COEXISTENCE OF MANY SPECIES IN RANDOM ECOSYSTEMS

by CARLOS A. SERVÁN, et al. (2018)

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❖ ***Backup slides***

INTRODUCTION

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

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

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 → parameters fine tuning
- we observe only a portions (*pruned by dynamics*) instead of the entire species' pool

DIFFERENT PERSPECTIVE

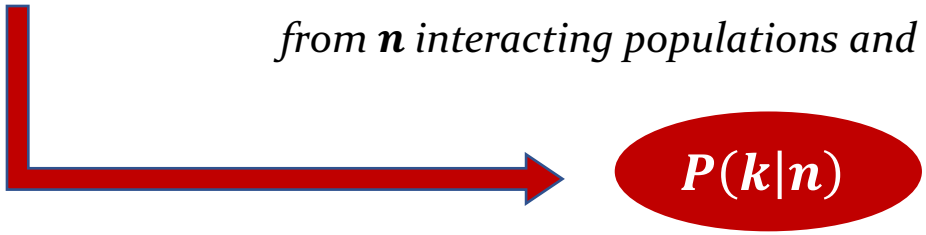
What is the probability that ***all*** the species in a community cohexist?

=

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:

COHEXISTANCE

STABILITY

BASIC CONCEPTS & GOALS

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$P(k|n)$

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↓

Dynamic evolution = *species pruning*

↓

Stationary solution *(Equilibria)*

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$P(k|n)$

We need two important feature:

COHEXISTANCE

↓

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

$$\Longrightarrow \quad \boldsymbol{x}^* = -A^{-1}\,\boldsymbol{r} \qquad [3]$$

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

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

Why **LDS** ?

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Why **LDS** ?

LDS *imply that* ∃ ***globally attractive*** *fixed point*

Non–invasible solution ⟹ ***GOAL***: *Distribution of non-invasible fixed point?*

STABILITY & FEASIBILITY

FEASIBILITY

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

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

STABILITY & FEASIBILITY *how are related to* ***COEXISTANCE?***

- **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

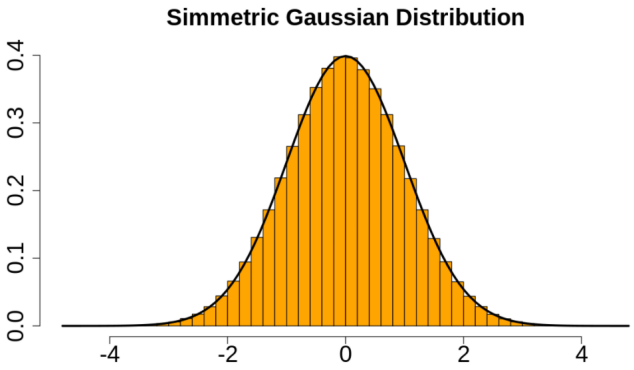
Considering the GLV system of equations **[1]**, the dynamic evolves with:

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

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

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

$d < 0$
(LDS)



Example: matrix $A_{(5x5)}$ 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

DISTRIBUTION – FIRST INTUITION

Easy Model → UNCOUPLED LOGISTIC EQUATION

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

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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*

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

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Binomial distribution

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

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

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For a *feasible equilibrium*: $\Longrightarrow \boldsymbol{x}^* = -A^{-1}\,\boldsymbol{r}$

Due to simmetry, 2^n *possible sign patterns for* x^* *that are equally probable.*

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Defining $D_k = (-1)^{\delta_{ik}}\,\delta_{ij}$ $\quad\Rightarrow (D_k A\, D_k) D_k\, x^* = -D_k\, r$

Since there is the simmetry hypothesis:

$(D_k A\, D_k) \rightarrow$ same distribution of A

$D_k\, r \rightarrow$ same distribution of r

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P(k|n) is the same as before

