Using motifs and to analyse (multiple) bipartite networks

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Outline

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Bipartite network

Two types of actors.

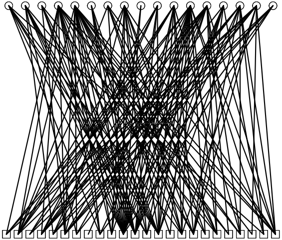
- Mutualistic: plant-pollinator
- Antagonistic: host-parasite

Topological analysis:
understanding the network organisation

Local: node or edge properties (degree, betweenness)

Global: density, connected components, nestedness

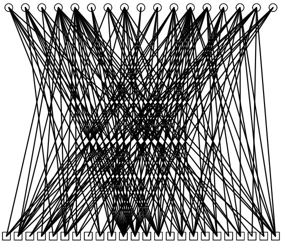
Zackenberg network: [SROB16]



Bipartite network: notations

Species.

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



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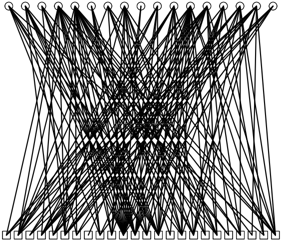

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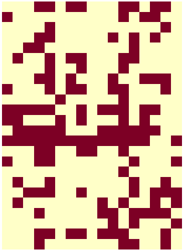


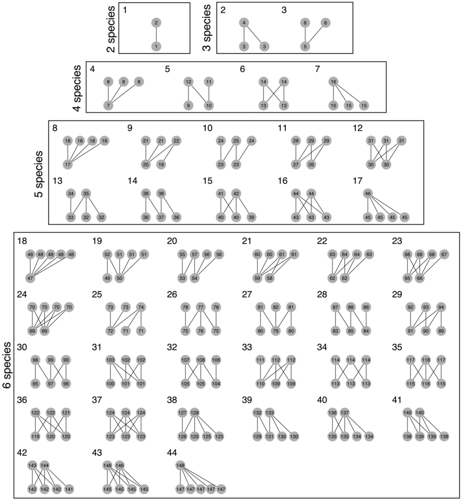
Interactions.

- $A_{ij} = 1$ if pollinator 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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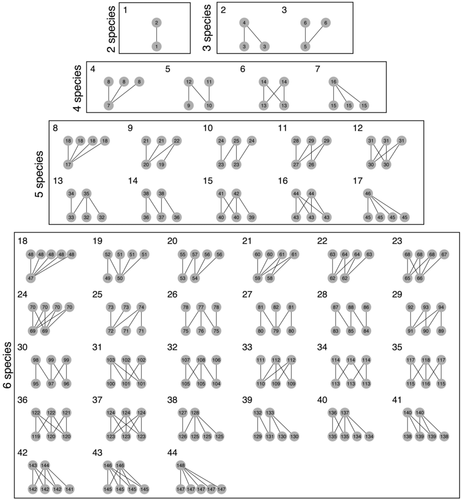

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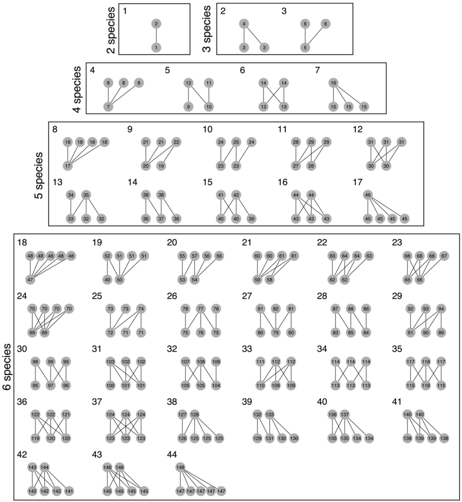

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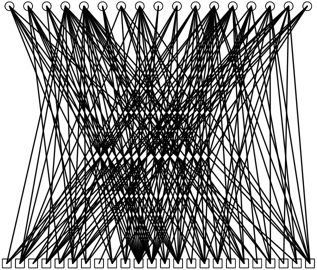
Existing tool. `bmotif` package [SSS+19]: counts motif occurrences

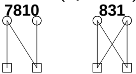
Example

Plant-pollinator network [SROB16]

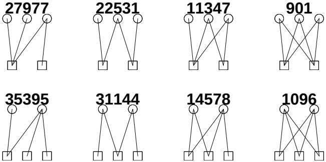


Motif counts.

