An exchangeable model for (ecological) bipartite networks

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joint work with S. Ouadah (AgroParisTech), P. Latouche (université Paris Cité)

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WG on Risk, ESSEC, Mar. 2022

Bipartite networks

Bipartite networks describe the connections between two set of entities

- authors / publications,
- actors / movies,
- hosts / parasites,
- plants / pollinators,
- etc.

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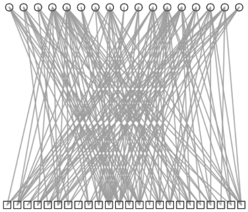


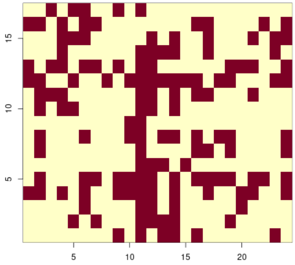
Example:

Top: Plants (○)

Bottom: Pollinators (□)

Zackenberg network from [OBEJ08,SROB16,CRR+18]:

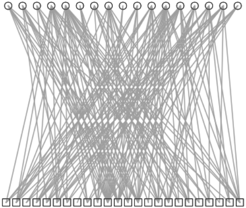
$$m = 17, \quad n = 24$$

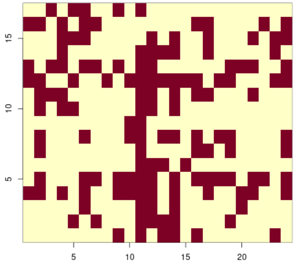


Species exchangeability

Aim. Describe the global organization ('topology') of the network to

- better understand the behavior of the ecosystem,
- or predict its response to a change





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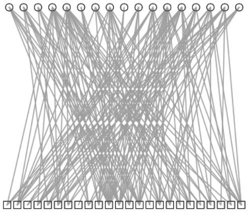

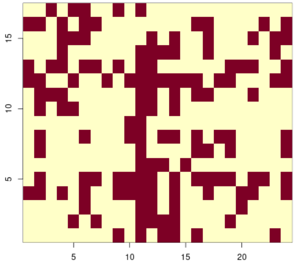

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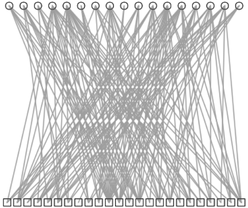

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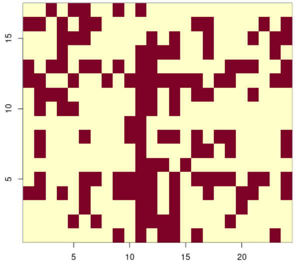

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- Species are not each considered *per se*.

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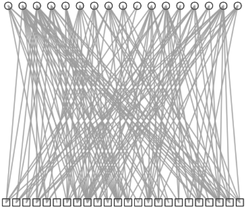

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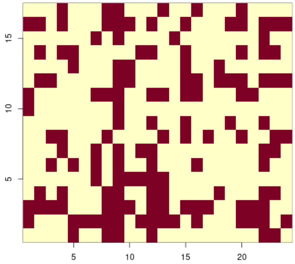

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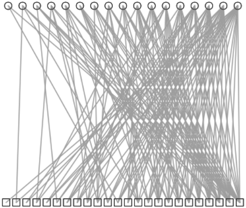

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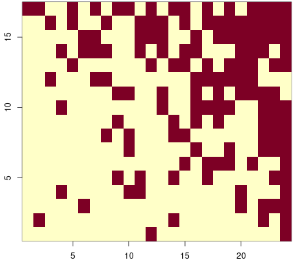

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Outline

Probabilistic formulation

Network. Can be seen either as

- a graph $\mathcal{G} = (\mathcal{V} = \text{set of vertices}, \mathcal{E} = \text{set of edges} \subset \mathcal{V} \times \mathcal{V})$, or
- an $m \times n$ adjacency matrix $Y = [Y_{ij}]$ where

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Probabilistic framework. The observed network is seen as a realization of a random graph ruled by some joint distribution $p(y)$, that is

$$p(y) = \mathbb{P}\{Y = y\} = \mathbb{P}\{Y_{11} = 1, Y_{12} = 0, \dots Y_{ij} = 1, \dots, Y_{mn} = 0\}$$

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Network analysis. Classical framework in statistical modelling:

- Questions of (ecological) interest have to be translated into
- Questions about the distribution p.

