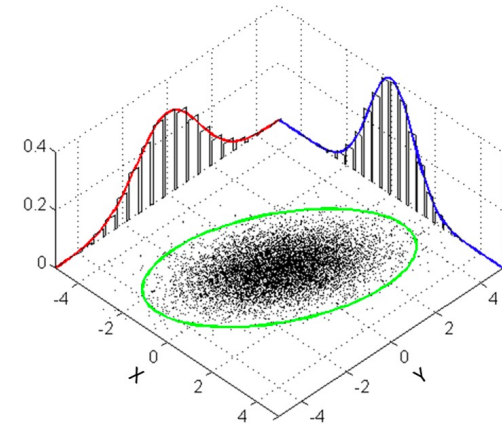
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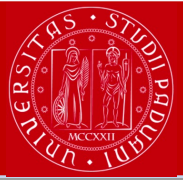
$$P(k|n, \alpha, \hat{\mu}, \gamma) = \frac{n(q + u) - 1}{\sqrt{2\pi n q(1 - q)K(\boldsymbol{\sigma}, n)}} e^{nF(\boldsymbol{\sigma}) + G(\boldsymbol{\sigma})}$$

[4]



$$\bullet \quad q = \frac{k}{n} \quad \bullet \quad u = \frac{\alpha}{\hat{\mu}} = \frac{\alpha}{n\mu} \quad \bullet \quad \boldsymbol{\sigma} = (q, u, v) \quad \bullet \quad v = \frac{\gamma(\alpha - \mu)}{\alpha - \mu + k\mu}$$

MULTIVARIATE NORMAL DISTRIBUTION



The **mode** of the distribution is:

$$u = \frac{\alpha}{\hat{\mu}} = \frac{e^{-[\Phi^{-1}(1-q^*)]^2/2} - \sqrt{2\pi} q^* \Phi^{-1}(1 - q^*)}{\sqrt{2\pi} [\Phi^{-1}(1 - q^*) + \gamma]} \quad [5]$$

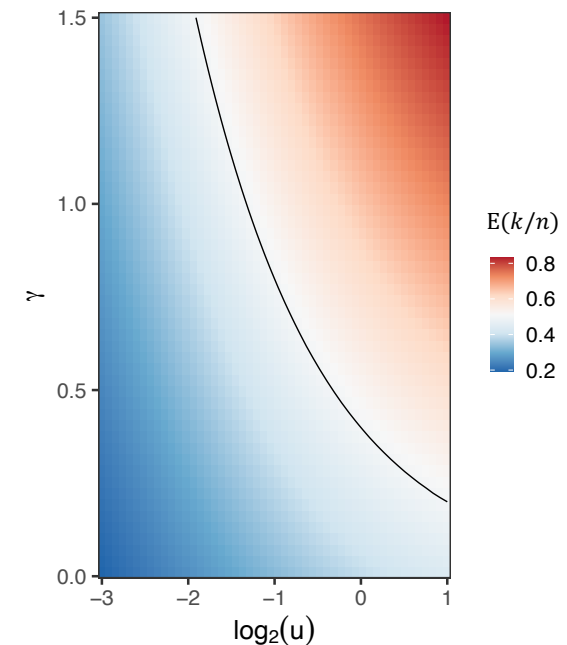
$$\left(\text{where: } \Phi^{-1}(q) = \sqrt{2} \operatorname{erf}^{-1}(2q - 1) \right)$$

A simple relation arises for the curve that separates left and right-skewed distributions by choosing:

