Motifs and bipartite networks

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Outline

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Bipartite network

Two types of actors.

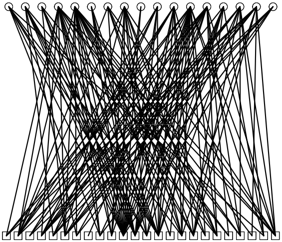
- Mutualistic: plant-pollinator
- Antagonistic: host-parasite

Topological analysis:
understanding the network organisation

Local: node or edge properties (degree, betweenness)

Global: density, connected components, nestedness

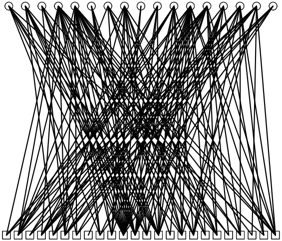
Zackenberg network: [SROB16]



Bipartite network: notations

Species.

- $i = 1, \dots m$ insects = rows = bottom nodes
- $j = 1, \dots n$ plants = columns = top nodes



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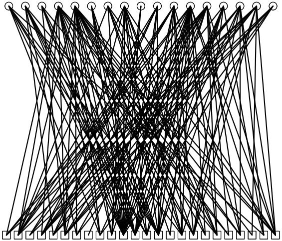

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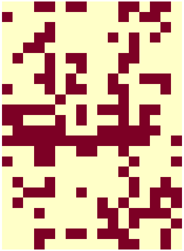


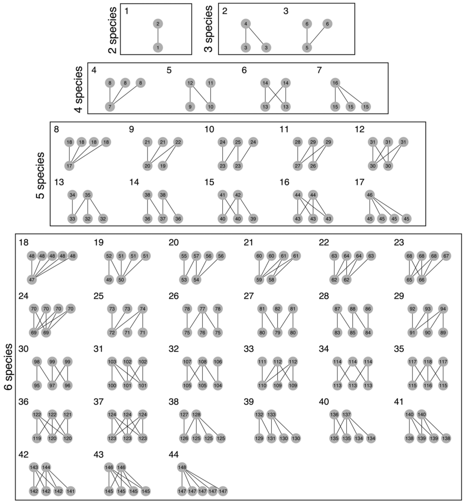
Interactions.

- $A_{ij} = 1$ if insect i interacts with plant j, 0 otherwise
$$A_{ij} = 1 \quad \Leftrightarrow \quad i \sim j$$
- adjacency matrix : $m \times n$
$$A = [A_{ij}]_{1 \leq i \leq m, 1 \leq j \leq n}$$

Bipartite motifs

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

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



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

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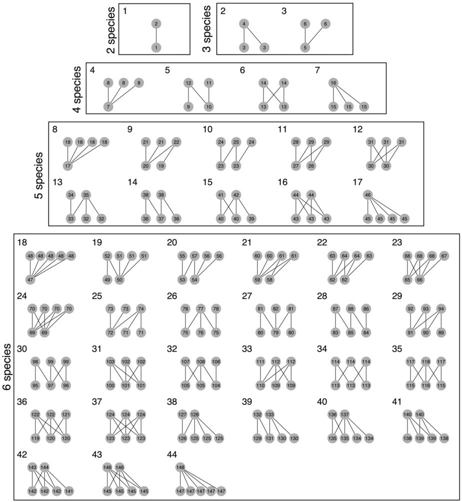

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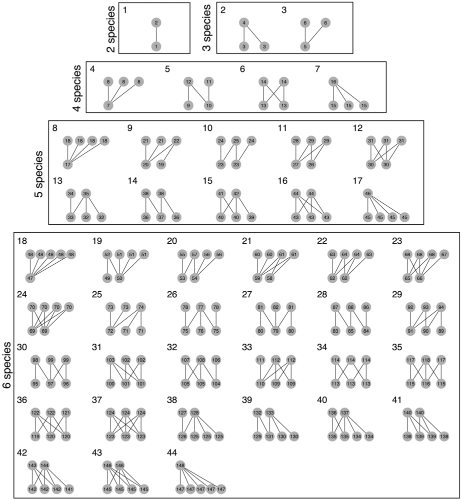
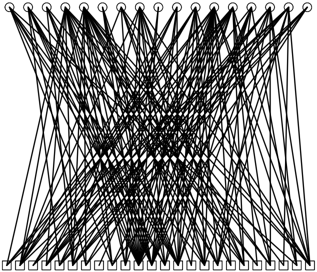
Existing tool. `bmotif` package [SSS+19]: counts motif occurrences



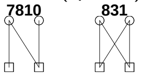
Example

Plant-pollinator network [SROB16]

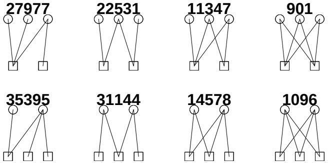


Motif counts.