Row-column exchangeability (RCE)

Exchangeability assumption. Species exchangeability means

- Plants can be exchanged with plants, insects can be exchanged with insects,
- That is: for any permutation σ_R of the rows and any permutation σ_C of the columns:

$$\mathbb{P}(Y = y) = \mathbb{P}(Y = y_{\sigma_R,\sigma_C}).$$

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Aldous-Hoover representation. A random graph $Y \sim p$ is RCE iff there exist a determistic function f such that

$$Y = f(T, U_1, \dots U_m, V_1, \dots, V_n, W_{11}, \dots W_{mn})$$

$$\text{with} \left\{ \begin{array}{ll} T, & \text{(whole graph)} \\ U_1, \dots U_m, & \text{(rows)} \\ V_1, \dots, V_n, & \text{(columns)} \\ W_{11}, \dots W_{mn} & \text{(edges)} \end{array} \right\} \text{iid} \ \sim \mathcal{U}[0,1].$$

Bipartite w-graph

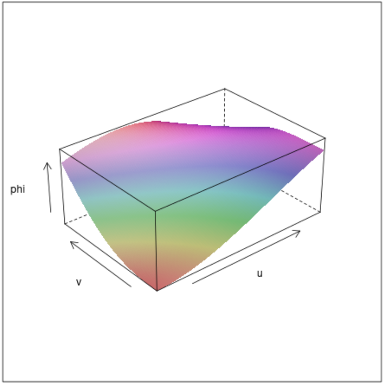
Model.

- Consider a 'graphon' function

$$\phi : [0,1] \times [0,1] \mapsto [0,1],$$

- draw $(U_1, \dots, U_m)$ iid $\sim \mathcal{U}[0,1]$,
- draw $(V_1, \dots, V_n)$ iid $\sim \mathcal{U}[0,1]$,
- draw $(Y_{11}, \dots, Y_{mn})$ independently:

$$\mathbb{P}\{Y_{ij} = 1\} = \phi(U_i, V_j).$$



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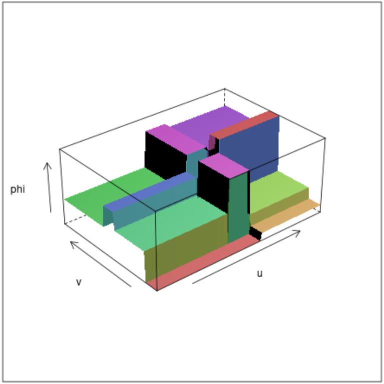
Latent block-model [GN05]. Block-wise constant function ϕ.



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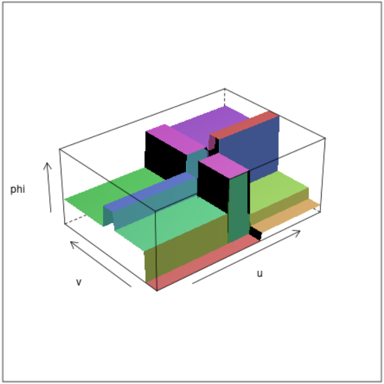

Latent block-model [GN05]. Block-wise constant function ϕ.

Dissociated models. No 'whole graph' random term T:

- Non-overlapping blocks of the adjacency matrix Y are independent.

Expected degree distribution model

A 'null' model. Product form w-graph:

$$\phi(u, v) = \rho\, f(u)\, g(v)$$

- $f : [0, 1] \mapsto \mathbb{R}^+$: row imbalance (generalist vs specialist plants),
- $g : [0, 1] \mapsto \mathbb{R}^+$: column imbalance (generalist vs specialist insects),
- $\rho \in [0, 1]$: network density[1].