SOME SIMULATIONS

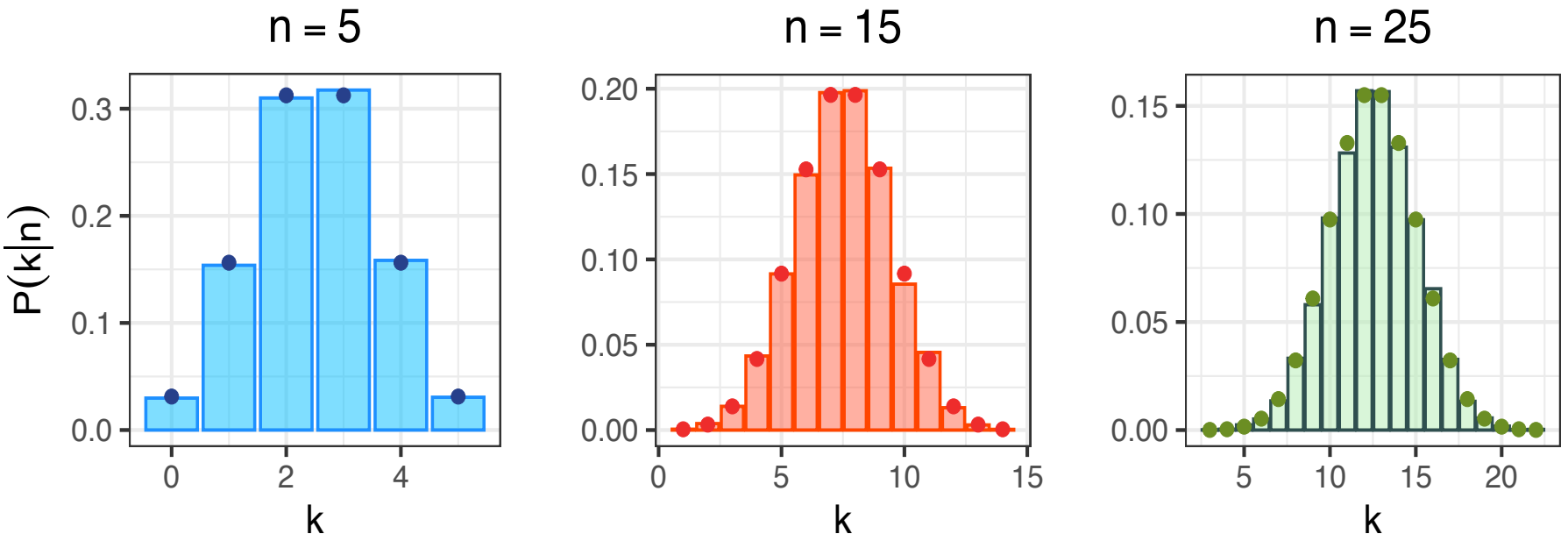

FIGURE 1: *Simulations of the number of coexisting species* ***k*** *with* 10000 *iterations, for systems with different initial value* ***n*** *of species. The dots are the expected values given by the Binomial distribution*

ADDING CORRELATION

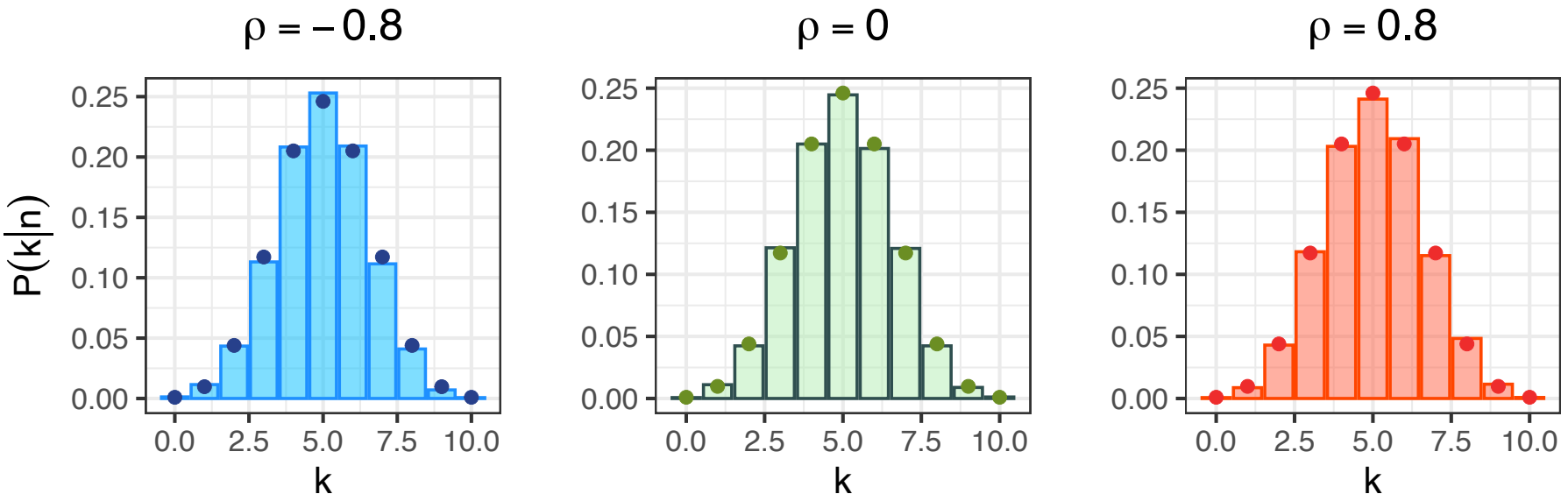

FIGURE 2: *Simulations of the number of coexisting species* $\boldsymbol{k}$ *with* 10000 *iterations, for systems with* $\boldsymbol{n = 10}$ *starting species, for different value of correlation* $\boldsymbol{\rho}$.

