Coexistence of many species in random ecosystems

by Carlos A. Serván, et al. (2018)

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Introduction

Lotka-Volterra population dynamics:

$$\frac{\mathrm{d}X_i(t)}{\mathrm{d}t} = X_i(t)\left(r_i + \sum_j A_{ij}X_j(t)\right) \tag{1}$$

- difficult with more species $\longrightarrow$ parameters fine tuning;
- we observe portions of a bigger pool (pruned by dynamics).

Change focus

What is the probability that *all* the species in a community cohexist?	$\Longrightarrow$	What is the probability of finding k species when we start from a pool of n species and let the dynamic evolve?

Key concepts and goal

Goal: finding the probability

$$\mathcal{P}(k|n)$$

of having **k** species...

$\hookrightarrow$ **Stably**

$\hookrightarrow$ **Cohexisting**

... when starting from **n** interacting populations and **random** parameters.

Key concepts and goal

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$$\mathcal{P}(k|n)$$

of having **k** species...

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$\downarrow$

After species pruning

$\downarrow$

Equilibria

$\hookrightarrow$ **Cohexisting**

... when starting from **n** interacting populations and **random** parameters.

Key concepts and goal

Goal: finding the probability

$$\mathcal{P}(k|n)$$

of having **k** species...

$\hookrightarrow$ **Stably**

$\downarrow$

After species pruning

$\downarrow$

Equilibria

$\hookrightarrow$ **Cohexisting**

$\downarrow$

possible drivers?

Impact of structure?

... when starting from **n** interacting populations and **random** parameters.

$$x_i^\star \left(r_i + \sum_j A_{ij} x_j^\star \right) = 0 \qquad \text{for } i = 1, 2, \ldots, n \tag{2}$$

$$\mathbf{x}^\star = -A^{-1}\mathbf{r} \tag{3}$$

$\hookrightarrow$ Equilibrium stability $\implies$ Lyapunov diagonally stable interaction matrix A

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

$\hookrightarrow$ Assumption of A negative definite $\implies$ $A + A^\top$ only evl< 0

Stability Goal

$$x_i^\star \left(r_i + \sum_j A_{ij} x_j^\star \right) = 0 \quad \text{for } i = 1, 2, \ldots, n$$

$\hookrightarrow$ Why LDS? $\Longrightarrow$ $\exists$ **globally attractive** fixed point!

$\hookrightarrow$ Non-invasible solution (*saturated* rest point)

Goal

Which is the **distribution** of the non-invasible fixed points?

Feasibility Definition

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

$$x_i^\star > 0$$

How are feasibility and stability related to coexistence?

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

$\hookrightarrow$ Finding an **analytical** solution for $\mathcal{P}(k|n)$ is possible!

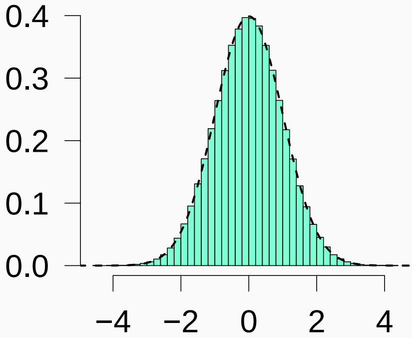
Food web caricature

Starting from Lotka-Volterra system of equations (1), evolve the dynamics with:

1. producers $\longrightarrow$ grow in isolation $\longrightarrow r_i > 0$
2. consumers $\longrightarrow$ grow with interactions $\longrightarrow r_i < 0$
3. **random** interactions A_{ij}

r_i and $A_{ij}, j \neq i$
Symmetric distribution around 0

A_{ii}
Symmetric distribution around 0 + d_i (<0 for LDS)



Toy model: uncoupled logistic equations

- Suppose that A is diagonal (species do not interact with each other).
- For LDS $\longrightarrow$ $A_{ii} < 0\ \forall i$. If p_i is the probability that $r_i > 0$, then, given that $x_i^\star = -A^{-1} r_i$...
- ... the probability that a **solution** $x^\star$ with k positive components is non-invasible is $P_{NI} = \prod_{i \in \{S\}_k} p_i \prod_{i \notin \{S\}_k} (1 - p_i)$
- but if r_i distribution is symmetric, then $p_i = \frac{1}{2}$ and $P_{NI} = \frac{1}{2^n}$.

Probability of coexistence is a **Binomial distribution** with $p = \frac{1}{2}$

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

... Could $\mathcal{P}(k|n)$ be a Binomial distribution also when species interacts?

Yes, indeed!