[1] $\int f(u)\, \mathrm{d}u = 1, \quad \int g(v)\, \mathrm{d}v = 1, \quad \rho \leqslant 1/(\max(f)\max(g))$

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Expected degrees.

$$\begin{aligned} D_i^\circ &= \text{ degree of top node } i: & \mathbb{E}(D_i^\circ \mid U_i = u) &= n\,\rho\, f(u), \\ D_j^\square &= \text{ degree of bottom node } j: & \mathbb{E}(D_j^\square \mid V_j = v) &= m\,\rho\, g(v). \end{aligned}$$

→ Bipartite version of the expected degree distribution (EDD) model [CL02].

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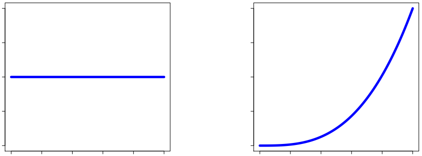
BEDD model

- Only individual effects matter: $f(U_i)$, $g(V_j)$.
- No specific interaction (U_i, V_j)

$g =$ $g =$



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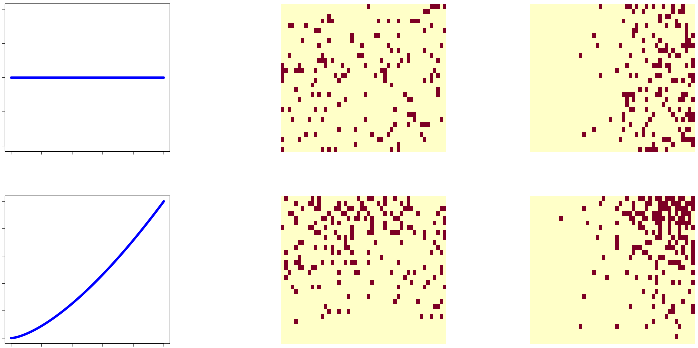


Outline

Bipartite network motifs

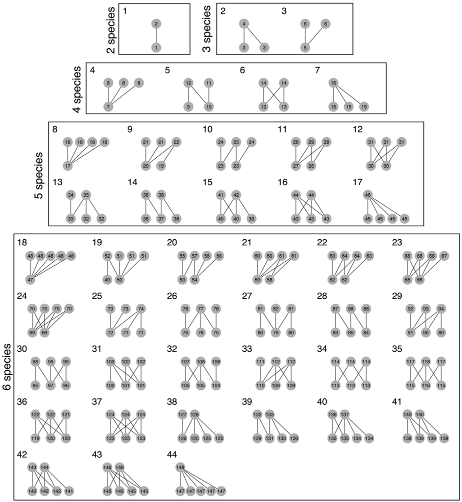
'Meso-scale' analysis. [SCB+19]

- Motifs ='building-blocks'
- between local (several nodes) and global (sub-graph)

Interest.

- Generic description of a network
- Enables network comparison
- Even when the nodes are different

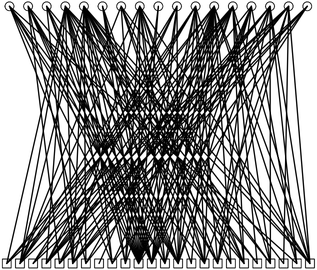
(+ 'species-role': see later?)



Existing tool. `bmotif` package [SSS+19]: counts motif occurrences

Example

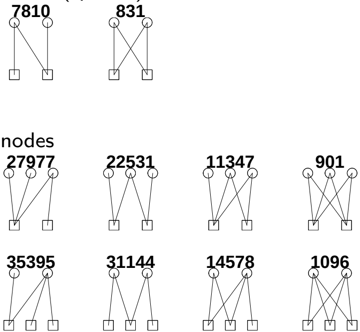
Zackenberg network.