STRUCTURE ADDITION

- 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: $Dk = (-1)^{\delta_{ik}}\,\delta_{ij}$ $\rightarrow$ $D_k A D_k$ 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

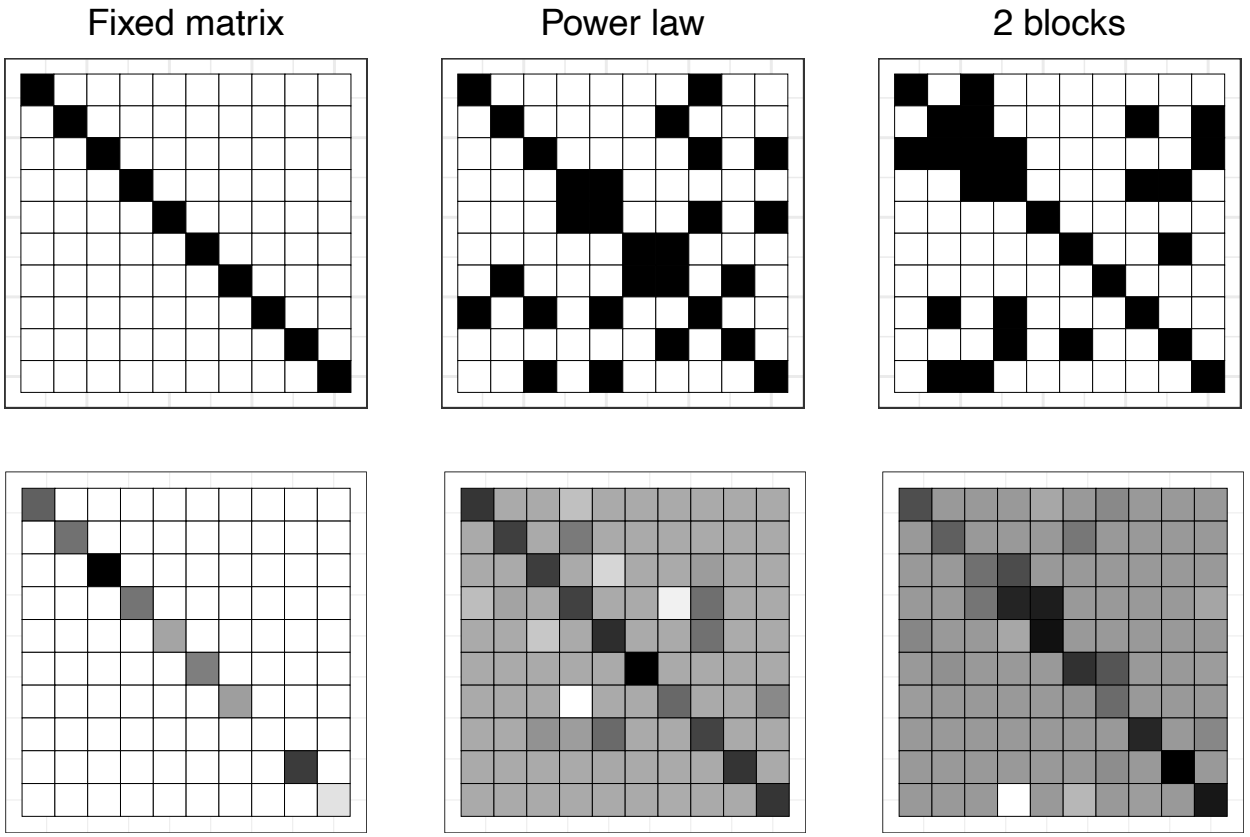

FIGURE 3: *Examples of 3 types of symmetric interaction matrix.*
TOP: *position of non-zero coefficients.*
BOTTOM: *LDS matrices where more negative values of* A_{ij} *are darker.*