4 nodes (species)



5 nodes



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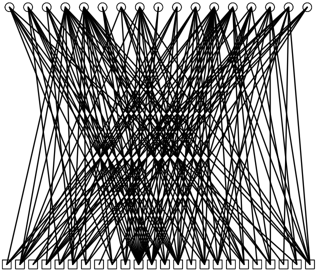

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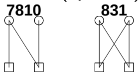

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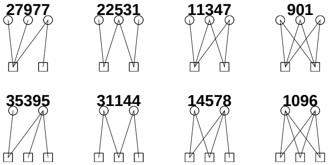
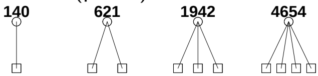
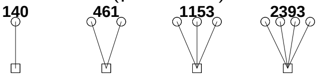


top 'stars' (plants)



bottom 'stars' (pollinators)



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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 pollinators)
- the imbalance between top-node degrees (specialist vs generalist plants)

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

- Consider m pollinators ($i = 1, \dots m$):
  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 pollinator i and plant j to interact is proportional to the product of their respective propensities.

BEDD model

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

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

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

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

(Bipartite version of the EDD model [CL02])

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Model parameters:

$$\theta = (\rho, g, h).$$

BEDD model

$$
\begin{aligned}
\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) \\
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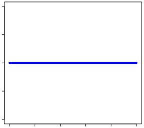
$h_0(v) =$



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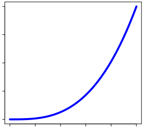

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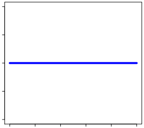

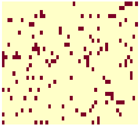

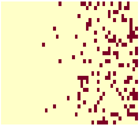

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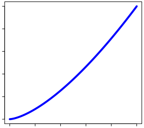

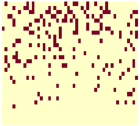

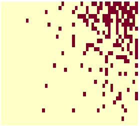

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Assumptions.

- No preferred or avoided specific connexion
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Sufficient statistics to fit BEDD:

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

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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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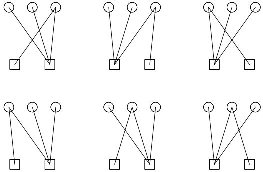

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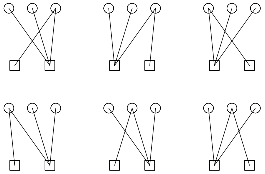


Motif count. Try all positions $\alpha = 1, \dots c_s$, define

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

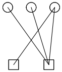
then count the number of matches:

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

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

Motif probability

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

$\Bigg($  $\Bigg) =$

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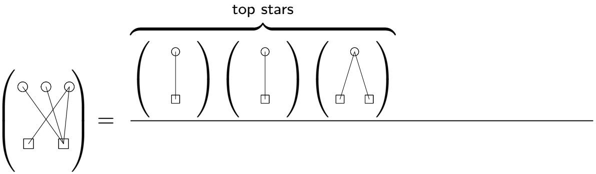

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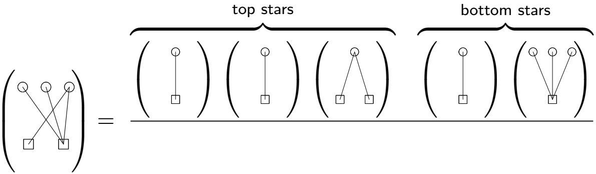

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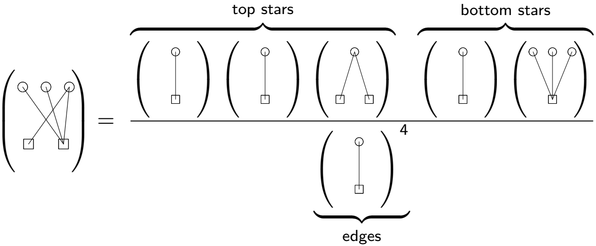