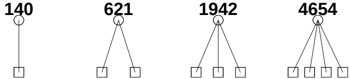
Motif counts.

4 nodes (species)

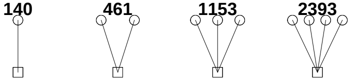
5 nodes



top 'stars' (plants)



bottom 'stars' (pollinators)



Counting motifs

Number of positions.

- Choose p nodes among m
- Choose q nodes among n
- Try all *automorphisms*

$$c_s := \binom{m}{p} \times \binom{n}{q} \times r_s$$

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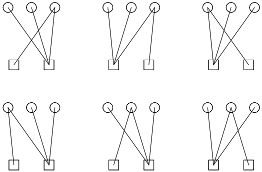

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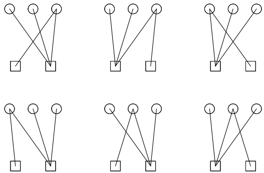


Motif count. Try all positions $\alpha = 1, \dots c_s$, define

$$Y_{s\alpha} = 1 \text{ if match}, \qquad 0 \text{ otherwise},$$

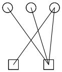
then count the number of matches:

$$N_s = \sum_\alpha Y_{s\alpha}$$

$\rightarrow$ Motif frequency: $F_s := N_s / c_s$

Motif probability

Occurrence probability $\overline{\phi}_s = \mathbb{P}\{Y_{s\alpha} = 1\}$. Under the BEDD model:

$\overline{\phi}_s := \mathbb{P}_{BEDD} \Big($  $\Big) = \frac{\quad}{\quad}$

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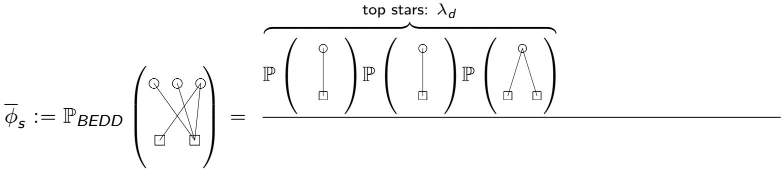

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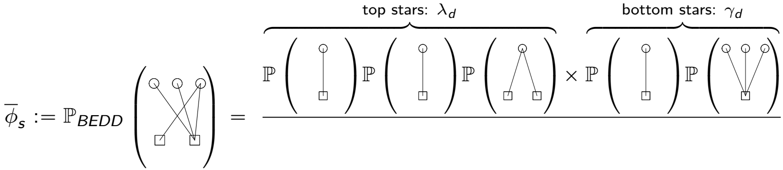

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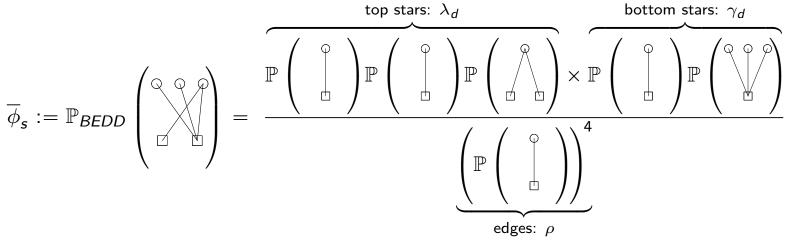

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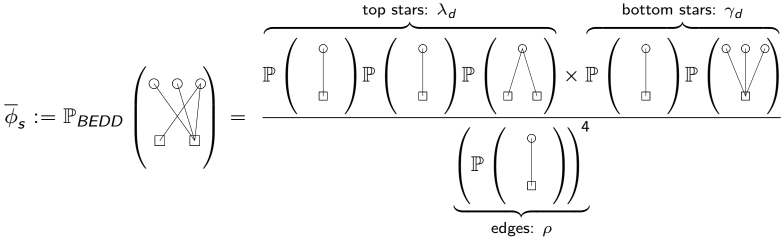

$$= \frac{\rho^2\lambda_2\rho\gamma_3}{\rho^4} \qquad = \frac{\lambda_2\gamma_3}{\rho}$$

where $\lambda_d = \rho^d \int f^d(u)\, \mathrm{d}u, \qquad \gamma_d = \rho^d \int g^d(v)\, \mathrm{d}v$