SIMULATIONS WITH STRUCTURE

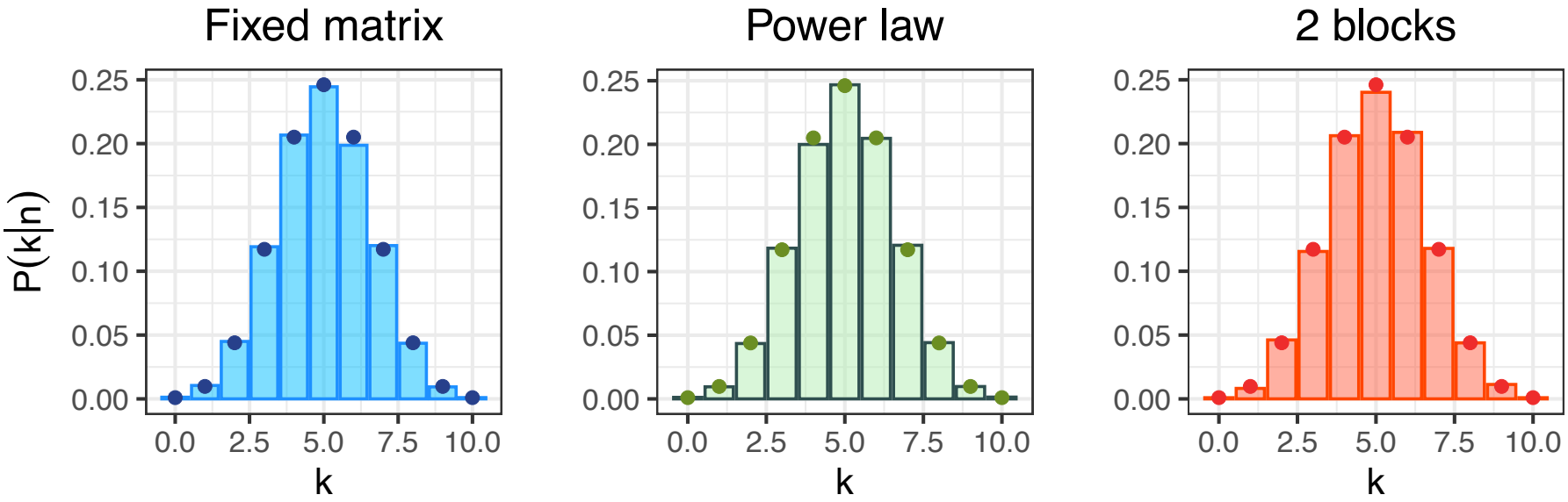

FIGURE 4: *Simulations of the number of coexisting species* $\boldsymbol{k}$ *with* 10000 *iterations, for systems with* $\boldsymbol{n = 10}$ *starting species, for different types of interaction matrix.*

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:

$A_{ij} = \mu = \frac{\widehat{\mu}}{n} < 0$ ← INTER-SPECIFIC INTERACTION ***(COMPETITIVE)***

$A_{ii} = d_i = \alpha < 0$ ← INTRA-SPECIFIC INTERACTION

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

!

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

ROLE OF MEAN ($\neq 0$)