For a *feasible* equilibrium:

$$x^\star = -A^{-1} r$$

2^n possible sign patterns for $x^\star$ that are equally probable (symmetry), hence it holds:

$$\mathcal{P}(n|n) = \frac{1}{2^n}$$

Let's define $D_k = (-1)^{\delta_{ik}} \delta_{ij}$

$$\implies (D_k A D_k) D_k x^\star = -D_k r$$

Because of symmetry hypothesis:

- $(D_k A D_k)$ has the same distribution of A
- $D_k r$ has the same distribution of r

D_k just flips sign of the $k-$th component $\longrightarrow$ applying D_k allows to obtain **any** pattern $\implies \mathcal{P}(k|n)$ is the same as before!

Some simulations

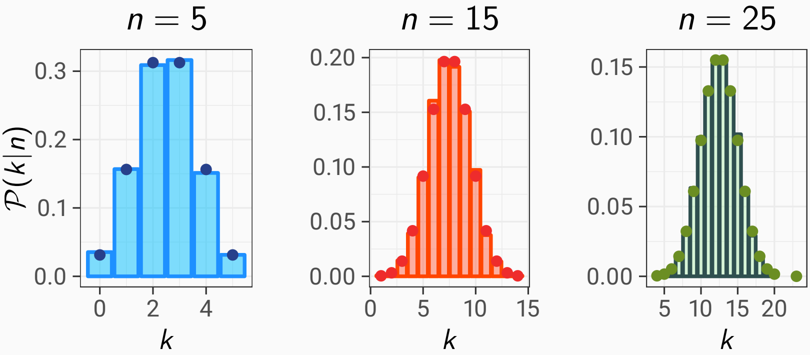


Figure 1 – Simulations of the number of coexisting species k with 50000 iterations, for systems with n starting species.
The dots are the expected values given by the Binomial distribution.

Adding correlation

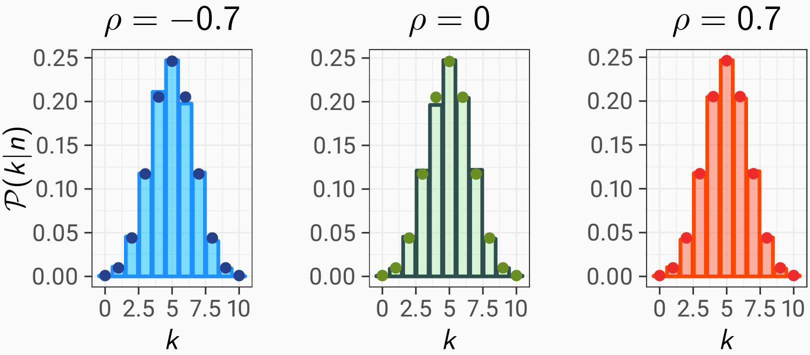


Figure 2 – Simulations of the number of coexisting species k with 10000 iterations, for systems with $n = 10$ starting species, for different correlations.

Adding structure Theoretical proof

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

Therefore

Adding network structure does not change the probability distribution!

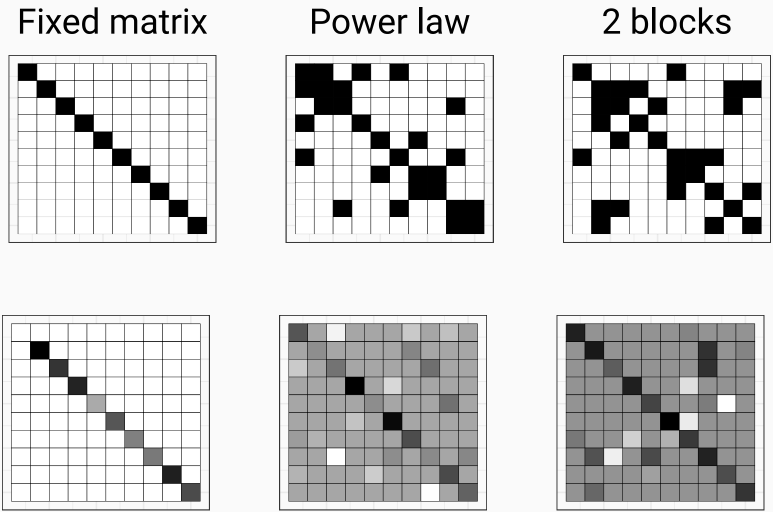


Figure 3 – Three types of interaction matrix. Upper row: position of non-zero coefficients. Bottom row: LDS matrices, the darker the colour, the more negative is A_{ij}.