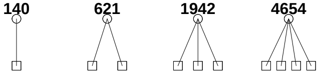
4 nodes (species)



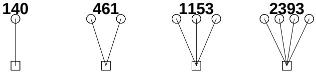
5 nodes



top 'stars' (plants)



bottom 'stars' (pollinators)



Outline

Need for a null model

Motif counts obviously depend on

- the size of the network: $n \times m$
- the density of the network
- the imbalance between bottom-node degrees (specialist vs generalist insects)
- the imbalance between top-node degrees (specialist vs generalist plants)

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Bipartite expected degree distribution (BEDD) model: (in words)

- Consider m insects ($i = 1, \dots m$):
  each plant i has a specific propensity to interact (degree of generalism)

- Consider n plants ($j = 1, \dots n$):
  each plant j has a specific propensity to interact (idem)

- The probability for insect i and plant j to interact is proportional to the product of their respective propensities.

BEDD model

Bipartite expected degree distribution (BEDD) model: (more formaly)

- $\rho =$ network density
- $g =$ top node degree imbalance ($\int g = 1$)
- $h =$ bottom node degree imbalance ($\int h = 1$)

$$\{U_i\}_{i=1,\dots m} \text{ iid } \sim \mathcal{U}[0,1] \qquad \{V_j\}_{j=1,\dots n} \text{ iid } \sim \mathcal{U}[0,1]$$

$$\mathbb{P}\{i \sim j \mid U_i, V_j\} = \rho \; g(U_i) \; h(V_j)$$

(Bipartite version of the EDD model [CL02])

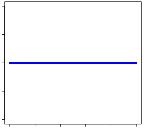
BEDD model

$$\mathbb{P}\{i \sim j \mid U_i, V_j\} = \rho\, g(U_i)\, h(V_j)$$

$$\mathbb{E}(D_i \mid U_i) = n\, \rho\, g(U_i)$$

$$\mathbb{E}(D_j \mid V_j) = m\, \rho\, g(V_i)$$

$h_0(v) =$



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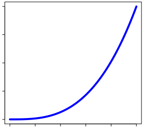

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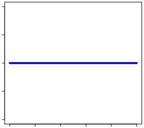

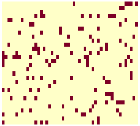

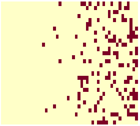

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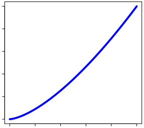

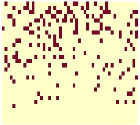

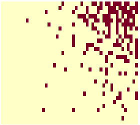

Properties of the BEDD model

Assumptions.

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- Graph-exchangeable model: insects and plants can be permuted simultaneously

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Sufficient statistics to fit BEDD:

- Insect degrees + plant degrees
- or, equivalently, star (single edge, top, bottom) frequencies

Outline

Counting motifs

Number of positions.

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

$$c_s := \left(\begin{array}{c} m \\ p \end{array} \right) \times \left(\begin{array}{c} n \\ q \end{array} \right) \times r_s$$

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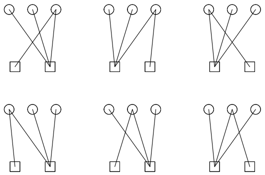

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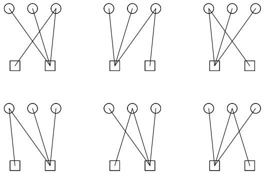


Motif count. Try all positions $\alpha = 1, \dots c_s$, define

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

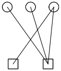
then count the number of matches:

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

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

Motif probability

Occurrence probability $\overline{\phi}_s = \mathbb{P}\{Y_{s\alpha} = 1\}$. Under the B-EDD model [OLR22]:

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

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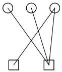
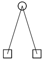
top stars

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

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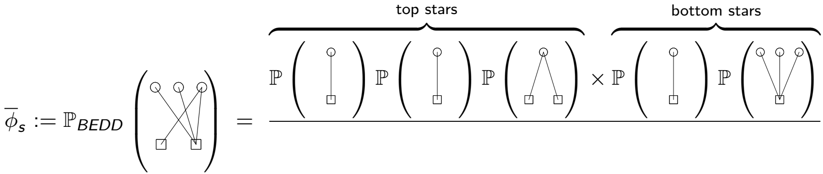