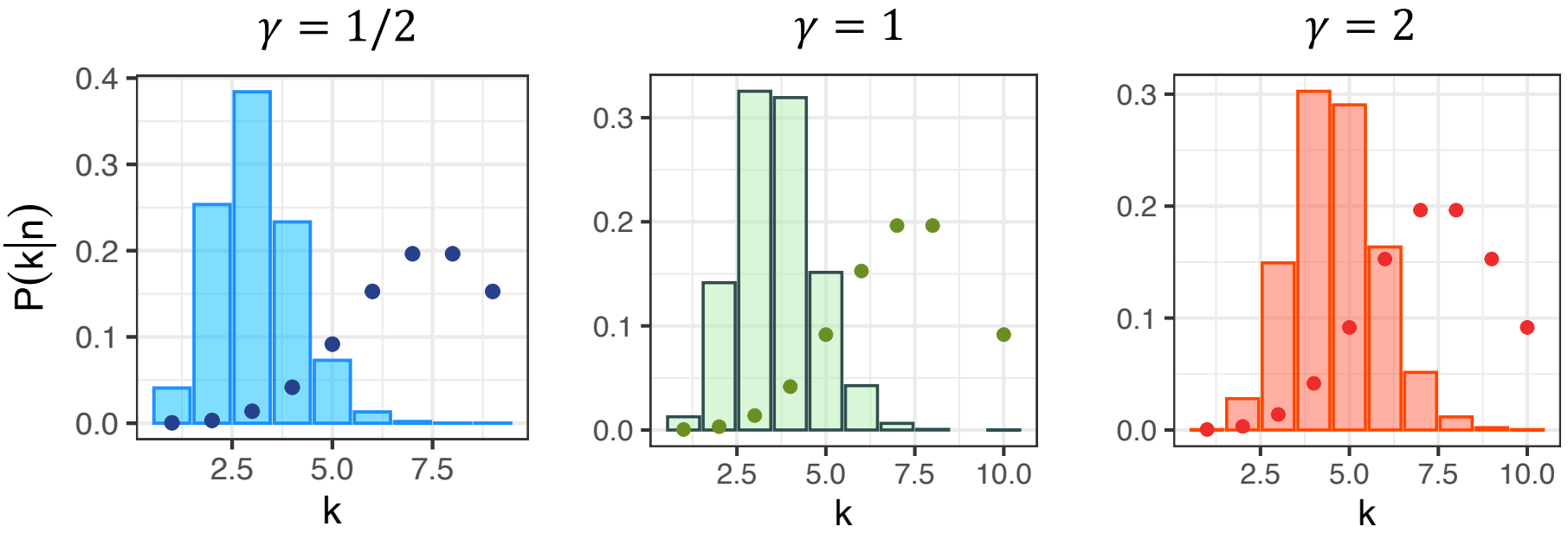

FIGURE 4: *Simulations of the number of coexisting species* $\boldsymbol{k}$ *with* 10000 *iterations, for systems with* $\boldsymbol{n = 15}$ *starting species, for different types of interaction matrix.*

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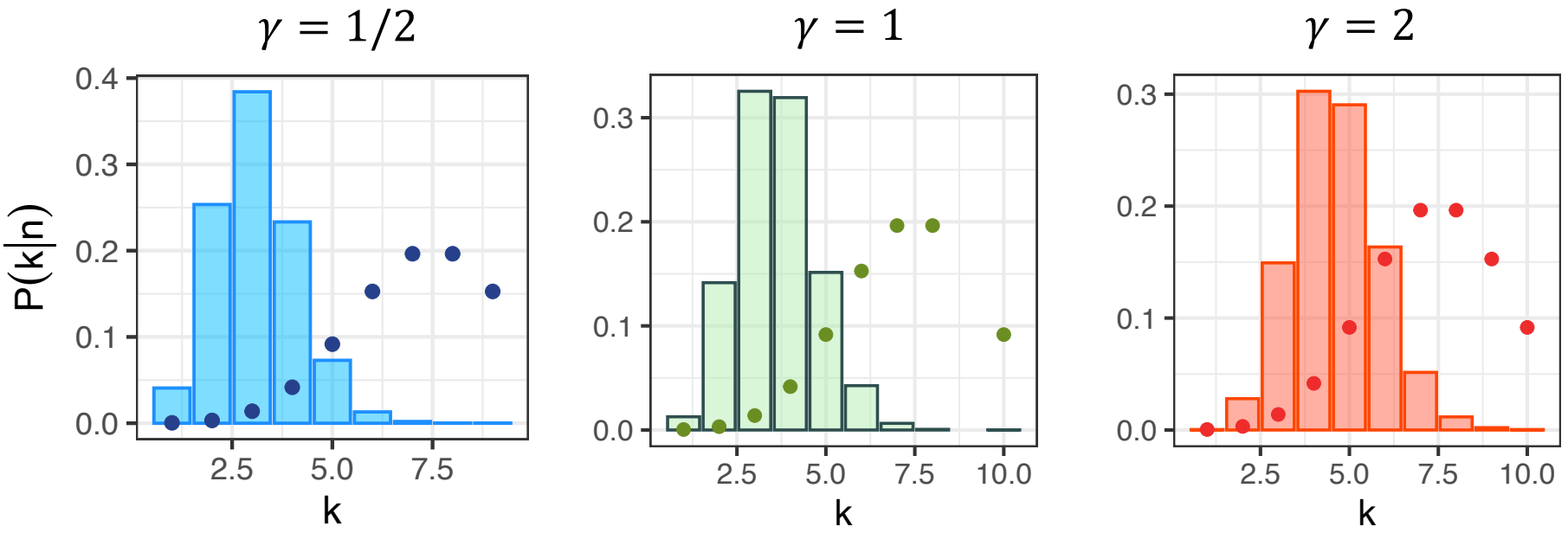

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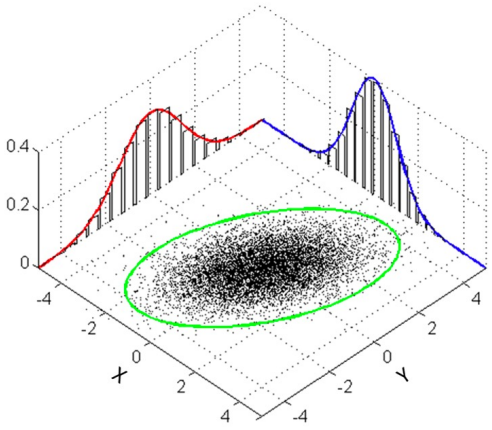
Which *distribution*?