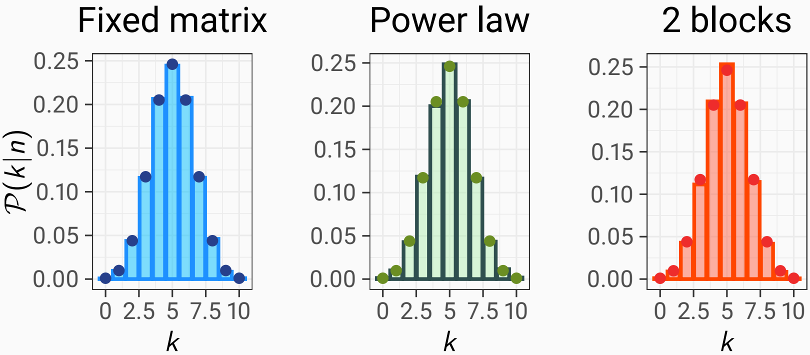


Figure 4 – Simulations of the number of coexisting species k with 10000 iterations, for systems with $n = 10$ starting species, for different types of interaction matrix.

Mean $\neq 0$ Hypothesis

Interacting competitors:

- $A_{ij} < 0, \forall i, j$
- r_i sampled from gaussian distribution with mean $\gamma \neq 0$

Competitive inter-specific interactions:

$$A_{ij} = \mu = \frac{\hat{\mu}}{n} < 0$$

Intra-specific interactions:

$$A_{ii} = d_i = \alpha < 0$$

To ensure LDS

$$\alpha < \mu < 0$$

In particular: $\mu = -0.5, \alpha = -1$

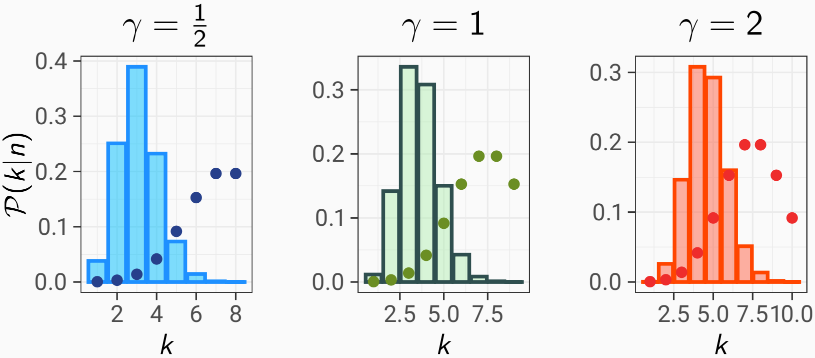


Figure 5 – Simulations of the number of coexisting species k with 10000 iterations, for systems with $n = 15$ starting species, for different means γ.

When $r_i \sim \mathcal{N}(\gamma, 1)$, then the equilibrium point of (3):

$$\mathbf{x}^\star = -A^{-1}\mathbf{r}$$

is described by a multivariate normal distribution.

Hence, $\mathcal{P}(k|n)$ can be written as a double integral $\longrightarrow$ computed numerically $\longrightarrow$ saddle-point approximation for $n \gg 1$, deriving:

$$\mathcal{P}(k|n, \alpha, \hat{\mu}, \gamma) = \frac{n(q+u)-1}{\sqrt{2\pi nq(1-q)K(\boldsymbol{\sigma}, n)}} e^{nF(\boldsymbol{\sigma})+G(\boldsymbol{\sigma})} \tag{4}$$

With:

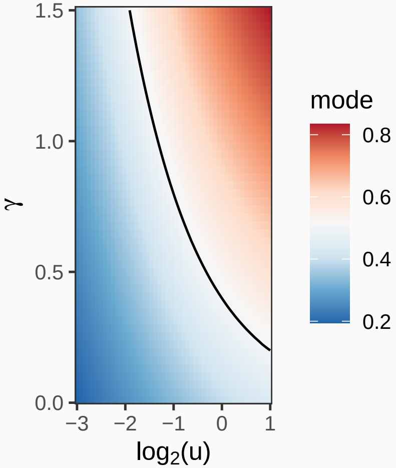
- $q = \dfrac{k}{n}$
- $u = \dfrac{\alpha}{\hat{\mu}} = \dfrac{\alpha}{n\mu}$
- $\boldsymbol{\sigma} = (q, u, v)$
- $v = \dfrac{\gamma(\alpha - \mu)}{\alpha - \mu + k\mu}$

