

Interaction networks, food webs, and complexity in ecology

20/03/2025

GDR TheoMoDive / FRB-CESAB workshop

Schedule

early morning

General introduction (FM)

later

Random interactions (MB)

afternoon

Complexity-stability relationship (CJ)

evening

Seminar “multiplexity” (SK)

Outline

1. Networks & associated definitions

2. Representations as matrices

Crash course: matrices, eigenvalues, Jacobian matrix

3. Theories & notable results

- Stability & feasibility
- Invariants
- Robustness to extinctions

4. A quick primer on network statistics

- degree distributions
- randomizations / null models
- modularity / block models
- nestedness

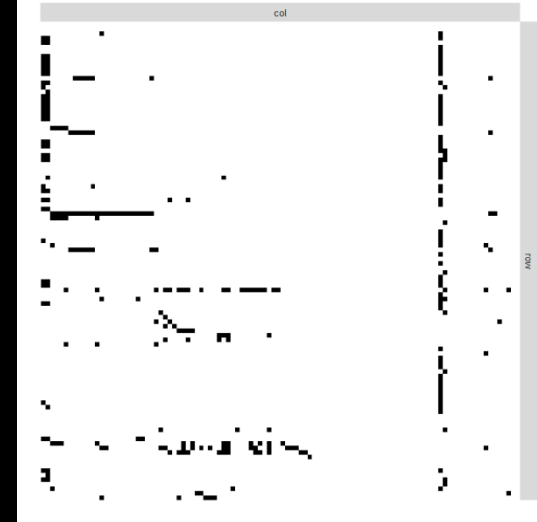
A food web example

```
library(cheddar)
library(igraph)
library(vegan)
library(sbm)
library(alluvial)
library(faux)
library(matlib)
library(calculus)
source('functions_network.R')
```

```
####In FWebs, there is a large list of food webs called mg1
sapply(1:length(mg1[[1]]),function(x)
  dim(as.matrix(mg1[[1]][[x]]))[1])
```

```
####Extract data from web 1,433
mat<-as.matrix(mg1[[1]][[433]])
plotMyMatrix(mat)
```

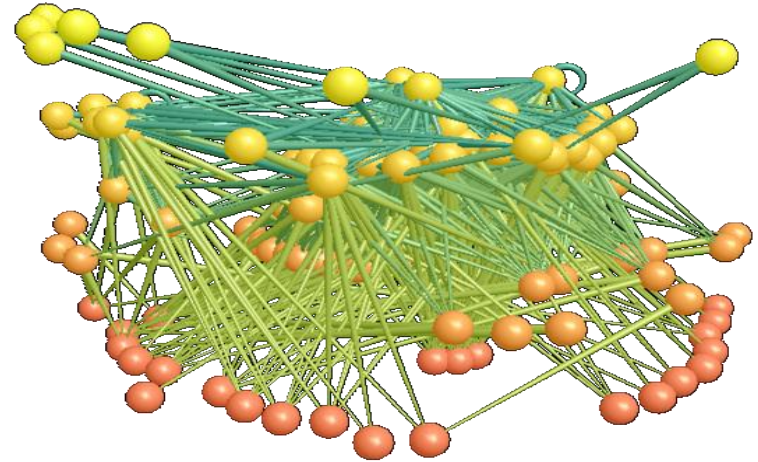
```
net.mat<-graph_from_adjacency_matrix(t(mat),mode="directed")
```



don't forget to change the
setwd line

What is a network?

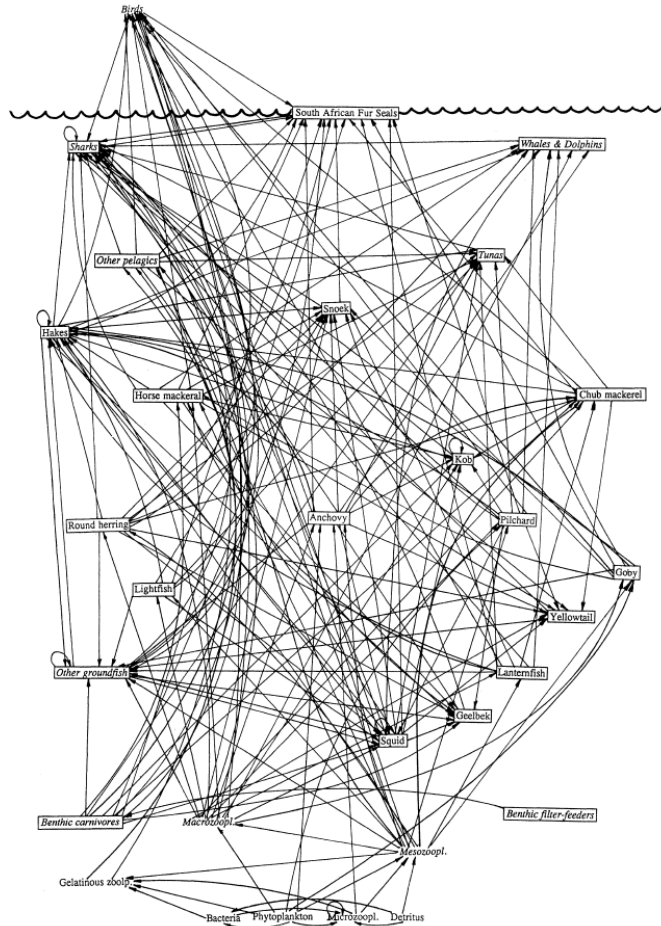
- Network or graph: **nodes** connected by **edges**
- Pairwise relationships
- Edges can be **directed** and/or **weighted**



