Using motifs and to analyse (multiple) bipartite networks

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Outline

Bipartite networks and motifs

A null model

Motif distribution

Network embedding

Goodness-of-fit and network comparison

Distance-based network comparison

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Bipartite network

Two types of actors.

► Mutualistic: plant-pollinator

Antagonistic: host-parasite

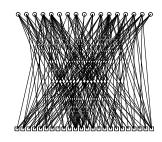
Topological analysis:

understanding the network organisation

Local: node or edge properties (degree, betweenness)

Global: density, connected components, nestedness

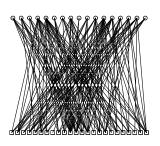
Zackenberg network: [SROB16]



Bipartite network: notations

Species.

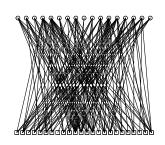
- $i = 1, \dots m$ pollinators = rows = bottom nodes
- $ightharpoonup j=1,\dots n$ plants = columns = top nodes



Bipartite network: notations

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



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 × n

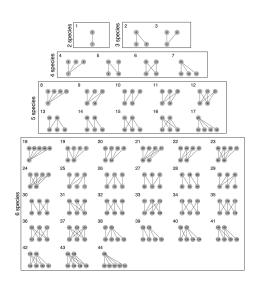
$$A = [A_{ij}]_{1 < i < m, 1 < j < n}$$



Bipartite motifs

'Meso-scale' analysis. [SCB⁺19]

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



Bipartite motifs

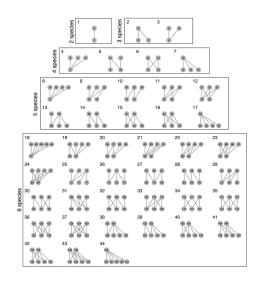
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Interest.

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

(+ 'species-role': out of the scope here)



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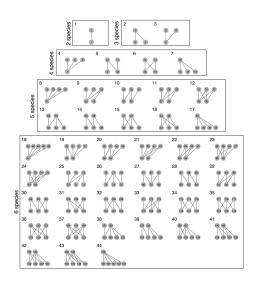
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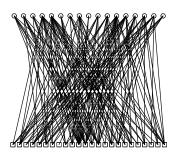
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Existing tool. bmotif package [SSS+19]: counts motif occurrences [#15] (Not an easy task!)

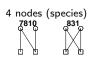


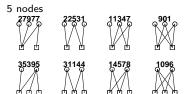
Example

Plant-pollinator network [SROB16]



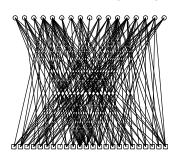
Motif counts.





Example

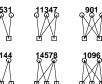
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bottom 'stars' (pollinators)









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Need for a null model

Motif counts obviously depend on

- \blacktriangleright 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, ... m): each plant i has a specific propensity to interact (degree of generalism)
- Consider n plants (j = 1,...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)

- $ho = {
 m network\ density}$
- $g = \text{top node degree imbalance } (\int g = 1)$
- ▶ $h = \text{bottom node degree imbalance } (\int h = 1)$

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

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

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

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

$$g_0(u) =$$

Properties of the BEDD model

Assumptions.

- ► No preferred or avoided specific connexion
- ► Graph-exchangeable model: pollinators can be permuted and plants can be permuted

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- Expected degree for pollinator i given U_i : $n \rho g(U_i)$.
- **Expected degree for plant** j given V_i : $m \rho h(V_i)$.
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Sufficient statistics to fit BEDD:

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

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Number of 'positions'.

- ightharpoonup Choose p nodes among m
- ightharpoonup 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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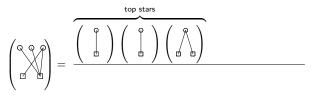
Motif count. Try all positions $\alpha = 1, \dots c_s$, define

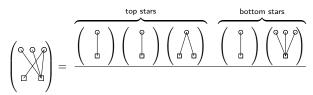
$$Y_{s\alpha} = 1$$
 if match, 0 otherwise,

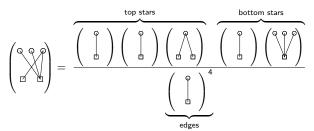
then count the number of matches:

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

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







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\end{pmatrix} \\
= \frac{(\phi_1^2 \phi_2) (\phi_1 \phi_4)}{(\phi_1 \phi_4)} = \frac{\phi_2 \phi_4}{(\phi_1 \phi_4)} \qquad [\#6]$$

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

Estimated probability \overline{F}_s .