Mean $\neq 0$ Mode of the distribution

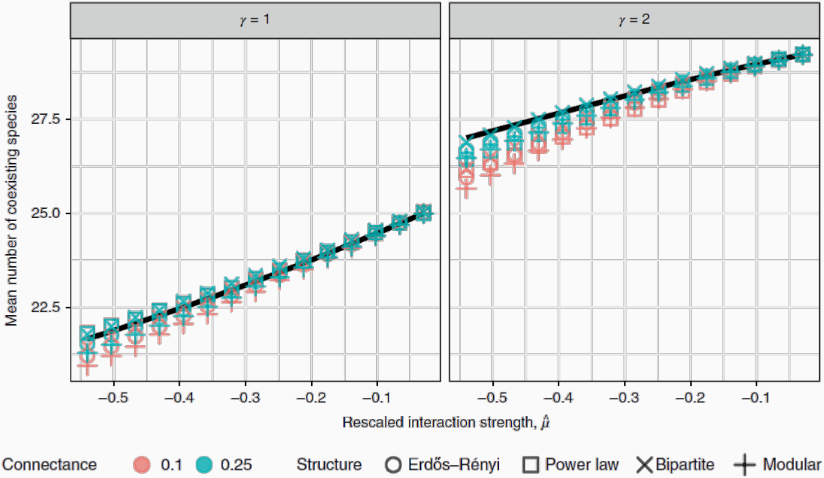
$$u = \frac{\alpha}{\hat{\mu}} = \frac{e^{-\left[\Phi^{-1}(1-q^*)\right]^2/2} - \sqrt{2\pi} q^\star \Phi^{-1}\left(1-q^\star\right)}{\sqrt{2\pi}\left[\Phi^{-1}\left(1-q^\star\right)+\gamma\right]} \quad (5)$$

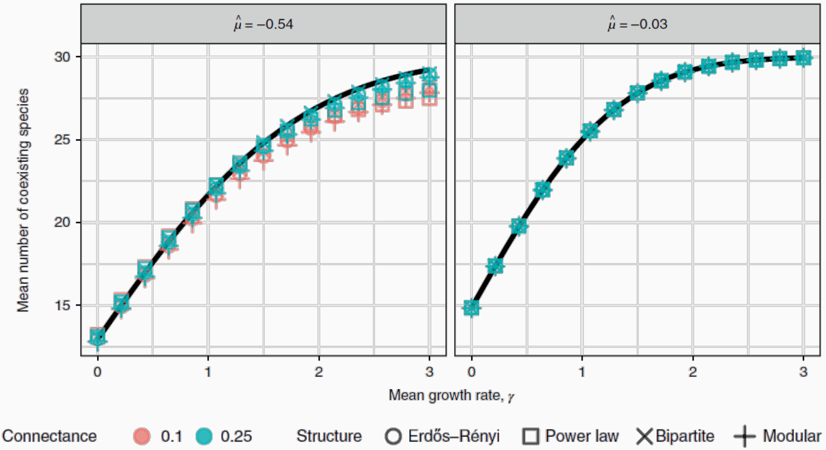
$$\frac{\alpha\gamma}{\hat{\mu}} = \frac{1}{\sqrt{2\pi}} \quad (6)$$

$$\frac{\alpha\gamma}{\mu} = \frac{n}{\sqrt{2\pi}} \quad (7)$$



Mean $\neq 0$ Adding structure




$\hat{\mu} = -0.54$
$\hat{\mu} = -0.03$
30
25
20
15
0
1
2
3
Mean number of coexisting species
Mean growth rate, γ
Connectance
0.1
0.25
Structure
Erdős–Rényi
Power law
Bipartite
Modular

- Food web → sampled A_{ij} and r_i independently → some "bad" species can be generated ($r_i < 0$, $A_{ij} < 0$) → extinction! $\implies$ **correlation**

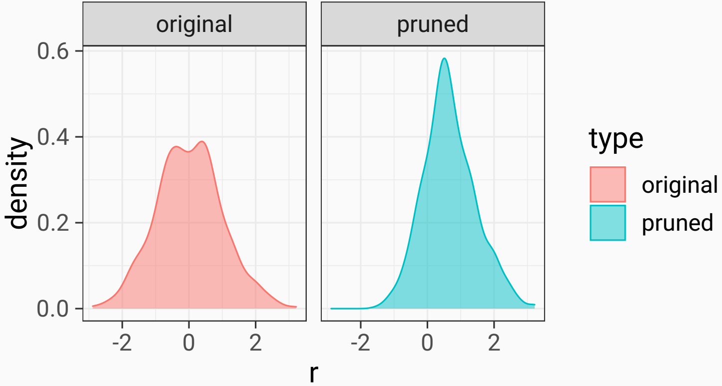


Figure 6 – Growth rates distribution before and after the dynamics has reached equilibrium, for a starting pool of $n = 1000$ species, with $k = 485$ species surviving.