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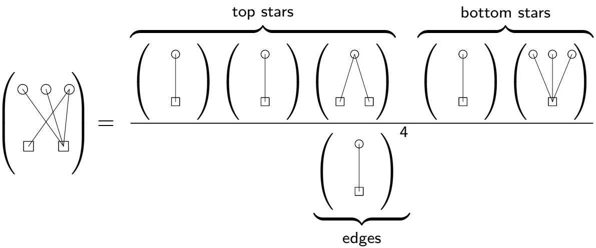
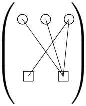


$\overline{\phi}_s = \mathbb{P}_{BEDD}$



$$= \frac{\left(\phi_1^2\phi_2\right)\left(\phi_1\phi_4\right)}{\left(\phi_1\right)^4} = \frac{\phi_2\phi_4}{\phi_1}$$

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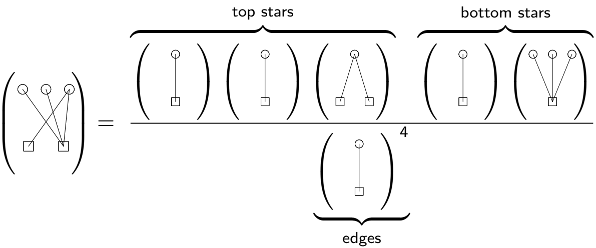
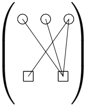


$\overline{\phi}_s = \mathbb{P}_{BEDD}$  $= \dfrac{(\phi_1^2\phi_2)\,(\phi_1\phi_4)}{(\phi_1)^4} \qquad = \dfrac{\phi_2\phi_4}{\phi_1}$

Estimated probability $\overline{F}_s$.

$$\overline{\phi}_s := \frac{\phi_2\phi_4}{\phi_1} \qquad \rightarrow \qquad \overline{F}_s := \frac{F_2F_4}{F_1}$$

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

Moments of the count

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- Asymptotic normality: [#33] [#34] $(F_s - \overline{F}_s) \Big/ \sqrt{\widehat{\mathbb{V}}(F_s)} \quad \xrightarrow{m,n\rightarrow\infty} \quad \mathcal{N}(0,1)$

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Network embedding: Multivariate analysis

Analysing multiple networks. Principle

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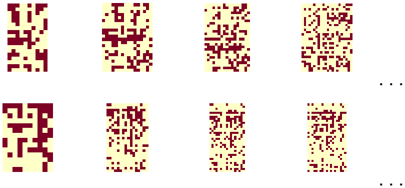
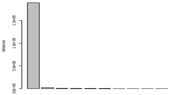
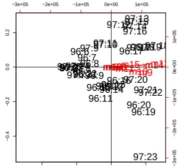
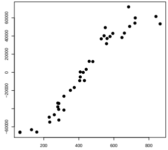
Zackenberg dataset. $K = 46$ networks

- 2 years
- 1 network observed every few days



Network embedding: Zackenberg's data [SROB16]

Raw counts			
  			

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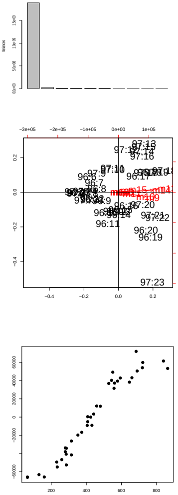	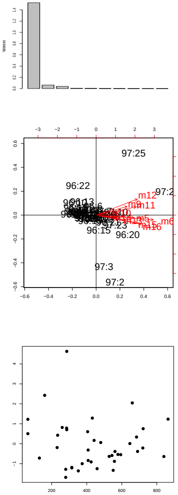		