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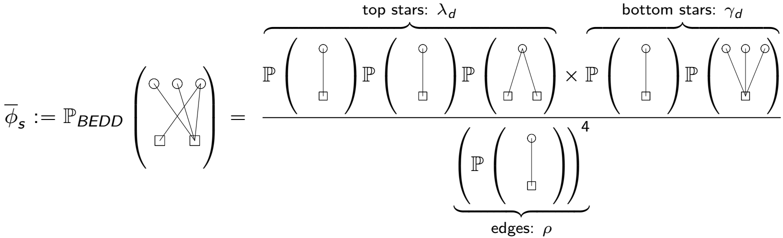

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Estimated probability.

$$\overline{\phi}_s := \frac{\lambda_2 \gamma_3}{\rho} \qquad \rightarrow \qquad \overline{F}_s := \frac{\Lambda_2 \Gamma_3}{R}$$

where Λ_2, Γ_3, R = empirical frequencies of top stars, bottom stars and edges.

Distribution of the count

Moments:

- Mean: $\mathbb{E}_{BEDD}(N_s) = c_s \times \overline{\phi}_s$

- Variance: Requires to evaluate $\mathbb{E}_{BEDD}(N_s^2) = \mathbb{E}_{BEDD}\left(\sum_\alpha Y_{s\alpha}\right)^2$

  $\rightarrow$ Need to account for overlap between positions (*super-motifs*: [PDK$^+$08])

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Asymptotic normality for non-star motifs [OLR22]. Under BEDD (and sparsity conditions):

$$(F_s - \overline{F}_s) \Big/ \sqrt{\widehat{\mathbb{V}}(F_s)} \quad \xrightarrow{m,n\to\infty} \quad \mathcal{N}(0,1)$$

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Proof:

- decompose

$$F_s - \overline{F}_s = \underbrace{(F_s - \phi_s)}_{\text{random fluctuations}} + \underbrace{(\phi_s - \overline{\phi}_s)}_{\text{null under BEDD}} + \underbrace{(\overline{\phi}_s - \overline{F}_s)}_{\text{estimation error }\to 0},$$

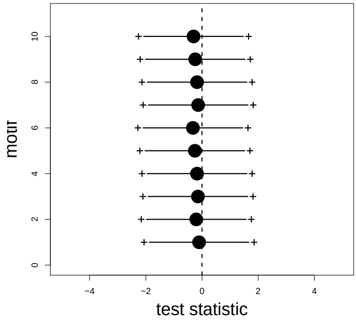
- construct a counting martingale [GL17] for $(F_s - \phi_s)$ + consistent estimate of $\widehat{\mathbb{V}}(F_s)$.

Goodness-of-fit (GOF) of the BEDD model

Raw test statistic:

$$T_s = \frac{N_s - \widehat{\mathbb{E}} N_s}{\sqrt{\widehat{\mathbb{V}} N_s}}$$

Zackenberg network.



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$$T'_s = \frac{N_s - (\widehat{\mathbb{E}} N_s - \widehat{\mathbb{B}}(\widehat{\mathbb{E}} N_s))}{\sqrt{\widehat{\mathbb{V}}(N_s - \widehat{\mathbb{E}} N_s)}}$$

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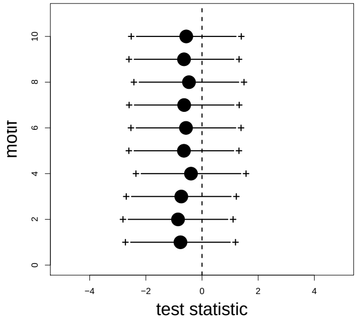