Networks in ecology

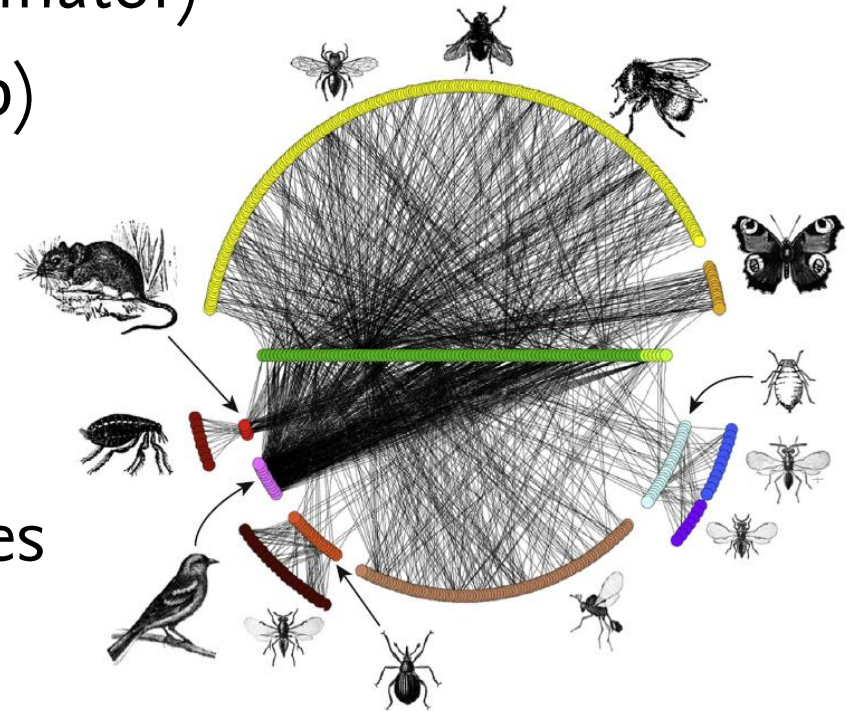
Different types of networks, depending on what an edge means

- Interaction networks
edge = interaction
- Spatial networks
edge = spatial connection
- Assembly network
edge = assembly transitions



Ecological interaction networks

- Different types of interactions => different networks
 - mutualistic (e.g. plant-pollinator)
 - antagonistic (e.g. food web)
 - ...
- Data on networks
 - interaction frequency (field)
 - co-abundances/occurrences
 - interaction potential (expe)



A little history

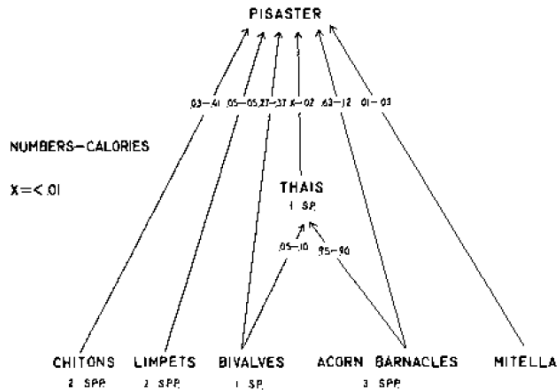


FIG. 1. The feeding relationships by numbers and calories of the *Pisaster* dominated subweb at Mukkaw Bay. *Pisaster*, N = 1049; *Thais*, N = 287. N is the number of food items observed eaten by the predators. The specific composition of each predator's diet is given as a pair of fractions; numbers on the left, calories on the right.

Paine 1966 *Am Nat*

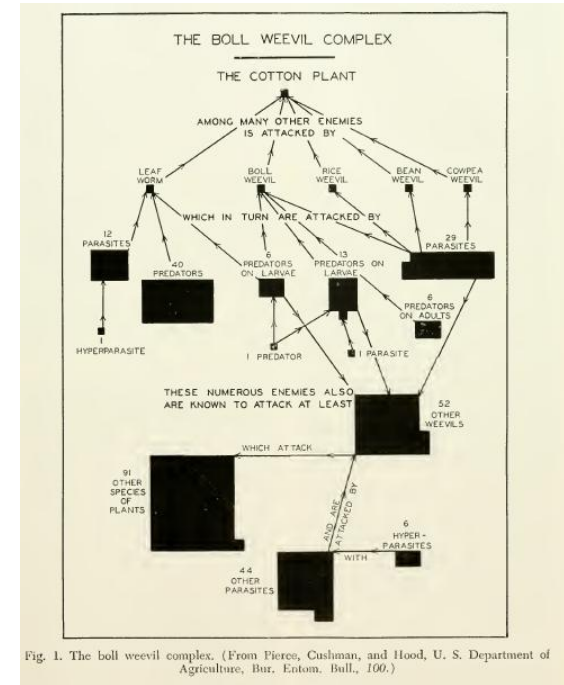


Fig. 1. The boll weevil complex. (From Pierce, Cushman, and Hood, U. S. Department of Agriculture, Bur. Entom. Bull., 100.)