Conclusions Applications and 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**)

Future work

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

In conclusion:

- 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 $= 0$

- $\mathcal{P}(k|n) = Bin(n, \frac{1}{2})$
- No effect due to network

Mean $\neq 0$

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

Backup slides

$\mathcal{P}(k|n)$ analytical computations Mean $= 0$

- $r_i \sim \mathcal{N}(\gamma, 1) \implies P(\mathbf{r}) = \frac{1}{\sqrt{(2\pi)^n}} \exp\left(-\sum_{i=1}^n \frac{(r_i-\gamma)^2}{2}\right) =$
  $\frac{1}{\sqrt{(2\pi)^n}} \exp\left(-\frac{1}{2}\left\|\mathbf{r}^{(s)} - \gamma \mathbf{1}_k\right\|^2 - \frac{1}{2}\left\|\mathbf{r}^{(n)} - \gamma \mathbf{1}_{n-k}\right\|^2\right)$
- **Def:** $\mathbf{z} = \mathbf{r}^{(n)} + A^{(ns)}\mathbf{x}$ for $n-k$ non-surviving species, $A^{(s)}\mathbf{x} = -\mathbf{r}^{(s)}$ for k surviving ones.
- Combining them, joint pdf is $f(\mathbf{x}, \mathbf{z} \mid A) =$
  $\frac{|\det \Lambda|}{(2\pi)^{n/2}} \exp\left(-\frac{1}{2}\left\|A^{(s)}\mathbf{x} + \gamma \mathbf{1}_k\right\|^2 - \frac{1}{2}\left\|\mathbf{z} - A^{(ns)}\mathbf{x} - \gamma \mathbf{1}_{n-k}\right\|^2\right)$
- with $\Lambda =$ Jacobian matrix of change of base $\mathbf{r} \longrightarrow (\mathbf{x}, \mathbf{z})$. Note that $|\det \Lambda| = |\det A^{(s)}|$
- Change of variables: $\left\|A^{(s)}\mathbf{x} + \gamma \mathbf{1}_k\right\|^2 = (\mathbf{x} - \boldsymbol{\xi})^T G (\mathbf{x} - \boldsymbol{\xi})$, with $\boldsymbol{\xi} = -\gamma \left(A^{(s)}\right)^{-1} \mathbf{1}_k$ and $G = \left(A^{(s)}\right)^T A^{(s)}$
- set that $\mathbf{x} > 0$ and $\mathbf{z} < 0$ (feasibility)

$$\mathcal{P}\left(\{S\}_k \mid A\right) \equiv \int d^k\mathbf{x} \left(\prod_{i=1}^{k} \Theta\left(x_i\right)\right) \int d^{n-k}\mathbf{z} \left(\prod_{j=k+1}^{n} \Theta\left(-z_j\right)\right) f(\mathbf{x}, \mathbf{z} \mid A) \tag{8}$$

$\mathcal{P}(k|n)$ analytical computations Mean $\neq 0$ - 1

- $A = (\alpha - \mu)I_n + \mathbf{1}_n \mathbf{1}_n^T$
- $\boldsymbol{\xi} = -\gamma \left(A^{(s)}\right)^{-1} \mathbf{1}_k = \xi^{(k)} \mathbf{1}_k = -\frac{\gamma}{\alpha + (k-1)\mu} \mathbf{1}_k$
- $G = \left(A^{(s)}\right)^T A^{(s)} = (\alpha - \mu)^2 I_k + \left[k\mu^2 + 2\mu(\alpha - \mu)\right] \mathbf{1}_k \mathbf{1}_k^T$
- change of variables $x_i' = x_i - \xi^{(k)}$ in (8)

$$\mathcal{P}\left(\{S\}_k \mid n\right) = \frac{\left|\det A^{(s)}\right|}{(2\pi)^{n/2}} \int d^k \mathbf{x} \prod_{i=1}^{k} \Theta\left(x_i + \xi^{(k)}\right) e^{-\frac{1}{2}\mathbf{x}^T G \mathbf{x}} \times$$
$$\times \int d^{n-k}\mathbf{z} \prod_{j=k+1}^{n} \Theta\left(-z_j\right) e^{-\frac{1}{2}\left\|\mathbf{z} - \left[\gamma + k\mu\xi^{(k)} + \mu\left(\mathbf{1}_k^T \mathbf{x}\right)\right]\mathbf{1}_{n-k}\right\|^2} \quad (9)$$