MULTIVARIATE NORMAL DISTRIBUTION

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



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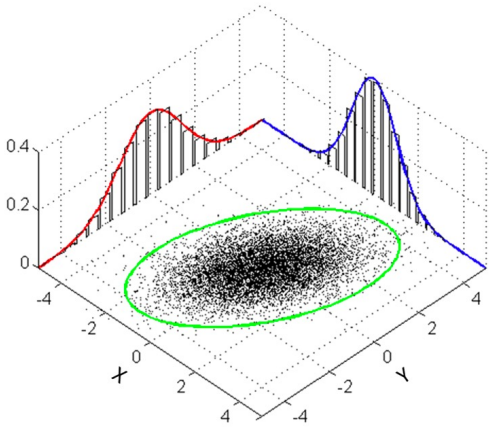
$P(k|n)$ can be written as double integral (***BAD BEAST***)

$\downarrow$

COMPUTED NUMERICALLY

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



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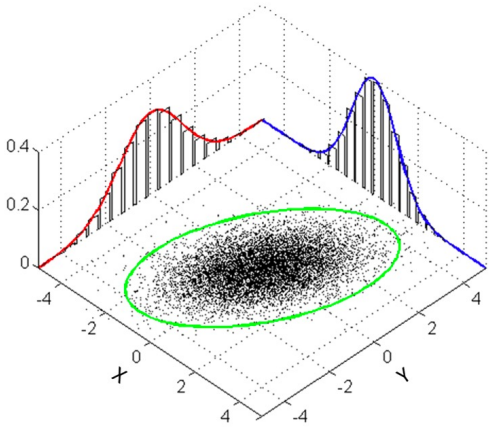
↓

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

[4]



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

MULTIVARIATE NORMAL DISTRIBUTION

The ***mode*** of the distribution is:

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

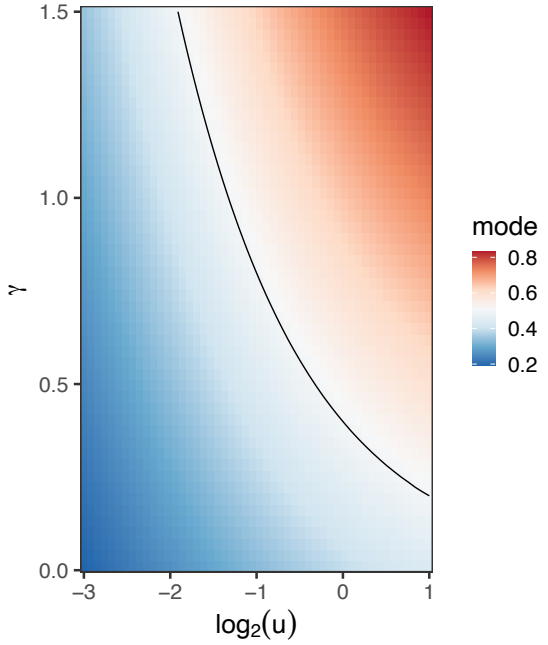
$$\left(\text{where: } \Phi^{-1}(q) = \sqrt{2}\,\mathrm{erf}^{-1}(2q - 1)\right)$$