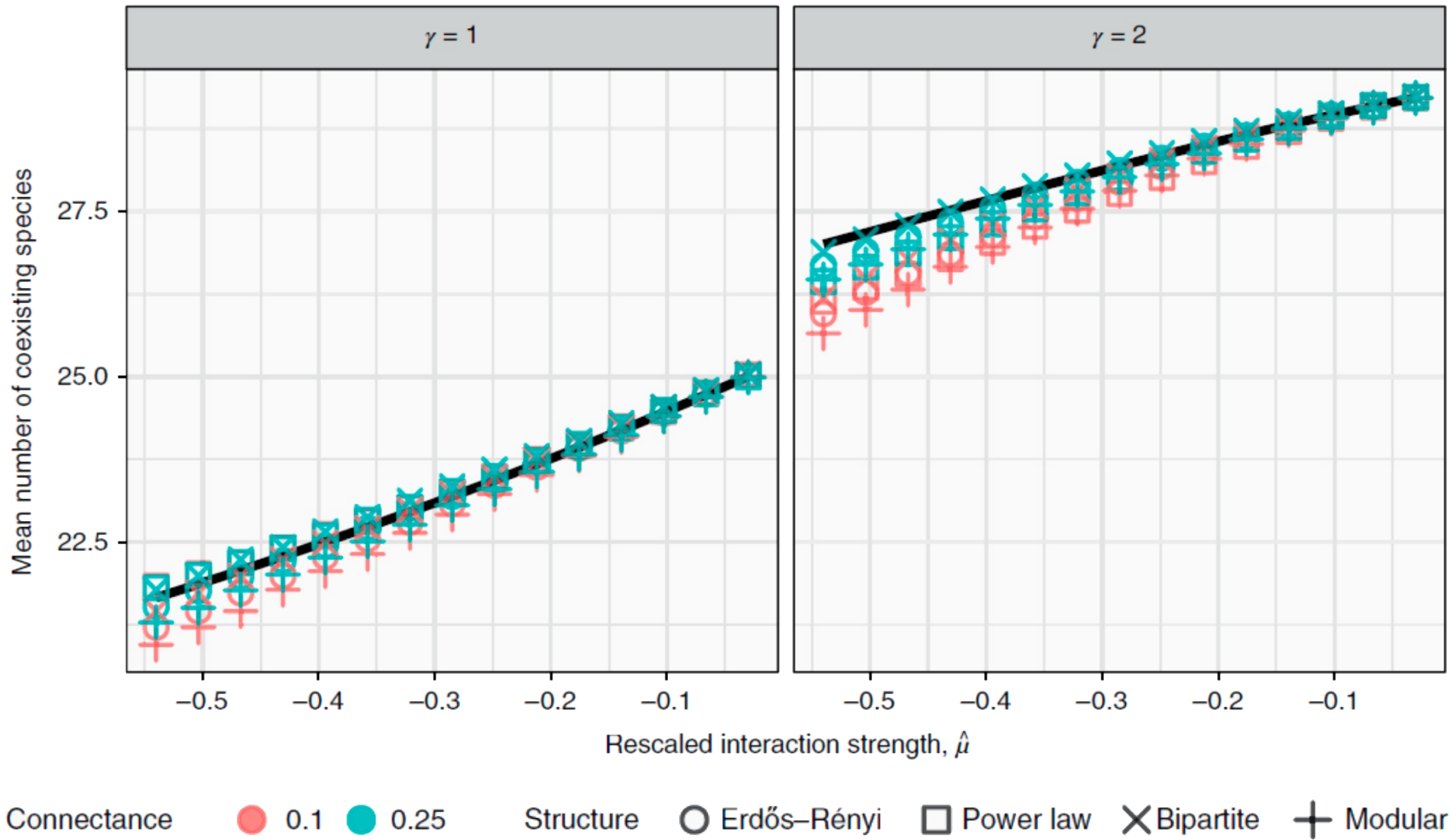
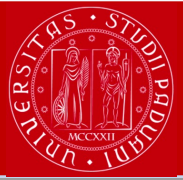
$$q^* = 1/2 \Rightarrow \Phi^{-1} \rightarrow 0$$