- change of variables: $z'_j = z_j - \gamma - k\mu\xi^{(k)}$
- $|\det A^{(s)}| = |\alpha - \mu|^{k-1}|\alpha + (k-1)\mu|$
- call all the exponent $g(\mathbf{x}, \mathbf{z})$

$$\mathcal{P}\left(\{S\}_k \mid n\right) = \frac{|\alpha - \mu|^{k-1}|\alpha + (k-1)\mu|}{(2\pi)^{n/2}} \int d^k\mathbf{x} \prod_{i=1}^{k} \Theta\left(x_i + \xi^{(k)}\right) \times$$
$$\times \int d^{n-k}\mathbf{z} \prod_{j=k+1}^{n} \Theta\left(-z_j - \gamma - k\mu\xi^{(k)}\right) e^{g(\mathbf{x},\mathbf{z})} \quad (10)$$

- apply **Hubbard-Stratonovich** transformation on g

$$e^{-bd^2/c^2 \pm de/c} = \frac{c}{2\pi} \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} e^{-\left(by^2 + ey + idw \pm icwy\right)} dw$$

$$\mathcal{P}\left(\{S\}_k \mid n\right) = \frac{|\alpha-\mu|^{k-1}|\alpha+(k-1)\mu|}{(2\pi)^{n/2+1}|\mu|}\int_{-\infty}^{\infty} dy \times$$

$$\times \int_{-\infty}^{\infty} e^{-\frac{1}{2}\left[n+2\left(\frac{\alpha}{\mu}-1\right)\right]y^2+i\frac{yw}{\mu\mu}} dw \int d^k\mathbf{x} \prod_{i=1}^{k} \Theta\left(x_i+\xi^{(k)}\right) \times$$

$$\times \int d^{n-k}\mathbf{z} \prod_{j=k+1}^{n} \Theta\left(-z_j-\gamma-k\mu\xi^{(k)}\right) e^{-\frac{1}{2}(\alpha-\mu)^2\mathbf{x}^T\mathbf{x}-i\left(\mathbf{1}_k^T\mathbf{x}\right)w} e^{-\frac{1}{2}\mathbf{z}^T\mathbf{z}-\left(\mathbf{1}_{n-k}^T\mathbf{z}\right)y} \tag{11}$$

- complete the squares + cumulative distribution function of $\mathcal{N}(0,1)$ $\Phi(x) = \frac{1}{2}\left[1+\mathrm{erf}\left(\frac{x}{\sqrt{2}}\right)\right]$

$$\mathcal{P}\left(\{S\}_k \mid n\right) = \frac{1}{2\pi}\left|k+\frac{\alpha}{\mu}-1\right|\int_{-\infty}^{\infty} dy \times$$

$$\times \int_{-\infty}^{\infty} e^{-\frac{1}{2}\left[k+2\left(\frac{\alpha}{\mu}-1\right)\right]y^2+i\left|\frac{\alpha}{\mu}-1\right|yw-\frac{1}{2}kw^2} dw \times$$

$$\times \left[1-\Phi\left(iw-|\alpha-\mu|\xi^{(k)}\right)\right]^k \left[\Phi\left(y-\gamma-k\mu\xi^{(k)}\right)\right]^{n-k} \tag{12}$$

$\mathcal{P}(k|n)$ analytical computations Mean $\neq 0$ - 4

- Note that $\gamma + k\mu\xi^{(k)} = \gamma\left(1 - \frac{k\mu}{\alpha+(k-1)\mu}\right) = \frac{\gamma(\alpha-\mu)}{\alpha+(k-1)\mu}$
- Define $s := \frac{\alpha}{\mu} - 1$ ($s > 0$ for LDS) and $v := \frac{\gamma(\alpha-\mu)}{\alpha-\mu+k\mu} = \frac{\gamma s}{k+s}$
- Then, given that $\alpha < \mu$, it holds that $|\alpha - \mu|\xi^{(k)} = -\frac{\gamma|\alpha-\mu|}{\alpha+(k-1)\mu} = v$

$$\mathcal{P}\left(\{S\}_k \mid n\right) = \frac{k+s}{2\pi}\int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} e^{-\frac{1}{2}(k+2s)y^2 + isyw - \frac{1}{2}kw^2} \times \\ \times \left[1 - \Phi(iw - v)\right]^k \left[\Phi(y - v)\right]^{n-k} dw \quad (13)$$

- (13) is a complex path integral, move integration on $\Gamma = \{w' \in \mathbb{C} | w' = iw + x_0\}$ with $x_0 \to 0$

$$\mathcal{P}\left(\{S\}_k \mid n\right) = \frac{k+s}{2\pi i}\int_{-\infty}^{\infty} dy \int_{\Gamma} e^{-\frac{1}{2}(k+2s)y^2 + syw - \frac{1}{2}kw^2} \times \\ \times \left[1 - \Phi(w - v)\right]^k \left[\Phi(y - v)\right]^{n-k} dw \quad (14)$$