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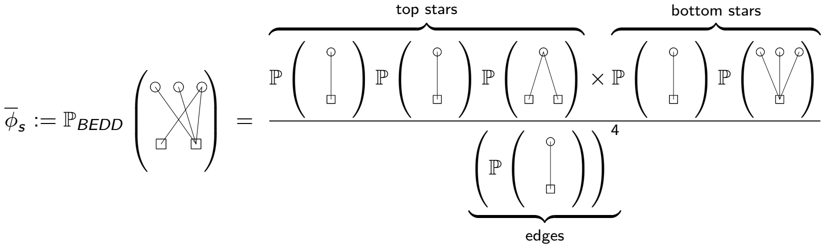

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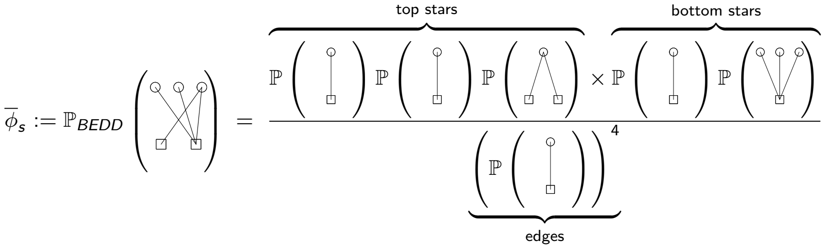

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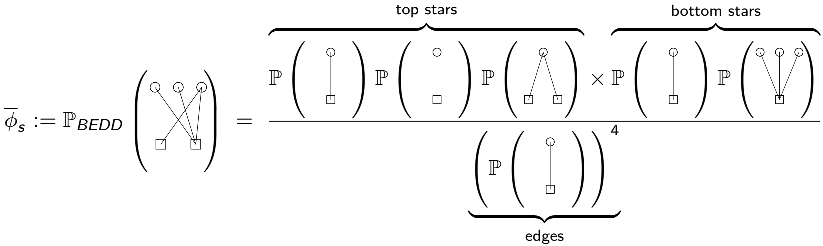

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Estimated probability.

$$\overline{\phi}_s := \frac{\phi_2 \phi_4}{\phi_1} \qquad \rightarrow \qquad \overline{F}_s := \frac{F_2 F_4}{F_1}$$

where F_1, F_2, F_4 = observed frequencies of edges, top stars and bottom stars.

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- Covariance: Same game to compute $\mathbb{C}\mathrm{ov}(N_s, N_{s'})$

Distribution of the count

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

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

Proof [OLR22]:

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

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Consequence. We know the expected behavior of motif counts under the BEDD model ($=$ 'null model').

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Aim. Test if the observed data arise from a given model.

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Example.

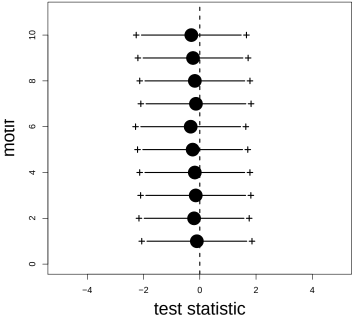
1. Data = observed plant-pollinator network
2. Statistic T = motif count N_s
3. Model = BEDD

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

Zackenberg network.

Raw statistic:

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



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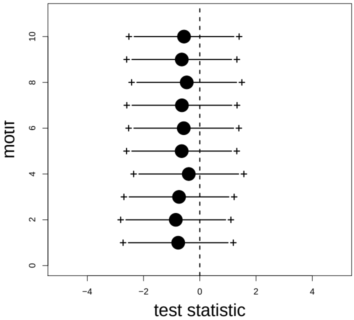

Raw statistic:

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

Corrected stat.: accounts for the estimation error in $\widehat{\mathbb{E}} N$

$$T_s' = \frac{N_s - (\widehat{\mathbb{E}} N_s - \widehat{\mathbb{B}}(\widehat{\mathbb{E}} N_s))}{\sqrt{\widehat{\mathbb{V}}(N_s - \widehat{\mathbb{E}} N_s)}}$$

Testing degree imbalance

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Statistical test.