Allee et al. 1949 *Principles of Animal Ecology*

INTERRELATIONS OF FOOD CHAINS

Biological communities do not consist of independent food chains, but of food webs, of such a kind that an individual at any level (corresponding to a link in a single chain) can use some but not all of the food provided by species in the levels below it.

Hutchinson 1959 *Am Nat*

Types of network

1. Unipartite networks

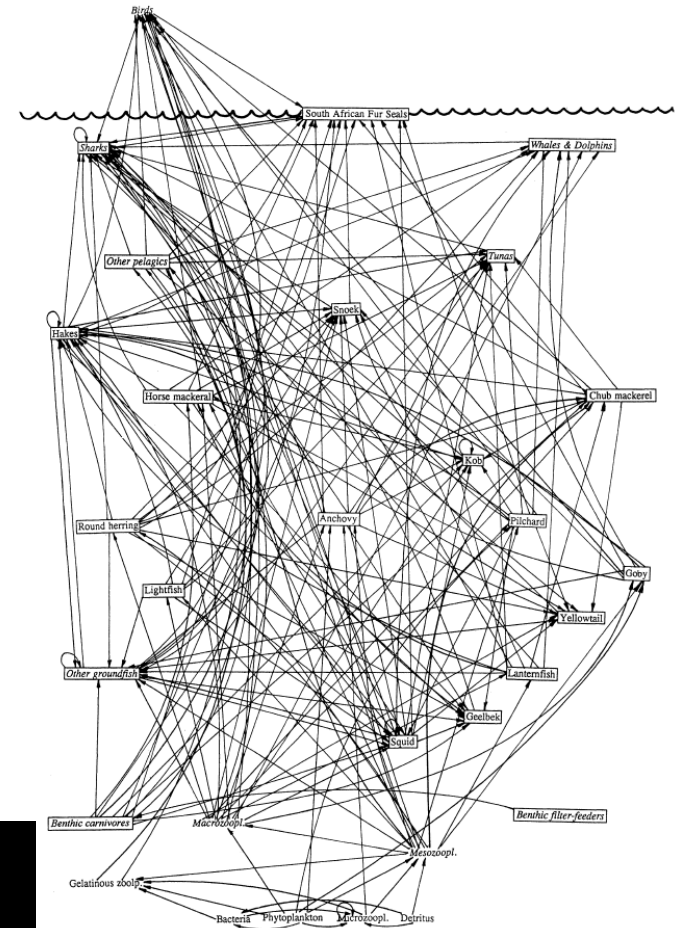
= “messy” ones

Interactions can occur between any two species

e.g. food webs, competition network

```
net<-sample_gnp(100,0.2,directed = FALSE)
plot(net)
net<-sample_gnp(100,0.2, directed =TRUE)
plot(net)
```

```
plot(net.mat, layout=layout_with_mds)
plot(net.mat, layout=layout_as_tree)
plot(net.mat, layout=layout_as_food_web5)
```



Types of network

2. Multipartite networks

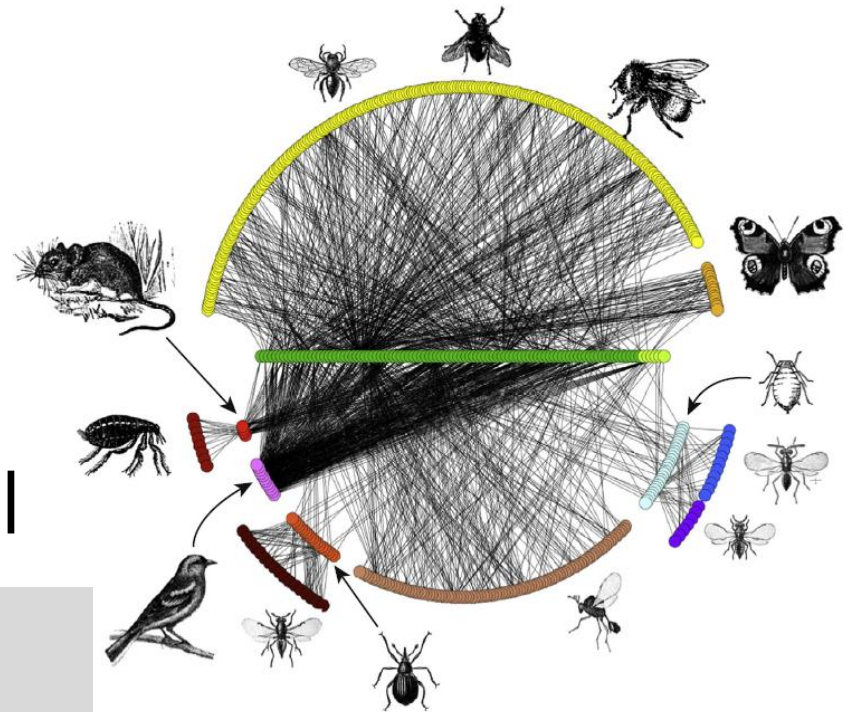
= neat ones

Each species has a “role”