- double integral of (13), (14) can be estimated numerically with FFT

$\mathcal{P}(k|n)$ analytical computations Mean $\neq 0$ - 5

- Probability of coexistence is $\mathcal{P}(k|n) = \binom{n}{k}\mathcal{P}\left(\{S\}_k \mid n\right)$, for $n \to \infty$ can be approximated with **saddle point** technique
- Defining $q = k/n$, grouping the y, w, q dependent terms in $\hat{h}(y, w; q) = \frac{q}{2}\left(y^2 - w^2\right) - q\log[1 - \Phi(w - v)] - (1 - q)\log\Phi(y - v)$, equation (14) becomes:

$$\mathcal{P}\left(\{S\}_k \mid n\right) = \frac{k + s}{2\pi i}\int_{-\infty}^{\infty} dy \int_{\Gamma} e^{-sy^2 + syw} e^{-n\hat{h}(y,w;q,v)} dw \tag{15}$$

- set $\mu = \hat{\mu}/n$ to have scaling in n
- set $s = n\alpha/\hat{\mu} - 1 = nu - 1$
- call $\boldsymbol{\sigma} = (q, u, v)$ and $h(y, w; \boldsymbol{\sigma}) = \hat{h}(y, w; q) + uy^2 - uyw$

$$\mathcal{P}\left(\{S\}_k \mid n\right) = \frac{k + nu - 1}{2\pi i}\int_{-\infty}^{\infty} dy \int_{\Gamma} e^{y^2 - yw} e^{-nh(y,w;\boldsymbol{\sigma})} dw \tag{16}$$

$\mathcal{P}(k|n)$ analytical computations Mean $\neq 0$ - 6

- $e^{-nh(y,w:\boldsymbol{\sigma})}$ is very peaked around global minimum of the real part of $h(y,w;\boldsymbol{\sigma}) \implies$ approximate the exponent up to second order
- find critical point by setting $dh/dy = 0$, $dh/dw = 0$
- compute discriminant of second derivative matrix, we find it is indeed a saddle point $\implies$ approximate $\mathcal{P}(k|n)$
- add also **Stirling** approximation for binomial coefficient:

$$\binom{n}{k} = \binom{n}{qn} \approx \frac{\exp(-n[q\log q + (1-q)\log(1-q)])}{\sqrt{2\pi nq(1-q)}}$$

$$P(k \mid n) = \frac{n(q+u)-1}{\sqrt{2\pi nq(1-q)K(\sigma,n)}} e^{nF(\sigma)+G(\sigma)} \tag{17}$$

With:

$$\begin{aligned} K(\boldsymbol{\sigma},n) :=& (nu-1)^2 + n^2\left[-q + (uy^\star + qw^\star)\left(v + \frac{uy^\star}{q}\right)\right] \\ &\times \left[\frac{2}{n} - 2u - q - (2uy^\star + qy^\star - uw^\star)\left(-v + \frac{y^\star - u\left(w^\star - 2y^\star\right)}{1-q}\right)\right] \end{aligned} \tag{18}$$

$$\begin{aligned} F(\boldsymbol{\sigma}) :=& \frac{q}{2}\left(w^{\star 2} - y^{\star 2}\right) + (1-q)\log\left[\Phi\left(y^\star - v\right)\right] + q\log\left[1 - \Phi\left(w^\star - v\right)\right] \\ &- uy^{\star 2} + uy^\star w^\star - q\log q - (1-q)\log(1-q) \end{aligned} \tag{19}$$

$$G(\boldsymbol{\sigma}) := y^\star\left(y^\star - w^\star\right) \tag{20}$$

$$v = \frac{\gamma(\alpha-\mu)}{\alpha-\mu+k\mu}\cdot\frac{\mu}{\mu} = \frac{\gamma(nu-1)}{k+nu-1}\cdot\frac{n}{n} \xrightarrow{n\gg 1} \frac{\gamma u}{q+u}$$

$$\begin{aligned}\frac{\partial F}{\partial q} = \frac{1}{2}\left(w^{\star 2}-y^{\star 2}\right) + q\left(w^{\star}w^{\star\prime}-y^{\star}y^{\star\prime}\right) - \log\Phi\left(y^{\star}-v\right) + \\ + \log\left(1-\Phi\left(w^{\star}-v\right)\right) + \left(w^{\star}-2y^{\star}\right)uy^{\star\prime} + \\ + uy^{\star}w^{\star\prime} + (1-q)\left(y^{\star\prime}-v^{\prime}\right)\frac{\Phi^{\prime}\left(y^{\star}-v\right)}{\Phi\left(y^{\star}-v\right)} - \\ - q\left(w^{\star\prime}-v^{\prime}\right)\frac{\Phi^{\prime}\left(w^{\star}-v\right)}{1-\Phi\left(w^{\star}-v\right)} + \log\frac{1-q}{q} \stackrel{!}{=} 0 \qquad (21)\end{aligned}$$