- Assume $A \sim BEDD(\rho, g, h)$,
$$H_0 = \{h = 1\}$$
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Example. (only one significant difference)

plant-pollinator

s	5	6	10	15	16
W_s	-6.45 10^{-2}	9.96 10^{-1}	-6.63 10^{-2}	7.52 10^{-1}	2.43

seed dispersal

s	5	6	10	15	16
W_s	-2.14 10^{-1}	-2.14 10^{-1}	-2.93 10^{-1}	-2.95 10^{-1}	-3.56 10^{-1}

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- For motif s, evaluate $\widehat{\mathbb{E}}_{\widehat{\rho}^A, \widehat{g}^B, \widehat{g}^A}(N_s^A)$ and $\widehat{\mathbb{E}}_{\widehat{\rho}^B, \widehat{g}^A, \widehat{g}^B}(N_s^B)$ and compare
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with $\mathcal{N}(0,1)$

Example. (no significant difference)

s	5	6	10	15	16
F_s^A	$9.21\ 10^{-5}$	$1.00\ 10^{-5}$	$8.12\ 10^{-6}$	$3.32\ 10^{-7}$	$4.47\ 10^{-8}$
$\widehat{\mathbb{E}}_0 F_s^A$	$1.96\ 10^{-4}$	$3.75\ 10^{-5}$	$1.74\ 10^{-5}$	$4.25\ 10^{-6}$	$1.33\ 10^{-6}$
F_s^B	$5.13\ 10^{-4}$	$1.15\ 10^{-4}$	$5.07\ 10^{-5}$	$1.79\ 10^{-5}$	$5.96\ 10^{-6}$
$\widehat{\mathbb{E}}_0 F_s^B$	$2.66\ 10^{-4}$	$2.92\ 10^{-5}$	$2.85\ 10^{-5}$	$1.50\ 10^{-6}$	$1.69\ 10^{-7}$
$F_s^B - F_s^A$	$-4.21\ 10^{-4}$	$-1.05\ 10^{-4}$	$-4.26\ 10^{-5}$	$-1.76\ 10^{-5}$	$-5.91\ 10^{-6}$
$\widehat{\mathbb{E}}_0(F_s^B - F_s^A)$	$-6.96\ 10^{-5}$	$8.37\ 10^{-6}$	$-1.11\ 10^{-5}$	$2.75\ 10^{-6}$	$1.16\ 10^{-6}$
$\sqrt{\widehat{\mathbb{V}}_0(F_s^A) + \widehat{\mathbb{V}}_0(F_s^B)}$	$2.25\ 10^{-4}$	$7.24\ 10^{-5}$	$3.26\ 10^{-5}$	$1.59\ 10^{-5}$	$7.38\ 10^{-6}$
W_s	-1.56	-1.56	-0.97	-1.28	-0.96

Outline

Network embedding: Multivariate analysis

Analysing multiple networks. Principle

- 'Embed' each network into a convenient space (e.g. $\mathbb{R}^d$)
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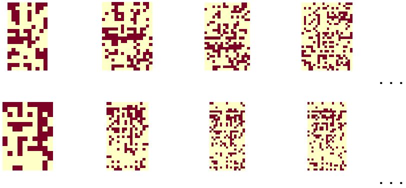
Zackenberg dataset. $K = 46$ networks

- 2 years
- 1 network observed every few days

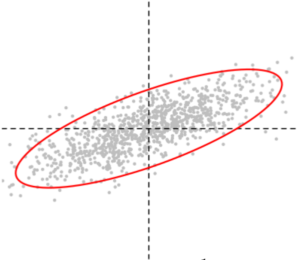


Choleski transform

Aim: 'Remove' correlation and variance heterogeneity

Covariance matrix (X_1, X_2):

$$\Sigma(X_1, X_2) = \left[\begin{array}{cc} \sigma_1^2 & \sigma_{12} \\ \sigma_{12} & \sigma_2^2 \end{array} \right]$$



Diagonalization: $\Sigma = P \Lambda P^{-1}$

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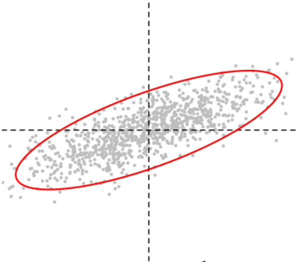

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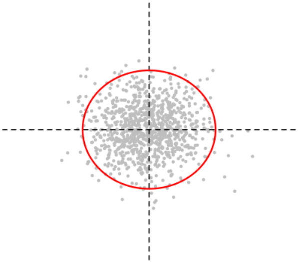
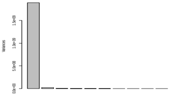
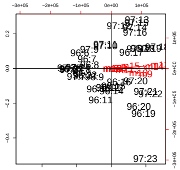
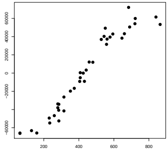
Choleski transform:

$$\begin{bmatrix} X_1' \\ X_2' \end{bmatrix} = \Sigma^{-1/2} \begin{bmatrix} X_1 \\ X_2 \end{bmatrix}$$