= belongs to a level

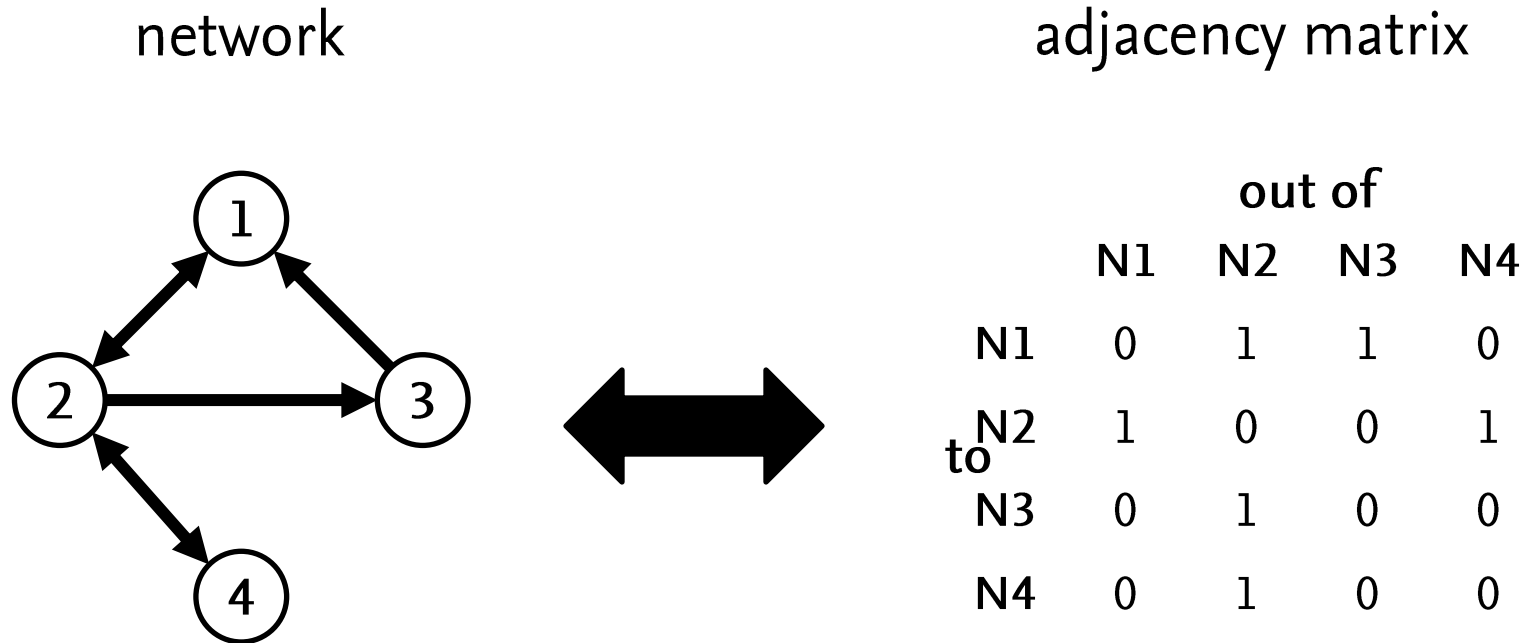
No interaction within a level

```
net<-  
sample_bipartite(50,50,"gnp",0.1)  
plot(net,layout=layout_as_bipartite)
```



Representations of networks

A network = a matrix

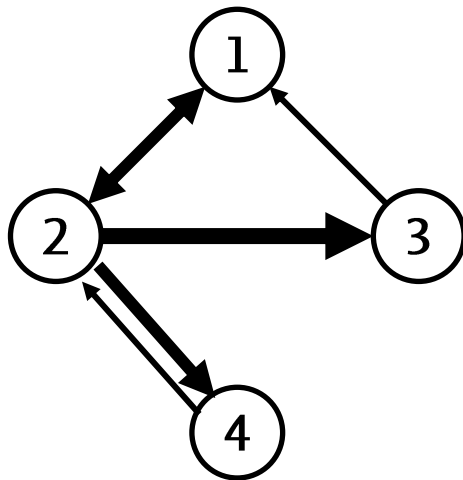


```
net<-sample_grg(100, 0.2)
as_adjacency_matrix(net)
```

Representations of networks

A network = a matrix

weighted network



weighted adjacency matrix

	out of			
	N1	N2	N3	N4
N1	0	5	2	0
N2	5	0	0	2
N3	0	10	0	0
N4	0	5	0	0

```
E(net)$weight<-rpois(length(E(net)),2)  
net[,]
```

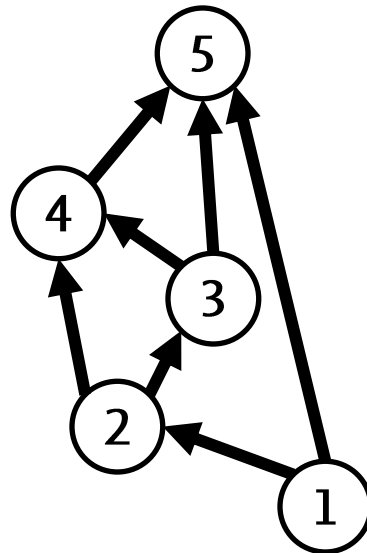
Network matrices

- Undirected network \Rightarrow symmetric matrix
- Directed network \Rightarrow non necessarily symmetric matrix

Potential misunderstanding over “food web matrices”?

who eats whom?