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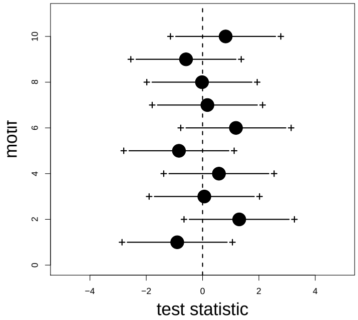
$$T'_s = \frac{N_s - (\widehat{\mathbb{E}} N_s - \widehat{\mathbb{B}}(\widehat{\mathbb{E}} N_s))}{\sqrt{\widehat{\mathbb{V}}(N_s - \widehat{\mathbb{E}} N_s)}}$$

Cholevski [2] transformation: accounts for the correlation between the counts

$$\Sigma_{s,s'} = \mathbb{C}\text{ov}(N_s - \widehat{\mathbb{E}} N_s, N_{s'} - \widehat{\mathbb{E}} N_{s'})$$

$$T'' = \widehat{\Sigma}^{-1/2} \left[N_s - (\widehat{\mathbb{E}} N_s - \widehat{\mathbb{B}}(\widehat{\mathbb{E}} N_s)) \right]$$

Zackenberg network.



[2] $\Sigma = P \Lambda P^\intercal$, $\Sigma = P \Lambda^{-1/2} P^\intercal$

Network comparison

Same degree imbalance for top nodes.

- Consider two networks $G^A \sim BEDD(\rho^A, f^A, g^A)$ and $G^B \sim BEDD(\rho^B, f^B, g^B)$ and

$$H_0 = \{f^A = f^B\}$$

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- Under H_0 [OLR22]

$$W_s = \frac{\left(F_s^A - \widehat{\mathbb{E}}_0(F_s^A)\right) - \left(F_s^B - \widehat{\mathbb{E}}_0(F_s^B)\right)}{\sqrt{\widehat{\mathbb{V}}_0(F_s^A) + \widehat{\mathbb{V}}_0(F_s^B)}} \xrightarrow{D} \mathcal{N}(0,1)$$

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Plant-pollinator vs Plant-seed disperser.

- $G^A = 546 \times 1044$ plant-pollinator network, $G^B = 207 \times 110$ plant-seed disperser network
- Is there the same degree imbalance between plants in the two networks ?

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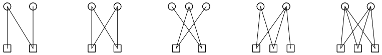
Results.



W'_s : -2.71 -1.90 -1.76 -1.34 -0.96

Outline

U-statistics

U-statistics.

- Consider a symmetric function (*kernel*) $h : \mathbb{R}^k \mapsto \mathbb{R}$:

$$h(y_1, \dots y_k) = h(y_{\sigma(1)}, \dots y_{\sigma(k)}) \qquad \text{for any permutation } \sigma$$

- Consider $(Y_1, \dots Y_n)$,
- Define

$$U_n = \binom{n}{k}^{-1} \sum_{1 \leqslant i_1 < \dots < i_k \leqslant n} h(Y_{i_1}, \dots Y_{i_k}),$$

- Asymptotic normality conditions for U_n when the $(Y_1, \dots Y_n)$ are iid [Hoe48] or exchangeable [NS63].

U-statistics for bipartite networks

U-statistics of order 2×2.

- Consider row-column symmetric kernel $h : \mathbb{R}^4 \mapsto \mathbb{R}$:

$$h(y_{11}, y_{12}, y_{21}, y_{22}) = h(y_{21}, y_{22}, y_{11}, y_{12}) = h(y_{12}, y_{11}, y_{22}, y_{21}),$$

- Consider $Y = [Y_{ij}]_{1 \leqslant i \leqslant m, 1 \leqslant j \leqslant n}$,
- Define

$$U_{m,n} = \binom{m}{2}^{-1} \binom{n}{2}^{-1} \sum_{1 \leqslant i_1 < i_2 \leqslant m} \sum_{1 \leqslant j_1 < j_2 \leqslant n} h(Y_{i_1 j_1}, Y_{i_1 j_2}, Y_{i_2 j_1}, Y_{i_2 j_2}).$$

- Tam Le Minh's PhD [LM21]: asymptotic normality of $U_{m,n}$ when Y is RCE dissociated[3], but not only with a product-form (i.e. includes *w*-graph).