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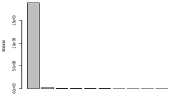
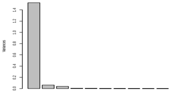
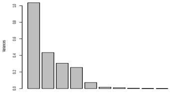
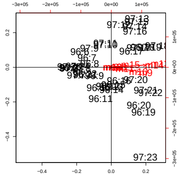
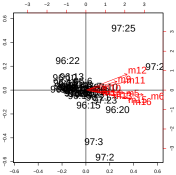
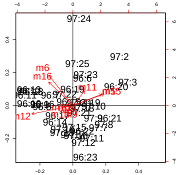
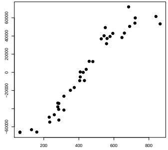
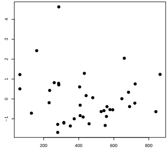
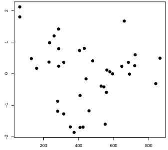
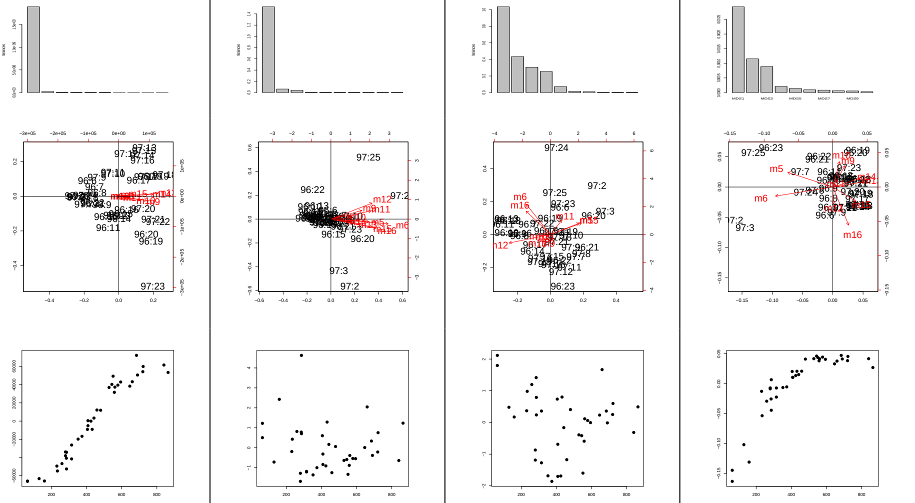
		
		
		

Network embedding: Zackenberg's data [SROB16]

Raw counts	Corrected stat.	Choleski [#36].	Bray-Curtis MDS



Outline

Goodness-of-fit (GOF)

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

More cautious: 'if the model fits the data reasonably well'

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Example.

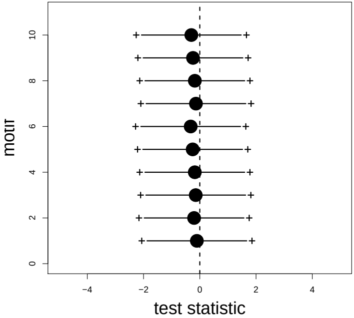
1. Data = observed plant-pollinator network
2. Statistic T = motif count N_s
3. Model = BEDD

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

Raw statistic:

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

Zackenberg network.



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

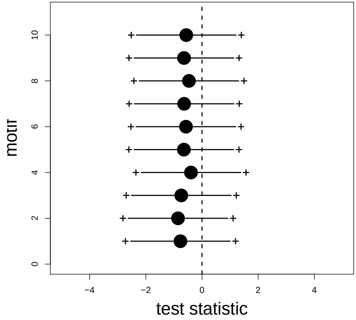
Zackenberg network.

Raw statistic:

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

Corrected stat.: accounts for the estimation error in $\widehat{\mathbb{E}} N$ [#37]

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



Testing degree imbalance

Question. Is there some degree imbalance between plants?

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Statistical test.