0	1	0	0	1
0	0	1	1	0
0	0	0	1	1
0	0	0	0	1
0	0	0	0	0



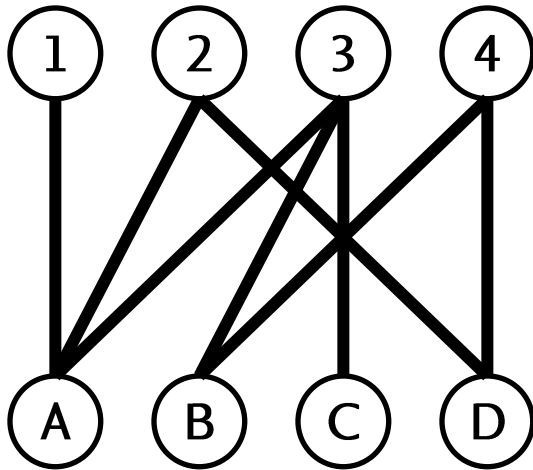
energy fluxes

0	1	0	0	1
-1	0	1	1	0
0	-1	0	1	1
0	-1	-1	0	1
-1	0	-1	-1	0

Network matrices

- Undirected network \Rightarrow symmetric matrix
- Directed network \Rightarrow non necessarily symmetric matrix
 - Potential misunderstanding over “food web matrices”?
- Binary or real-valued matrix
- Adjacency matrix vs. incidence matrices in multipartite networks

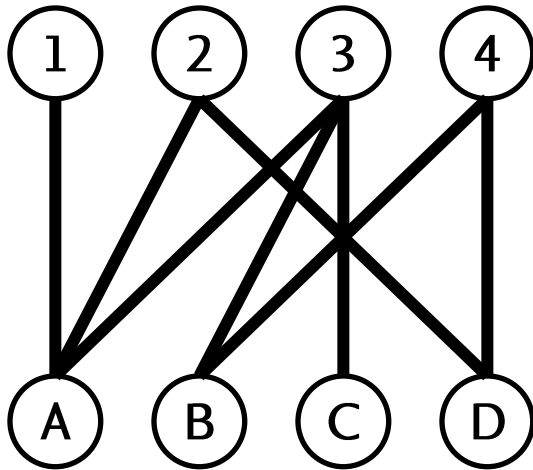
Matrices for multipartite networks



adjacency matrix

	A	B	C	D	1	2	3	4
A	0	0	0	0	1	1	1	0
B	0	0	0	0	0	0	1	1
C	0	0	0	0	0	0	1	0
D	0	0	0	0	0	1	0	1
1	1	0	0	0	0	0	0	0
2	1	0	0	1	0	0	0	0
3	1	1	1	0	0	0	0	0
4	0	1	0	1	0	0	0	0

Matrices for multipartite networks



adjacency matrix

	A	B	C	D	1	2	3	4
A	0	0	0	0	1	1	1	0
B	0	0	0	0	0	0	1	1
C	0	0	0	0	0	0	1	0
D	0	0	0	0	0	1	0	1
1	1	0	0	0	0	0	0	0
2	1	0	0	1	0	0	0	0
3	1	1	1	0	0	0	0	0
4	0	1	0	1	0	0	0	0

```
net<-sample_bipartite(4,4,"gnm",m=8)  
net[,]
```


Matrices for multipartite networks

incidence matrix

	A	B	C	D
1	1	0	0	0
2	1	0	0	1
3	1	1	1	0
4	0	1	0	1

adjacency matrix

	A	B	C	D	1	2	3	4
A	0	0	0	0	1	1	1	0
B	0	0	0	0	0	0	1	1
C	0	0	0	0	0	0	1	0
D	0	0	0	0	0	1	0	1
1	1	0	0	0	0	0	0	0
2	1	0	0	1	0	0	0	0
3	1	1	1	0	0	0	0	0
4	0	1	0	1	0	0	0	0

```
as_biadjacency_matrix(net)
```

Degrees

For binary adjacency matrices A (=1 if there is an edge, 0 otherwise), one can compute:

- node i degree = total number of connections in an undirected network

$$d_i = \sum_j a_{ij}$$

degree(net)

- node i in-degree and out-degree = number of connections coming in or going out of node i

$$d_i^- = \sum_j a_{ji}$$

degree(net, mode="in")

$$d_i^+ = \sum_j a_{ij}$$

degree(net, mode="out")

Connectance and degree distribution

Connectance = nb of realized interactions/nb of potential interactions

```
####Compute the connectance of the empirical network
```

```
Compute the connectance of net.mat
```

```
####Plot its degree distribution
```

```
Make a histogram of the degrees of net.mat
```

```
Plot the cumulative distribution of the degrees of net.mat
```