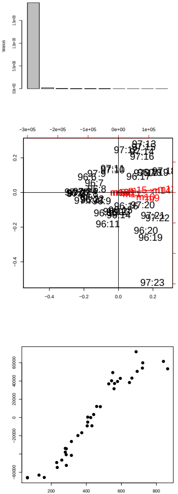
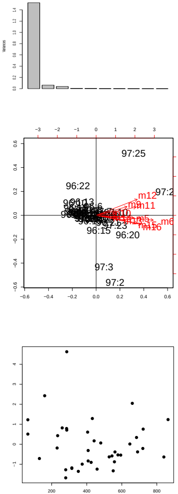


$$\Sigma(X_1', X_2') = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

Network embedding: Zackenberg's data [SROB16]

Raw counts			
			
			
			

Network embedding: Zackenberg's data [SROB16]

Raw counts	Corrected stat.		
			

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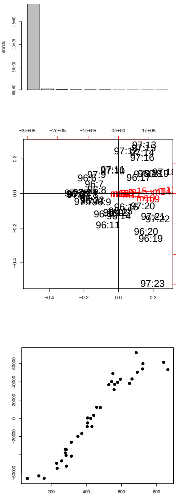
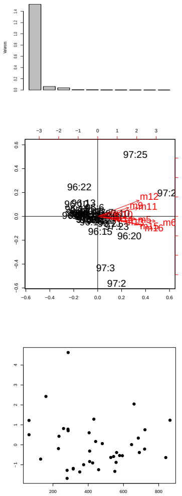
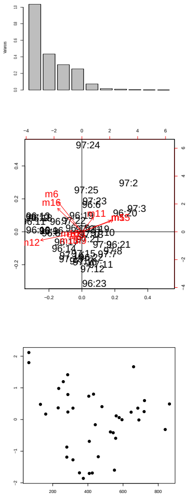
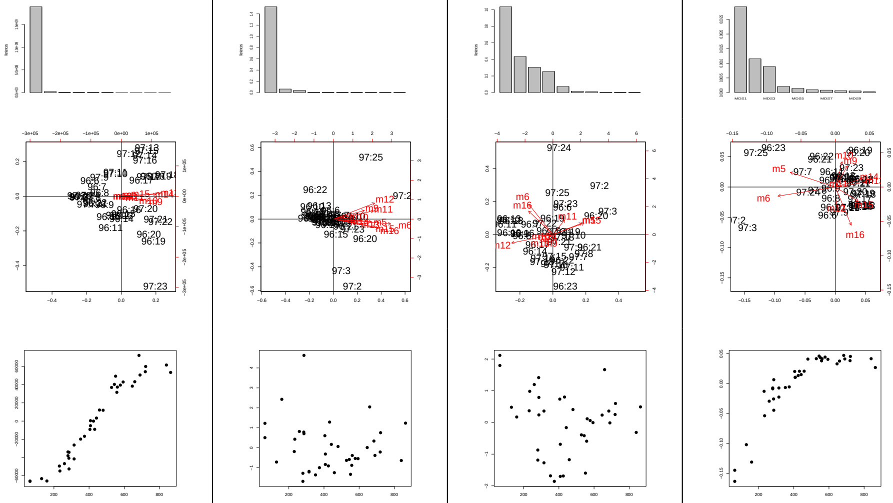
		

Network embedding: Zackenberg's data [SROB16]

Raw counts	Corrected stat.	Choleski	Bray-Curtis MDS



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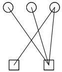
Super-motifs

Motif:



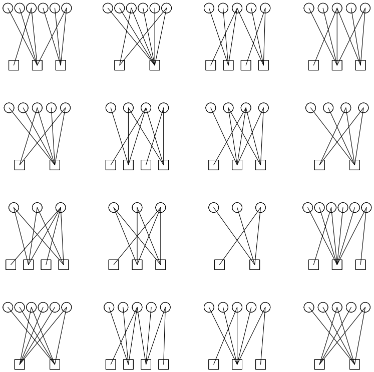
Variance:

$$N_s^2 = \left(\sum_\alpha Y_{s\alpha}\right)^2$$

$$= \sum_{\alpha,\beta:\alpha\cap\beta=\emptyset} Y_{s\alpha} Y_{s\beta}$$

$$+ \sum_{\alpha,\beta:\alpha\cap\beta\neq\emptyset} \underbrace{Y_{s\alpha} Y_{s\beta}}_{\text{occurrence of a super-motif}}$$