- Assume $A \sim BEDD(\rho, g, h)$,

$$H_0 = \{h = 1\}$$

- For motif s, evaluate $\widehat{\mathbb{E}}_0(N_s)$ and $\widehat{\mathbb{V}}_0(N_s)$ and compare

$$W_s = (N_s - \widehat{\mathbb{E}}_0(N_s))/\sqrt{\widehat{\mathbb{V}}_0(N_s)}$$

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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}

Comparing network imbalances

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- Assume $A \sim BEDD(\rho^A, g^A, h^A)$ and $B \sim BEDD(\rho^B, g^B, h^B)$

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$$W_s^{(g)}(A, B) = \frac{(N_s^A - \widehat{\mathbb{E}}_0(N_s^A)) - (N_s^B - \widehat{\mathbb{E}}_0(N_s^B))}{\sqrt{\widehat{\mathbb{V}}_0(N_s^A) + \widehat{\mathbb{V}}_0(N_s^B)}}$$

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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	$5.13\ 10^{-4}$	$1.15\ 10^{-4}$	$5.07\ 10^{-5}$	$1.79\ 10^{-5}$	$5.96\ 10^{-6}$
$\widehat{\mathbb{E}}_0 F_s^B$	$2.66\ 10^{-4}$	$2.92\ 10^{-5}$	$2.85\ 10^{-5}$	$1.50\ 10^{-6}$	$1.69\ 10^{-7}$
W_s	-1.56	-1.56	-0.97	-1.28	-0.96

Outline

Plant-pollinator networks in space & time

Questions. Does the structure of plant (herbaceous species) pollinator (native wild bees and hoverflies) network differ[1]:

- along the environmental gradient?
- across sites within the season?

[1] Joint work with Natasha de Manincor & François Massol + Sarah Ouadah & Pierre Latouche

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Dataset.

- 6 sites: 3 regions $\times$ 2 sites per region
- 2 years
- 7 months (April to October) per year

$$\rightarrow \quad n = 82 \text{ networks}, \quad [4, 39] \text{ plants}, \quad [8, 80] \text{ insects}$$

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Approach. Define a motif-based distance between each pair of networks.

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Distance-based network comparison

Network distance. For a pair of networks (A, B)

- for a given comparison (insect imbalance):

$$H_0^{(g)} = \{g^A = g^B\},$$

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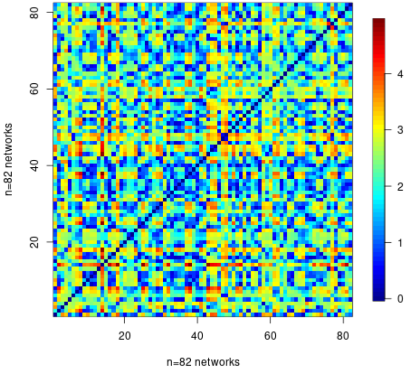

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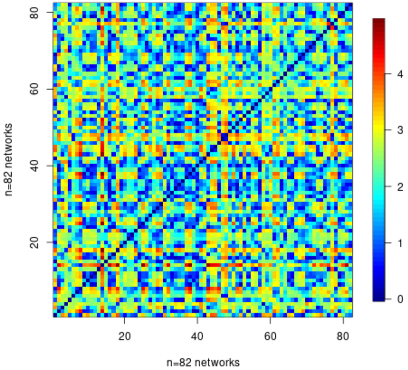

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The same for

- plant imbalance: $H_0^{(h)} = \{h^A = h^B\} \to W_s^{(h)} \to D^{(h)}(A, B)$
- both imbalance: $H_0^{(gh)} = \{g^A = g^B, h^A = h^B\} \to W_s^{(gh)} \to D^{(gh)}(A, B)$

Distance-based analysis of variance ('Adonis')

Data at hand. n networks ($A = 1, \dots n$)

- network covariates: e.g. region, year, month, ...
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Analysis of variance for distance matrices [And01]. Briefly speaking:

- Think of the regular linear model (regression, analysis of variance)
- Do as if the distance was computed on pseudo variable rules by a linear model
- 'Model':

$$D(A, B) = f(\text{region}_A, \text{region}_B, \text{month}_A, \text{month}_B, \\ (\text{region*month})_A, (\text{region*month})_B, \dots)$$

- Compute a pseudo F statistics for each effect of interest
- Assess significance using permutation tests.

(see [MA01, ZS06] [#38], `vegan` R package –`adonis2`–)

Results

Insect imbalance $D^{(g)}$.