Connectance and degree distribution

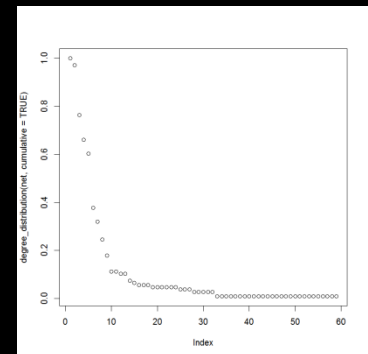
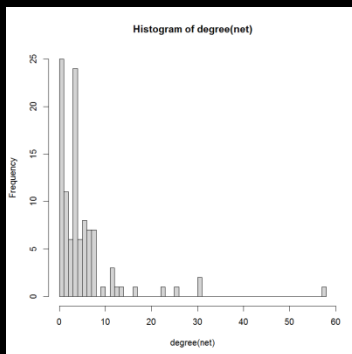
Connectance = nb of realized interactions/nb of potential interactions

```
#### Compute the connectance of the empirical network  
conn<-mean(as.matrix(net.mat[, ]))
```

```
#### Plot its degree distribution
```

```
hist(degree(net.mat), breaks=0:max(degree(net.mat)))
```

```
plot(degree_distribution(net.mat, cumulative = TRUE))
```



Crash course: matrices

Matrices = mathematical objects as 2-way tables
“Strange” multiplication with vectors (and matrices)

$$\begin{array}{|c|c|c|} \hline a & b & c \\ \hline d & e & f \\ \hline g & h & i \\ \hline \end{array} \cdot \begin{array}{|c|} \hline x \\ \hline y \\ \hline z \\ \hline \end{array} = \begin{array}{|c|} \hline ax+by+cz \\ \hline dx+ey+fz \\ \hline gx+hy+iz \\ \hline \end{array}$$

```
m<-matrix(rbinom(9,1,0.5),nrow=3)
x<-rnorm(3)
m*x
m%*%x
```

Crash course: matrix eigenvalues

Spectrum of matrix M = list of values λ such that there is a non-zero vector x verifying

$$Mx = \lambda x$$

λ 's are called eigenvalues, x 's eigenvectors

$\text{Sp}(M)$ is always finite (= discrete set of numbers), at most the smallest dimension of the matrix

Crash course: Jacobian matrices

A set of ODEs written as

$$\frac{d\vec{x}}{dt} = \vec{F}(\vec{x})$$

with an equilibrium at \vec{x}^*

can be linearized around this equilibrium:

$$\frac{d(\vec{x} - \vec{x}^*)}{dt} \approx J(\vec{x}^*) \cdot (\vec{x} - \vec{x}^*)$$

Crash course: Jacobian matrices

Matrix $J(\vec{x}^*)$ is called the Jacobian matrix of the dynamical system at equilibrium \vec{x}^*

$$J(\vec{x}^*) = \left(\frac{\partial F_i}{\partial x_j} \right) \Big|_{x=x^*}$$

Local stability at \vec{x}^* is obtained when all eigenvalues of $J(\vec{x}^*)$ have negative real parts

```
jacobian(c("r*n1*(1-n1/k)-a*n1*n2/(1+h*n1)", "b*n1*n2/(1+h*n1)-d*n2"), var = c("n1", "n2"))
```


Lotka-Volterra and networks

The classic (dimensionless) LV system

$$\frac{dx_i}{dt} = x_i \left[r_i - x_i + \sum_j a_{ij} x_j \right]$$

can be seen as a network, with matrix A as its “weighted” adjacency matrix

May's stability result

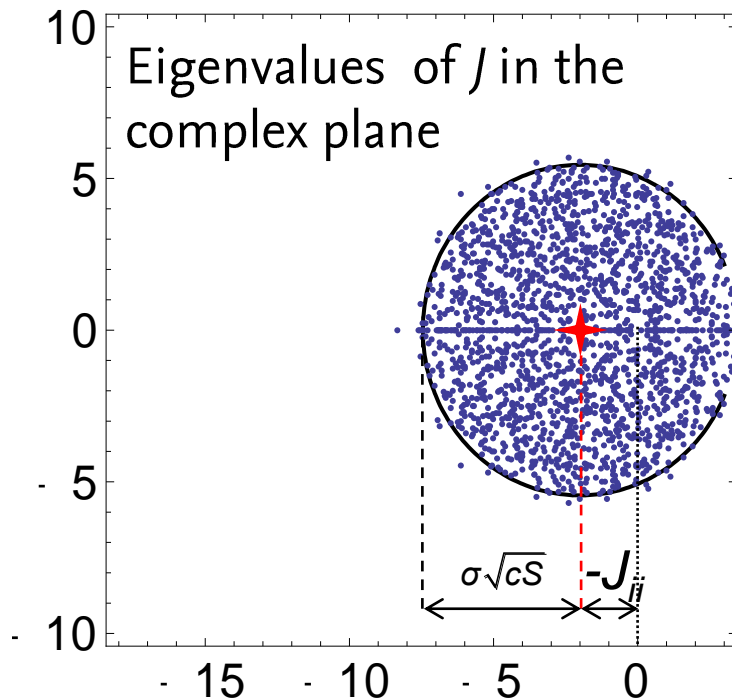
Assume species abundances follow a large system of ODEs (= many species, S) and have an equilibrium \vec{x}^*

If the Jacobian matrix at this equilibrium is random, with non-diagonal elements equal to 0 with probability $1 - c$ and otherwise equal to the drawing of a normal distribution of mean = 0 and variance σ^2 , the system is stable when:

$$\sigma\sqrt{cS} < -\overline{J_{ii}}$$

May's stability result

Graphical representation



Here, m is the average diagonal element of J

This follows from the circular law: for random matrices with variance $1/S$ and mean 0, eigenvalues are distributed uniformly in the disk of center 0 and radius 1.

```
m<-matrix(rnorm(10^6),nrow=10^3)
plot(eigen(m)$values,asp=1)
```

May's stability result

Interpretation:

Stable systems should have low diversity (S) and/or low connectance (c) and/or low variability of non-diagonal Jacobian elements (σ) and/or highly negative diagonal Jacobian elements

Intuitively, does not seem to conform to reality

⇒ some of the assumptions must be false

- transient dynamics (not at equilibrium)?
- structure of interactions not random?