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

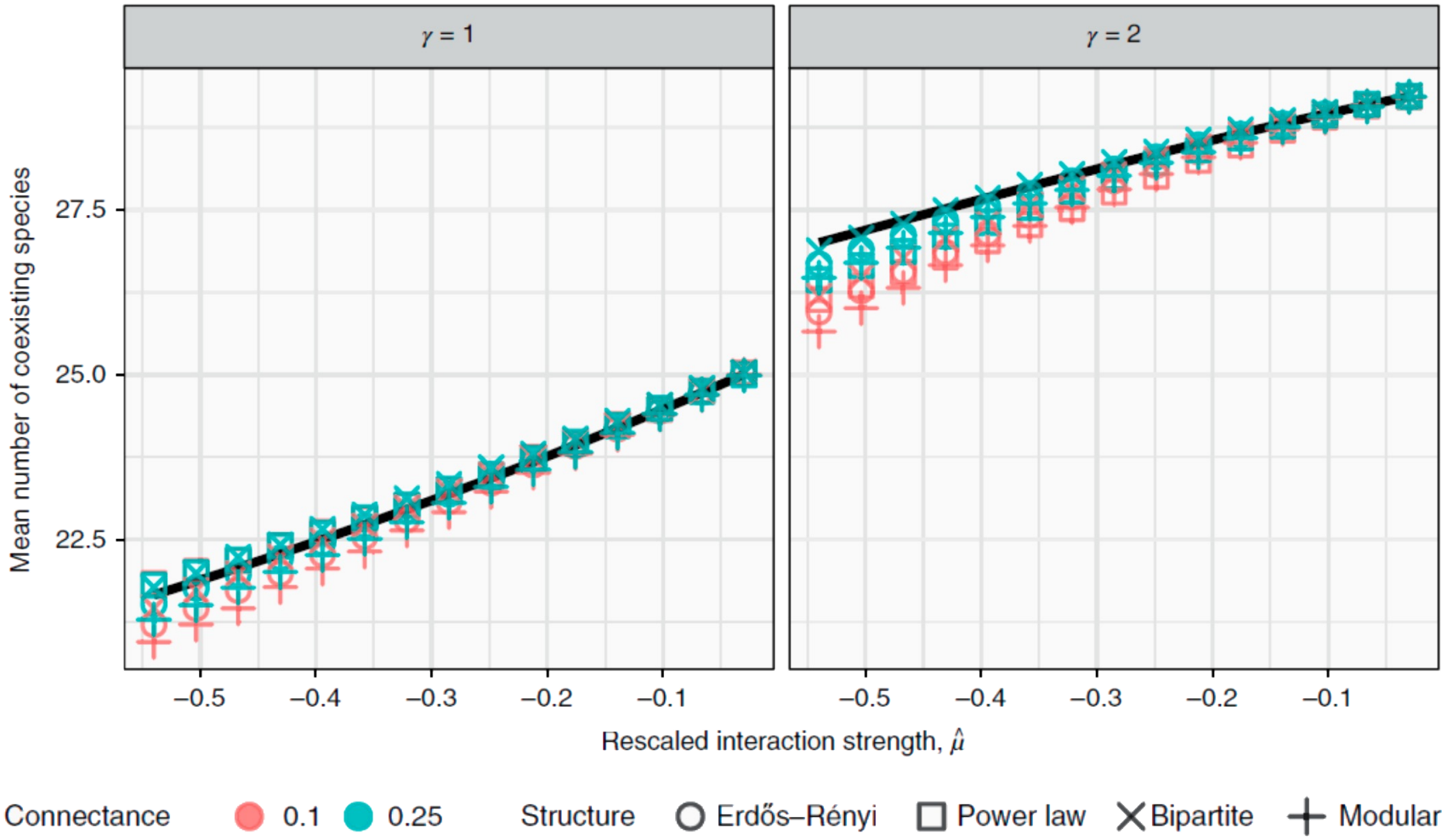
$$q^* = 1/2 \implies \Phi^{-1} \to 0$$

$$\downarrow$$

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



...WITH STRUCTURE



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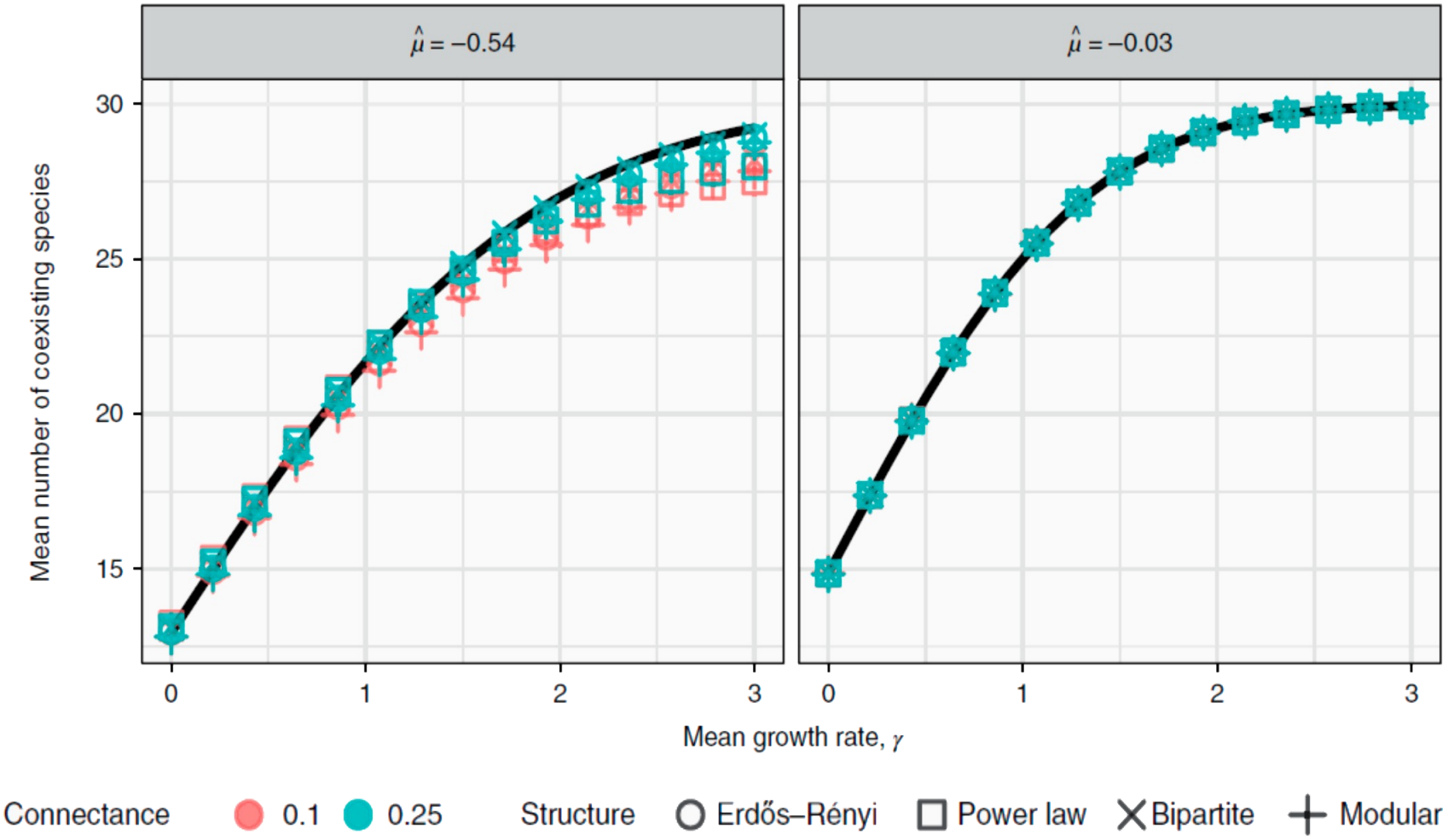

CONCLUSIONS

FOOD WEB ⟶ sampled A_{ij} and r_i independently

↓

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

↓

surely **EXTINCTED!** $\Longrightarrow$ ***CORRELATION***

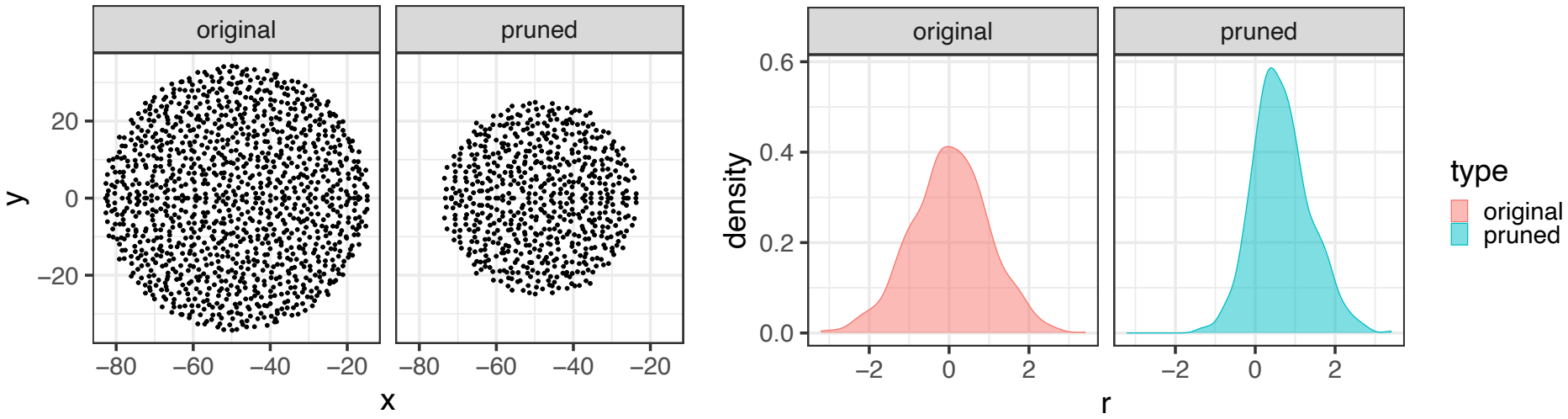

FIGURE 6: ***LEFT:*** *$\Re(z)$ vs $\Im(z)$ parts of eigenvalues (z) of interaction matrix A ...**

RIGHT: *Growth rates distribution ...**

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

Related application & future work

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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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

SUMMARY

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

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

MEAN ≠ 0

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