[3] plus technical conditions

Weighted BEDD model

Weighted networks.

- Interactions Y_{ij} may be valued ('weighted').
- Example: Y_{ij} = number of visits from insect j to plant i within a given period of time.

[4] $\int f(u) \, \mathrm{d}u = 1, \quad \int g(v) \, \mathrm{d}v = 1$

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Weighted BEDD model: Poisson BEDD.

- $f : [0,1] \mapsto \mathbb{R}^+$: row imbalance (generalists vs specialists),
- $g : [0,1] \mapsto \mathbb{R}^+$: column imbalance (generalists vs specialists),
- $\lambda \in \mathbb{R}^+$: mean interaction intensity[4],

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- $\lambda \in \mathbb{R}^+$: mean interaction intensity[4],
- Draw

$$(U_1, \dots, U_m) \text{ iid} \sim \mathcal{U}[0,1], \qquad (V_1, \dots, V_n) \text{ iid} \sim \mathcal{U}[0,1],$$

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$$(U_1, \dots, U_m) \text{ iid} \sim \mathcal{U}[0,1], \qquad (V_1, \dots, V_n) \text{ iid} \sim \mathcal{U}[0,1],$$
- Draw $(Y_{11}, \dots, Y_{mn})$ independently conditionally on $(U_1, \dots, U_m), (V_1, \dots, V_n)$,
$$Y_{ij} \mid U_i, V_j \sim \mathcal{P}(\lambda f(U_i) g(V_j)).$$

[4] $\int f(u)\,\mathrm{d}u = 1, \quad \int g(v)\,\mathrm{d}v = 1$

Some kernels

Mean intensity.

$$h_1 = \frac{1}{4}(Y_{11} + Y_{12} + Y_{21} + Y_{22}) \qquad \Rightarrow \qquad \mathbb{E}_{PBEDD} h_1 = \lambda,$$

$$h_3 = \frac{1}{2}(Y_{11} Y_{22} + Y_{21} Y_{12}) \qquad \Rightarrow \qquad \mathbb{E}_{PBEDD} h_3 = \lambda^2.$$

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Row imbalance. Denoting $F_2 = \int f^2(u)\, \mathrm{d}u$,

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- Test $H_0 = \{F_2 = 1\}$ = 'no imbalance among rows'
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Over-dispersion (wrt Poisson):

$$h_4 = \frac{1}{4}(Y_{11}^2 + Y_{12}^2 + Y_{21}^2 + Y_{22}^2) \quad \Rightarrow \quad \mathbb{E}_{PBEDD} h_4 = \lambda + \lambda^2.$$

- Test $H_0 = \{\mathbb{V}(Y_{ij} \mid U_i, V_j) = \mathbb{E}(Y_{ij} \mid U_i, V_j)\}$ = 'no over-dispersion'

Variance degeneracy

Technical conditions in [LM21] impose that $\mathbb{V} U_{m,n}$ is controlled by the 'leading' covariances

$$\mathbb{C}\text{ov}(h(Y_{11}, Y_{12}, Y_{21}, Y_{22}), h(Y_{13}, Y_{14}, Y_{33}, Y_{33})) \qquad \text{(one common row)}$$

$$\text{and} \quad \mathbb{C}\text{ov}(h(Y_{11}, Y_{12}, Y_{21}, Y_{22}), h(Y_{31}, Y_{33}, Y_{41}, Y_{43})) \qquad \text{(one common column)}$$

(if not: wrong scaling for the TCL).

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(if not: wrong scaling for the TCL).