(A) From $dh/dy = 0$ it holds $\frac{\Phi'(y^\star-v)}{\Phi(y^\star-v)} = \frac{qy^\star+2uy^\star-uw^\star}{1-q} = \frac{e^{-(y^\star-v)^2/2}}{\sqrt{2\pi}\Phi(y^\star-v)}$

(B) From $dh/dw = 0$ it holds $\frac{\Phi'(w^\star-v)}{1-\Phi(w^\star-v)} = \frac{uy^\star+qw^\star}{q} = \frac{e^{-(w^\star-v)^2/2}}{\sqrt{2\pi}[1-\Phi(w^\star-v)]}$

Mode of $\mathcal{P}(k|n)$ Mean $\neq 0$ - 2

Simplifying (21):

$$\frac{\partial F}{\partial q} = \frac{1}{2}\left(w^{\star 2} - y^{\star 2}\right) - v\left(w^{\star} - y^{\star}\right) - \log\Phi\left(y^{\star} - v\right) + \\ + \log\left(1 - \Phi\left(w^{\star} - v\right)\right) + \log\frac{1-q}{q} \overset{!}{=} 0$$

From which we derive:

$$\left(1 - q^{\star}\right) e^{w^{\star 2}/2 - v w^{*}} \left[1 - \Phi\left(w^{\star} - v\right)\right] = q^{\star} e^{y^{*2}/2 - v y^{*}} \Phi\left(y^{\star} - v\right), \qquad (22)$$

where the functions $y^{\star}(\sigma), w^{\star}(\boldsymbol{\sigma})$ and $v(q)$ are evaluated at $q = q^{\star}$. On the other hand, given (A) and (B):

$$(1-q)e^{-(y^{\star}-v)^2/2} = \sqrt{2\pi}\Phi\left(y^{\star} - v\right)\left(q y^{\star} + 2 u y^{\star} - u w^{\star}\right),$$

$$q e^{-(w^{\star}-v)^2/2} = \sqrt{2\pi}\left[1 - \Phi\left(w^{\star} - v\right)\right]\left(u y^{\star} + q w^{\star}\right)$$

Substituting these expressions into equation (22) yields, after some algebra, this simple condition for the mode of the distribution, $q^{\star}$:

$$y^{\star}\left(q^{\star}, u, v\left(q^{\star}\right)\right) = w^{\star}\left(q^{\star}, u, v\left(q^{\star}\right)\right). \qquad (23)$$

Mode of $\mathcal{P}(k|n)$ Mean $\neq 0$ - 3

Meaning that (22) reduces to:

$$\log \frac{1-\Phi\left(y^\star - v\right)}{\Phi\left(y^\star - v\right)} = \log \frac{q^\star}{1-q^\star} \implies \Phi\left(y^\star - v\right) = 1 - q^\star \tag{24}$$

Inverting (24) and putting it into (A) we obtain

$$\sqrt{2}\gamma u + 2\left(q^\star + u\right)\operatorname{erf}^{-1}\left(1-2q^\star\right) = \frac{e^{-\left[erf^{-1}(1-2q^*)\right]^2}}{\sqrt{\pi}}$$

which is a transcendental equation that determines the mode of the distribution $q^\star = \frac{k^\star}{n}$ as a function of interaction strengths and growth rates.

Equivalently, with $\Phi^{-1}(q) = \sqrt{2}\operatorname{erf}^{-1}(2q-1)$, the transcendental condition for the mode can be expressed as

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

Mode of $\mathcal{P}(k|n)$ Mean $\neq 0$ - 4

By choosing $q^\star = \frac{1}{2}$, we get:

$$\frac{\alpha\gamma}{\hat{\mu}} = \frac{1}{\sqrt{2\pi}} \implies \frac{\alpha\gamma}{\mu} = \frac{n}{\sqrt{2\pi}} \tag{25}$$

In the limit of small interaction strengths ($\hat{\mu} \ll \alpha$) of the mean zero case ($\gamma = 0$), (25) reproduces the expected (binomial) behaviour:

$$\frac{k^\star}{n} \approx \frac{1}{2} - \frac{1}{2\pi}\frac{\hat{\mu}}{\alpha} + \frac{1}{4\pi}\left(\frac{\hat{\mu}}{\alpha}\right)^2,$$