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

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

Number of positions: c_s (frequency: $F_s = N_s / c_s$)

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- ▶ Mean: $\mathbb{E}_{BEDD}(N_s) = c_s \times \overline{\phi}_s$
- ▶ Variance: Same game, requires to evaluate $\mathbb{E}_{BEDD}(N_s^2) = \mathbb{E}_{BEDD}\left(\sum Y_{s\alpha}\right)^2$
 - → Need to account for overlap between positions (super-motifs: [PDK+08] [#32])











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- ► Covariance: Same game to compute $\mathbb{C}ov(N_s, N_{s'})$
- ► Asymptotic normality: [#33] [#34] $(N_s \overline{N}_s) / \sqrt{\widehat{\mathbb{V}}(N_s)} \stackrel{m,n \to \infty}{\longrightarrow} \mathcal{N}(0,1)$

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Network embedding: Multivariate analysis

Analysing multiple networks. Principle

- ightharpoonup 'Embed' each network into a convenient space (e.g. \mathbb{R}^d)
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Using motifs. K networks

$$(\mathsf{Network})_k \quad o \quad (N_1^k, \dots, N_S^k) \in \mathbb{R}^S$$

but need to correct for: network sizes, correlation between motif frequencies, etc...

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Zackenberg dataset. K = 46 networks

- 2 years
- 1 network observed every few days







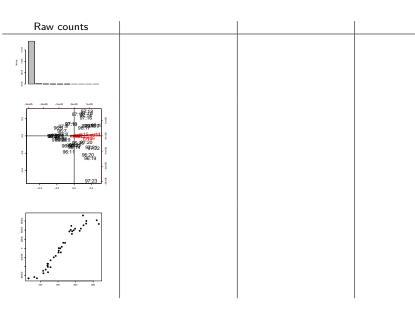


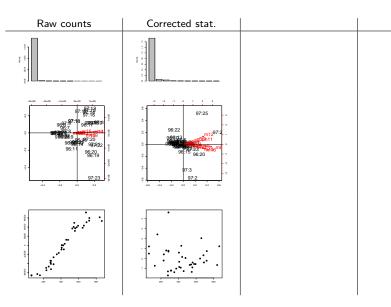


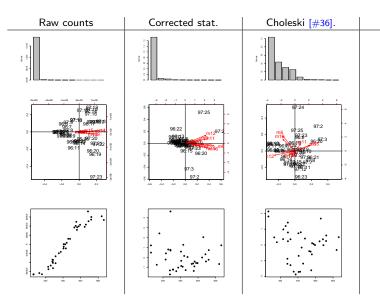


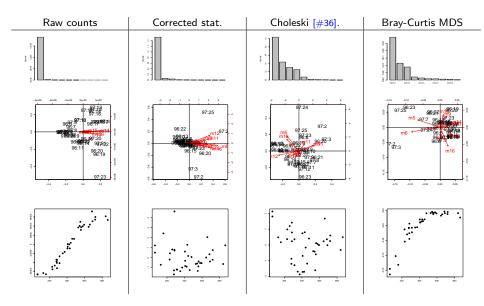












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Typical approach.

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Example.

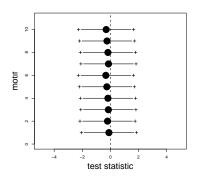
- 1. Data = observed plant-pollinator network
- 2. Statistic $T = \text{motif count } N_s$
- 3 Model = BFDD

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

Raw statistic:

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

Zackenberg network.



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

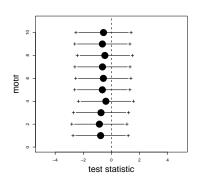
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Corrected stat.: accounts for the estimation error in $\widehat{\mathbb{E}}N$ [#37]

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

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Testing degree imbalance

Question. Is there some degree imbalance between plants?

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Statistical test.

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

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

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

with $\mathcal{N}(0,1)$

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Example. (only one significant difference)

nlant-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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$$H_0 = \{g^A = g^B\}$$

 $\blacktriangleright \ \, \text{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}$

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

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with $\mathcal{N}(0,1)$

Example. (no significant difference)

S	5	6	10	15	16
F_s^A	$9.21\ 10^{-5}$	$1.00\ 10^{-5}$	$8.12 \ 10^{-6}$	$3.32\ 10^{-7}$	$4.47 \ 10^{-8}$
$\widehat{\mathbb{E}}_0 \overset{s}{F_s^A}$	$1.96 \ 10^{-4}$	$3.75 \ 10^{-5}$	$1.74 \ 10^{-5}$	$4.25 \ 10^{-6}$	$1.33 \ 10^{-6}$
F_s^{B}	$5.13 \cdot 10^{-4}$	$1.15 \ 10^{-4}$	$5.07 \ 10^{-5}$	$1.79 \ 10^{-5}$	$5.96 \ 10^{-6}$
$\widehat{\mathbb{E}}_{0}F_{s}^{B}$	$2.66 \ 10^{-4}$	$2.92\ 10^{-5}$	$2.85 \ 10^{-5}$	$1.50\ 10^{-6}$	$1.69 \ 10^{-7}$
W_s	-1.56	-1.56	-0.97	-1.28	-0.96

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Plant-pollinator networks in space & time

Questions. Does the structure of plant (herbaceous species) pollinator (native wild bees and hoverflies) network differ¹:

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

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- lacktriangle 6 sites: 3 regions (Hauts-de-France, Normandie and Occitanie) imes 2 sites per region
- 2 years (2016, 2017)
- ▶ 7 months (April to October) per year
 - \rightarrow N = 82 networks, [4, 39] plants, [8, 80] 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 (e.g. insect imbalance):