↓

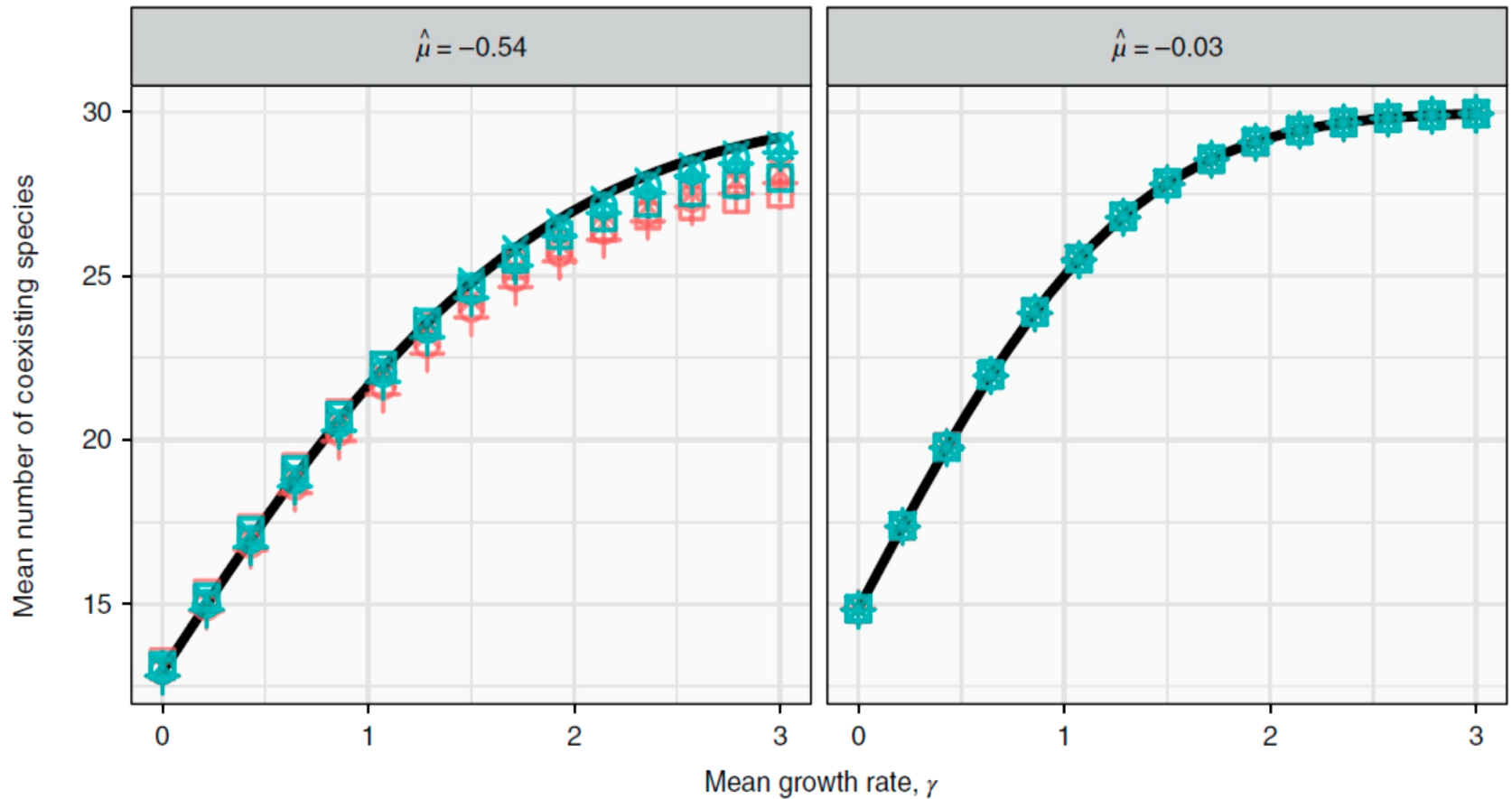
$$u = \frac{1}{\sqrt{2\pi}\gamma} \Rightarrow \frac{\alpha\gamma}{\mu} = \frac{n}{\sqrt{2\pi}} \quad [6]$$