	Df	Sum Of Sqs	R^2	F	Pr(F)
insectNb	1	69.9	0.2595	42.69	**1e-05**
plantNb	1	31.17	0.1157	19.04	**1e-05**
Year	1	2.66	0.0099	1.62	0.22212
Month	6	24.8	0.092	2.52	**0.00959**
Region	2	8.67	0.0322	2.65	**0.04531**
Year:Month	6	4.81	0.0179	0.49	0.88756
Year:Region	2	5.51	0.0204	1.68	0.1787
Month:Region	12	32.41	0.1203	1.65	**0.06346**
Year:Month:Region	12	27.26	0.1012	1.39	0.15884
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- No effect is found for the plant imbalance distance $D^{(h)}$ [#40]

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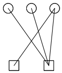
Super-motifs

Motif:



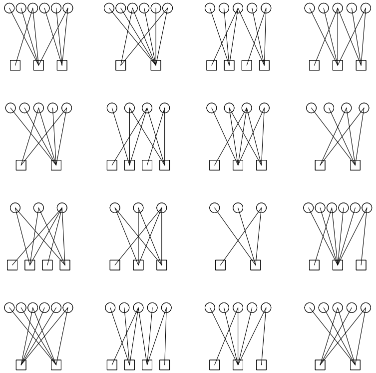
Variance:

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

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

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

Some super-motifs:



. . . 396 super-motifs

Covariance: same game, for $Y_{s\alpha} Y_{s'\beta}$ with $s \neq s'$ [#16]

Asymptotic distribution of the count

Estimated probability.

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

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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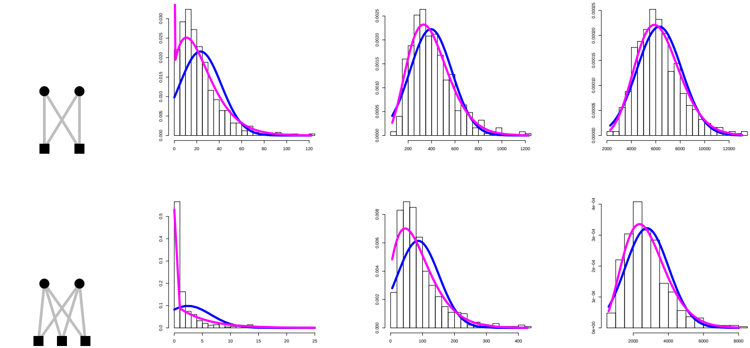
Test statistic. Under BEDD:

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

[#16]

In practice: Asymptotic normality

$(n = 2m/3)$ $\quad m = 50 \quad m = 100 \quad m = 200$



Normal distribution, Poisson-geometric distribution with same mean and variance [Sta01, PDK+08] [#16]

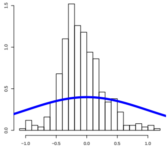
In practice: Test statistic

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

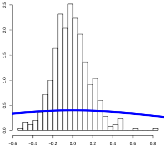
Regular stat.:

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

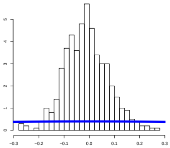
$m = 50$



$m = 100$



$m = 200$



In practice: Test statistic

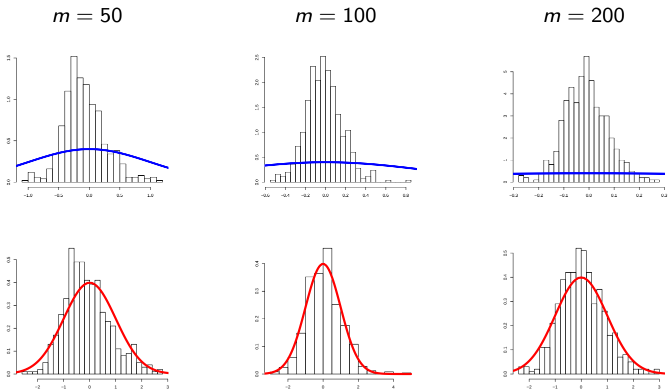
Need to account for the estimation error of $\widehat{\mathbb{E}}N$

Regular stat.:

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

Correction:

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



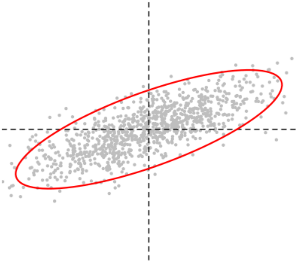
- Need to evaluate $\mathbb{V}(N - \widehat{\mathbb{E}}(N))$ and $\mathbb{B}(\widehat{\mathbb{E}}N)$: resort to Taylor expansion ($\Delta-$method) [#22]

Choleski transform

Aim: 'Remove' correlation and variance heterogeneity

Covariance matrix of (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: $\Sigma = P \Lambda P^{-1}$

Choleski matrix: $\Sigma^{-1/2} = P \Lambda^{-1/2} P^{-1}$

Choleski transform

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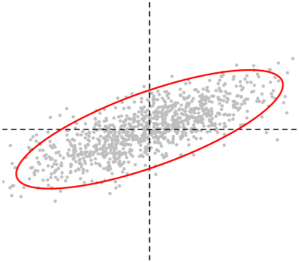
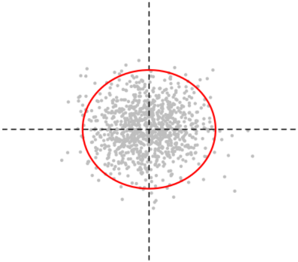


Diagonalization: $\Sigma = P\Lambda P^{-1}$

Choleski matrix: $\Sigma^{-1/2} = P\Lambda^{-1/2}P^{-1}$

Choleski transform:

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



$$\Sigma_{X_1',X_2'} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

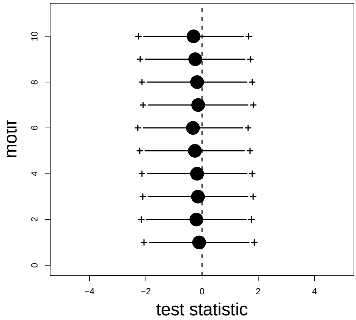
[#19]

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

Raw statistic:

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

Zackenberg network.



[#22]

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

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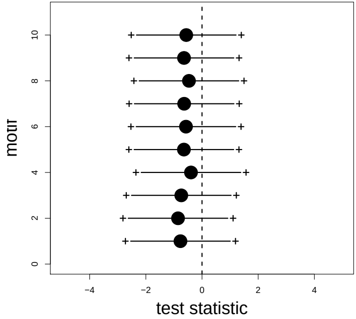
Zackenberg network.



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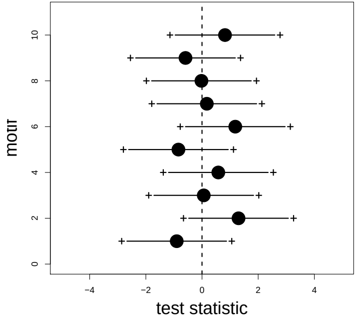
Cholevski [2] transformation: accounts for the correlation between the counts

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

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

Zackenberg network.



[#22]

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

An intuition for Adonis

Variance. Remind that $\sum_{i=1}^{n}(y_i - \overline{y})^2 = \frac{1}{2n}\sum_{i=1}^{n}\sum_{i'=1}^{n}(y_i - y_{i'})^2$

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Analysis of variance. Remind that, for g groups, with r replicates ($n = r\,g$),

$$\underbrace{\sum_{i=1}^{g}\sum_{j=1}^{r}(y_{ij} - \overline{y})^2}_{\text{Total}} = \underbrace{\sum_{i=1}^{g} r\,(\overline{y}_i - \overline{\overline{y}})^2}_{\text{Between}} + \underbrace{\sum_{i=1}^{g}\sum_{j=1}^{r}(y_{ij} - \overline{y}_i)^2}_{\text{Within}}$$

Anova test statistic $\quad F \propto \text{Between/Within}$

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Anova test statistic $F \propto$ Between/Within

Distance. p variables $y_{ij} = (y_{ijk})_{k=1\dots p}$: $D^2(y_{ij}, y_{i'j'}) = \sum_{k=1}^{p}(y_{ijk} - y_{i'j'k})^2$