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

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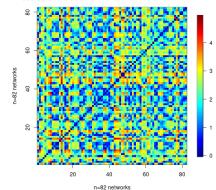
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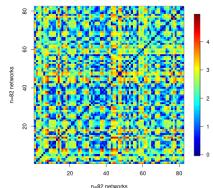
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Distance matrix:



The same for

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

Distance-based analysis of variance ('Adonis')

Data at hand. N networks (A = 1, ... N)

- network covariates: e.g. region, year, month, . . .
- buildraw distance matrix D = [D(A, B)] for all pairs of networks

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- distance matrix D = [D(A, B)] for all pairs of networks

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':

$$D(A, B) = f(region_A, region_B, month_A, month_B,$$

 $(region*month)_A, (region*month)_B, ...)$

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

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

	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
Residual	38	62.22	0.2309		
Total	81	269.42	1		

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

	Df	Sum Of Sqs	R^2	F	Pr(F)
insectNb	1	69.9	0.2595	42.69	1e-05
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▶ Because of small network sizes, need to correct for the number of insects and plants [#39]

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- ▶ Because of small network sizes, need to correct for the number of insects and plants [#39]
- Significant effect of the region and the month, indicating change of the insect imbalance both in space and time
- ► The pattern is conserved from year to the next (not year effect)
- No effect is found for the plant imbalance distance $D^{(h)}$ [#40]

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Super-motifs

Motif:



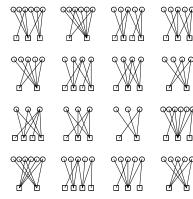
Variance:

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

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

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

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 [OLR22]. Under BEDD (and sparsity conditions):

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

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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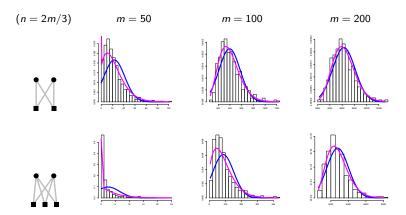
lacktriangle construct a counting martingale [GL17] for $F_s-\phi_s$

Test statistic. Under BEDD:

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

[#16]

In practice: Asymptotic normality



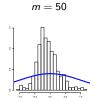
Normal distribution, Poisson-geometric distribution with same mean and variance [Sta01, PDK⁺08] [#16]

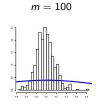
In practice: Test statistic

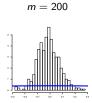
Need to account for the estimation error of $\widehat{\mathbb{E}}N$

Regular stat.:

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







In practice: Test statistic

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

Regular stat.:

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





$$m = 100$$









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







▶ Need to evaluate $\mathbb{V}(N-\widehat{\mathbb{E}}(N))$ and $\mathbb{B}(\widehat{\mathbb{E}}N)$: resort to Taylor expansion (Δ -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: $\Sigma = P \wedge P^{-1}$

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

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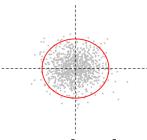
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Choleski transform:

$$\left[\begin{array}{c} X_1' \\ X_2' \end{array}\right] = \Sigma^{-1/2} \left[\begin{array}{c} X_1 \\ X_2 \end{array}\right]$$



$$\Sigma_{X_1',X_2'} = \left[\begin{array}{cc} 1 & 0 \\ 0 & 1 \end{array} \right]$$

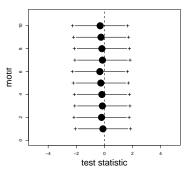
[#19]

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]

 $^{^{2}\}Sigma = P\Lambda P^{\mathsf{T}}, \ \Sigma = P\Lambda^{-1/2}P^{\mathsf{T}}$

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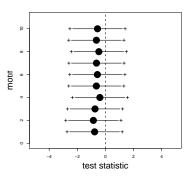
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Corrected stat.: accounts for the estimation error in $\widehat{\mathbb{E}}N$

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

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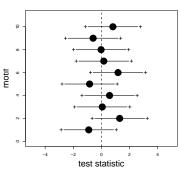
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Cholevski ² transformation: accounts for the correlation between the counts

$$\begin{split} & \Sigma_{s,s'} = \mathbb{C}\text{ov}(N_s - \widehat{\mathbb{E}}N_s, N_{s'} - \widehat{\mathbb{E}}N_{s'}) \\ & T'' = \widehat{\Sigma}^{-1/2} \left[N_s - (\widehat{\mathbb{E}}N_s - \widehat{\mathbb{B}}(\widehat{\mathbb{E}}N_s)) \right] \end{split}$$

Zackenberg network.



[#22]

 $^{^{2}\}Sigma = P\Lambda P^{\mathsf{T}}, \ \Sigma = P\Lambda^{-1/2}P^{\mathsf{T}}$

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 $F \propto \text{Between/Within}$

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

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Adonis. Define Between = Total - Within, where

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

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Null simulations

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

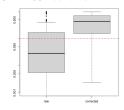
Without correction.

	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		

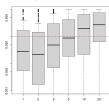
With correction.

	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		

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		