...WITH STRUCTURE



...WITH STRUCTURE



Connectance ● 0.1 ● 0.25 Structure ○ Erdős-Rényi □ Power law × Bipartite + Modular

CONCLUSIONS

FOOD WEB



sampled A_{ij} and r_i independently



generation of "bad" species ($r_i < 0$ & $A_{ij} < 0$)



surely **EXTINCTED!** \Rightarrow **CORRELATION**

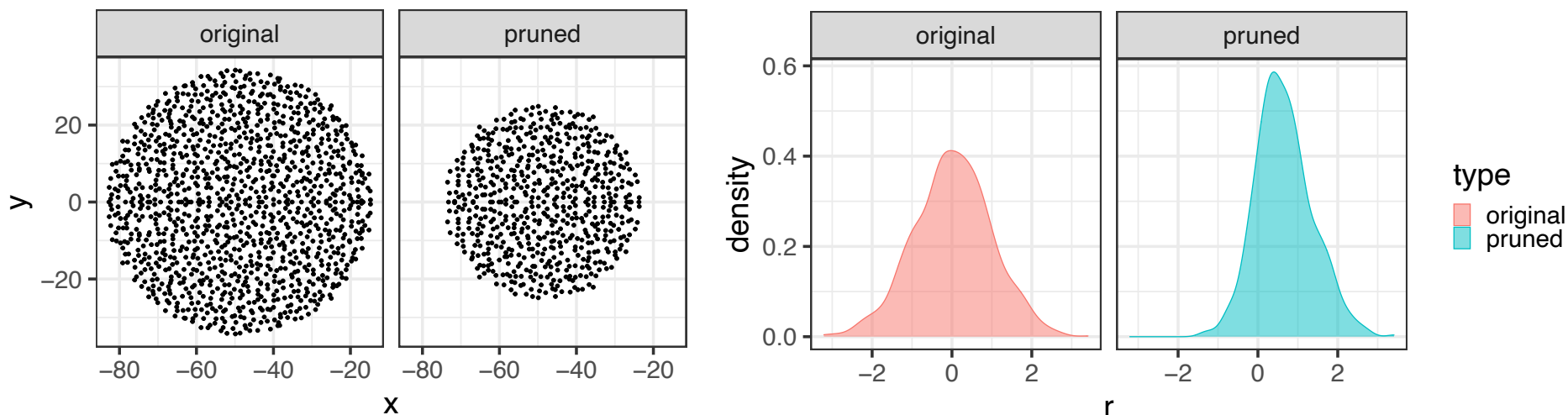


FIGURE 6: *LEFT: $\Re(z)$ vs $\Im(z)$ parts of eigenvalues (z) of interaction matrix A ...**
*RIGHT: Growth rates distribution ...**

*...before and after the dynamics has reached equilibrium. (initial $n = 3000$ species; survived $k = 1525$ species).



APPLICATIONS

- Application to local communities composed of subsets of the same pool of species (*metacommunities*): model the distribution of the number of species found in local patches
- Application to microbial communities (*assembly*)

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- Application to microbial communities (*assembly*)

FUTURE WORK

- Consider stronger form of networks, in which also the non-zero coefficient have a pattern
- Relaxing LDS condition → very challenging
- Understanding the process of assembly in which communities are built

SUMMARIZING:

- ✓ Large communities can stably coexist thanks to the selection imposed by the dynamical pruning of a large species pool
- ✓ Successfully tested many different structures, no particular impact from network once stability is reached

MEAN = 0

- $P(k|n) = \text{Bin}\left(n, \frac{1}{2}\right)$
- No differences caused by the network

MEAN \neq 0

- $P(k|n)$ not binomial
 - ↳ but with strong central tendency and known mode
- Little effect due to network