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Distance. p variables $y_{ij} = (y_{ijk})_{k=1\dots p}$: $D^2(y_{ij}, y_{i'j'}) = \sum_{k=1}^{p}(y_{ijk} - y_{i'j'k})^2$

Adonis. Define Between = Total - Within, where

$$\text{Total} = \frac{1}{2n}\sum_{i=1}^{g}\sum_{i'=1}^{g}\sum_{j'=1}^{r} D^2(y_{ij}, y_{i'j'}), \qquad \text{Within} = \frac{1}{2}\sum_{i=1}^{g}\sum_{j=1}^{r}\sum_{j'=1}^{r} D^2(y_{ij}, y_{i'j'}),$$

and determine the p-value for F = Between/Within by permutation. [#28]

Null simulations

100 sets of 83 synthetic networks, with dimensions as the original ones and fixed ρ, g, and h

Without correction.

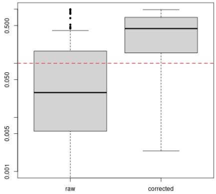
	Df	SumOfSqs	R^2	F	Pr(F)
Year	1	1.5	0.0114	0.94	0.443
Month	6	25.17	0.1914	2.61	**0.012**
Region	2	0.69	0.0052	0.21	0.845
Year:Month	6	7.46	0.0568	0.77	0.653
Year:Region	2	2.52	0.0191	0.78	0.543
Month:Region	12	12.55	0.0954	0.65	0.831
Year:Month:Region	12	17.39	0.1322	0.9	0.578
Residual	40	64.23	0.4884		
Total	81	131.51	1		

With correction.

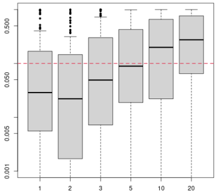
	Df	SumOfSqs	R^2	F	Pr(F)
insectNb	1	10.55	0.0803	7.17	**0.003**
plantNb	1	7.32	0.0556	4.97	**0.015**
Year	1	0.77	0.0059	0.53	0.622
Month	6	8.96	0.0681	1.01	0.458
Region	2	4.39	0.0334	1.49	0.241
Year:Month	6	8.54	0.0649	0.97	0.496
Year:Region	2	2.17	0.0165	0.74	0.569
Month:Region	12	13.99	0.1064	0.79	0.699
Year:Month:Region	12	18.9	0.1437	1.07	0.421
Residual	38	55.93	0.4253		
Total	81	131.51	1		

[#29]

Over 100 networks.



Increasing the networks' size.



Results for other motif distances

Plant imbalance $D^{(h)}$.

	Df	Sum Of Sqs	R^2	F	Pr(F)
insectNb	1	9.81	0.1935	19.53	**1e-05**
plantNb	1	1.42	0.028	2.83	**0.06594**
Year	1	0.67	0.0133	1.34	0.27518
Month	6	4.14	0.0818	1.38	0.20713
Region	2	0.99	0.0196	0.99	0.43126
Year:Month	6	2.61	0.0514	0.86	0.58258
Year:Region	2	1.87	0.037	1.87	0.1283
Month:Region	12	4.33	0.0854	0.72	0.8062
Year:Month:Region	12	5.75	0.1135	0.95	0.53039
Residual	38	19.09	0.3766		
Total	81	50.69	1		

Both imbalance $D^{(gh)}$.

	Df	Sum Of Sqs	R^2	F	Pr(F)
insectNb	1	56.21	0.265	48.58	**1e-05**
plantNb	1	16.44	0.0775	14.21	**1e-05**
Year	1	0.83	0.0039	0.71	0.56559
Month	6	24.41	0.1151	3.52	**0.00012**
Region	2	8.83	0.0417	3.82	**0.00321**
Year:Month	6	10.09	0.0476	1.45	0.14299
Year:Region	2	3.15	0.0149	1.36	0.25071
Month:Region	12	29.92	0.1411	2.16	**0.0028**
Year:Month:Region	12	18.24	0.086	1.31	0.16496
Residual	38	43.96	0.2073		
Total	81	212.09	1		

[#29]