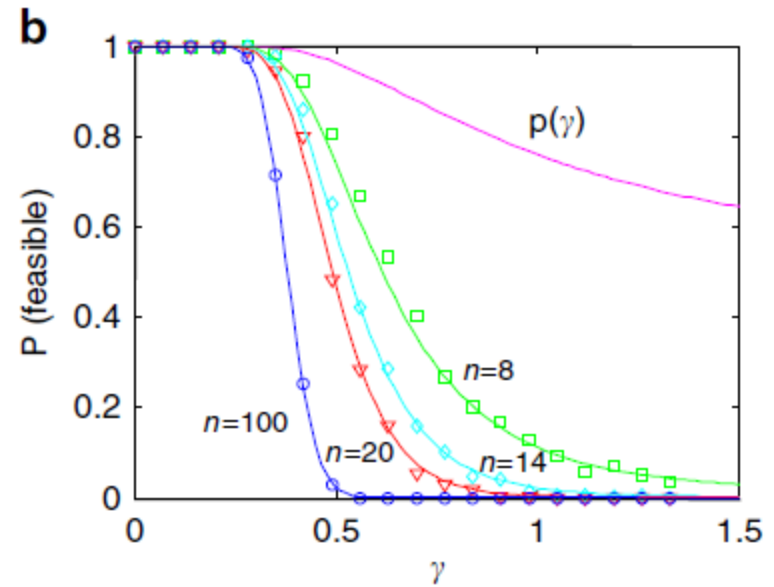
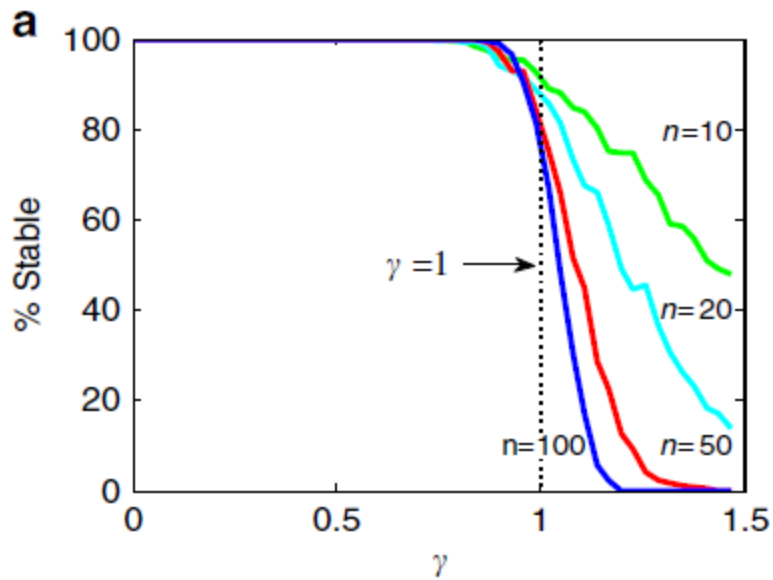
Feasibility vs. stability

One strong argument against May's result:
It might be harder to get an equilibrium (with all the species) than to get stability

For a certain class of LV systems (Bizeul-Najim), feasibility of equilibrium is obtained only when

$$\sigma \sqrt{2S \log(S)} < -\overline{J_{ii}}$$

Feasibility vs. stability



Results obtained from simulations of random LV systems

Food web invariants

Two models from the 80-90's:

1. the **cascade model** (Cohen-Briand): predators eat species that are smaller than them with probability c/S

⇒ connectance decreases as $1/S$

```
m<-cascade_matrix(10,20)
sum(m)/(dim(m)[1]*(dim(m)[1]-1))
```

```
m<-cascade_matrix(10,200)
sum(m)/(dim(m)[1]*(dim(m)[1]-1))
```

Food web invariants

Two models from the 80-90's:

2. the **niche model** (Williams-Martinez): predators eat all species that are within a size interval

⇒ connectance stays constant

Food web invariants

Two models from the 80-90's:

2. the **niche model** (Williams-Martinez): predators eat all species that are within a size interval

⇒ connectance stays constant

```
niche<-niche_matrix(0.2,100)
m<-niche$matrix
sum(m)/(dim(m)[1]^2)
```

```
niche<-niche_matrix(0.2,200)
m<-niche$matrix
sum(m)/(dim(m)[1]^2)
```

Generating the niche model

In the `functions_network.R` file, there is a function `niche_matrix` to generate niche model-based food webs

```
####Generate 100 virtual food webs based on the niche  
model with the actual connectance
```

```
Create 100 instances of niche_matrix with lapply
```

```
Create a list of the 100 matrices corresponding to the simulated food webs
```