Some super-motifs:



... 396 super-motifs

Covariance: same game, for $Y_{s\alpha} Y_{s'\beta}$ with $s \neq s'$

Asymptotic distribution of the count

Estimated probability.

$$\overline{\phi}_s := \phi_2 \phi_4 \,/ \phi_1 \qquad \to \qquad \overline{F}_s := F_2 F_4 \,/ F_1$$

where F_1, F_2, F_4 = observed frequencies of top stars, bottom stars and edges.

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

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

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 $F_s - \phi_s$

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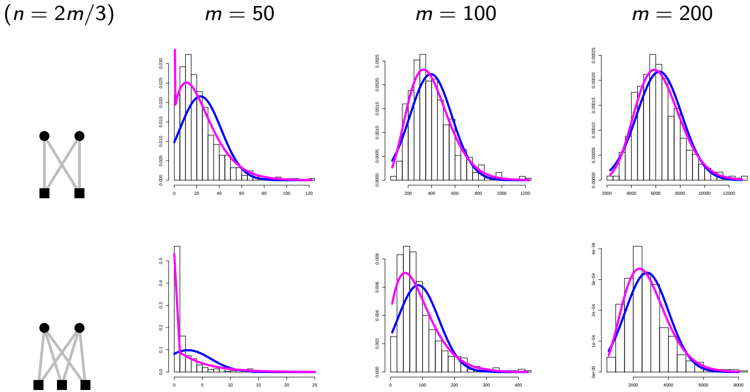
Test statistic. Under BEDD:

$$N_s \approx \mathcal{N}\left(\widehat{\mathbb{E}}(N_s), \widehat{\mathbb{V}}(N_s)\right) \qquad \Leftrightarrow \qquad \left(N_s - \widehat{\mathbb{E}}(N_s)\right) \Big/ \sqrt{\widehat{\mathbb{V}}(N_s)} \approx \mathcal{N}(0,1)$$

In practice: Asymptotic normality

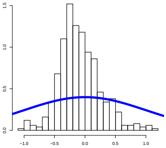


Normal distribution, Poisson-geometric distribution with same mean and variance [Sta01,PDK+08]

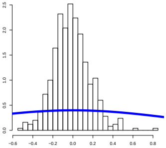
In practice: Test statistic

Need to account for the estimation error of $\widehat{\mathbb{E}}N$

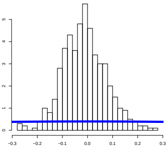
$m = 50$



$m = 100$



$m = 200$



Regular stat.:

$$\frac{N - \widehat{\mathbb{E}}N}{\sqrt{\widehat{\mathbb{V}}N}}$$

In practice: Test statistic

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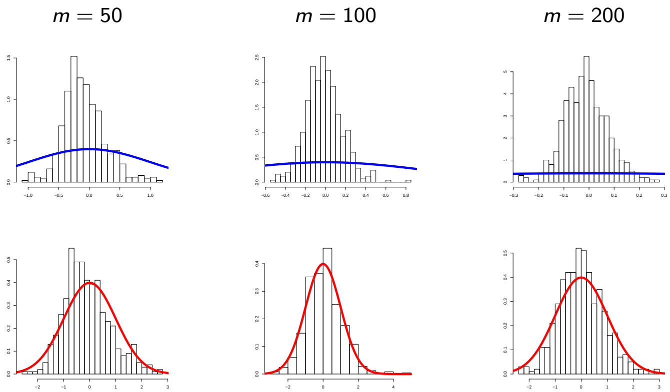
Regular stat.:

$$\frac{N - \widehat{\mathbb{E}}N}{\sqrt{\widehat{\mathbb{V}}N}}$$

Correction:

$$\frac{N - (\widehat{\mathbb{E}}N - \widehat{\mathbb{B}}(\widehat{\mathbb{E}}N))}{\sqrt{\widehat{\mathbb{V}}(N - \widehat{\mathbb{E}}N)}}$$



- Need to evaluate $\mathbb{V}(N - \widehat{\mathbb{E}}(N))$ and $\mathbb{B}(\widehat{\mathbb{E}}N)$: resort to Taylor expansion ($\Delta-$method)