Not only a technical issue. To test $H_0 = \{F_2 = 1\}$ ('no imbalance among rows'), natural kernel:

$$h = h_2 - h_3 = \frac{1}{2}(Y_{11}Y_{12} + Y_{21}Y_{22} - Y_{11}Y_{22} - Y_{21}Y_{12})$$

$$\Rightarrow \quad \mathbb{E}h = \lambda^2(F_2 - 1) \overset{H_0}{=} 0$$

but then, both leading covariances are 0...

Outline

Future works

Summary.

- RCE models provide a generic framework for the analysis of bipartite networks
- The product-form BEDD model is non-naive null model
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- Unclear connection between motif and alternative H_1
- Species role in networks can be characterized by their precise position in each motif
- 'Phenologic' motif: time labeled motifs to investigate mutualistic interactions along time

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- Unclear connection between motif and alternative H_1
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- 'Phenologic' motif: time labeled motifs to investigate mutualistic interactions along time

Future for network U-statistics.

- Better understand variance degeneracy: define a relevant Hoeffding decomposition?
- Motif counts are actually U-statistics: easier way to prove joint normality?

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Overlapping motifs

$\lvert\alpha^t \cap \beta^t\rvert$	0	0	1	1
$\lvert\alpha^b \cap \beta^b\rvert$	1	2	0	1

Power study: goodness-of-fit

Alternative: 2-block stochastic block model

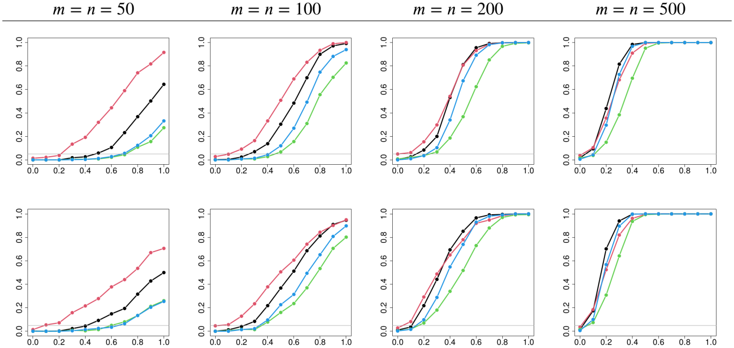

Figure 5: Empirical power of the goodness-of-fit tests, averaged over $S = 500$ simulations. Top: scenario I (easy: $\gamma_{\max} = 0.95$); bottom: scenario II (hard: $\gamma_{\max} = 0.5$). From left to right: $m = n = 50, 100, 200, 500$. Color = motif: black=5, red=6, green=10, blue=15.

Power study: network comparison

Alternative: $f^A(u) = 2u, \quad f^* \equiv 1, \quad f^B = (1-\alpha)f^A + \alpha f^*$

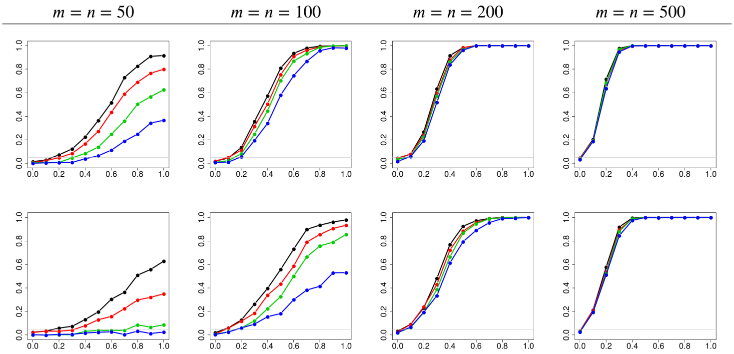

Figure 6: Empirical power of the network comparison test for $H_0 = \{g^A = g^B\}$, averaged over $S = 500$ simulations. Top: scenario I (easy); bottom: scenario II (hard). From left to right: $m = n = 50, 100, 200, 500$. Color = motif: same legend as Figure 5.