Generating the niche model

In the functions_network.R file, there is a function niche_matrix to generate niche model-based food webs

```
####Generate 100 virtual food webs based on the niche  
model with the actual connectance  
niches<-lapply(1:100,function(x)  
  niche_matrix(conn,dim(mat)[1]))  
ms<-lapply(1:100,function(x) niches[[x]]$matrix)
```

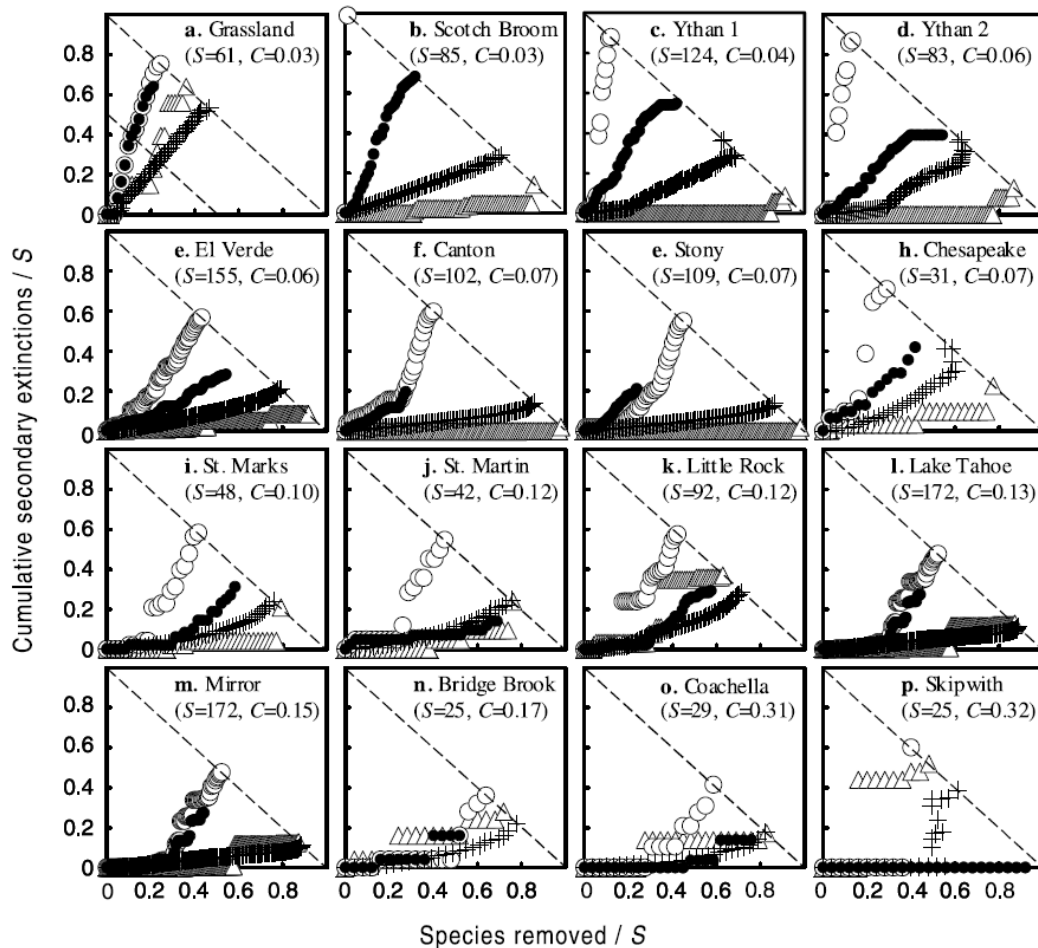
Robustness to secondary extinctions

General idea: if one species is removed, what happens to the remaining ones?

Under certain rules, secondary extinction

Robustness analysis = how many species are lost when R species are removed?

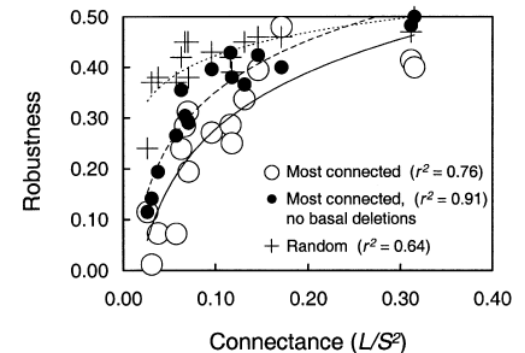
Robustness to secondary extinctions



Examples based on a variety of datasets

Secondary extinction when a species loses all its prey items (except itself if cannibalistic)

Different scenarios based on how removed species are chosen



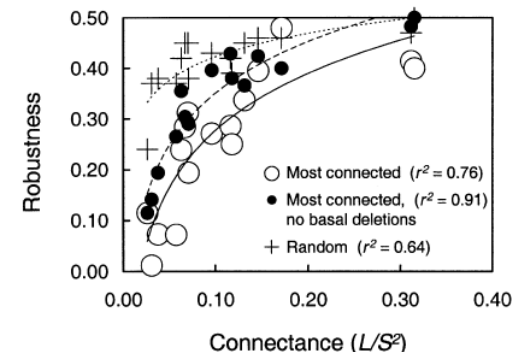
Robustness to secondary extinctions

```
net<-  
graph_from_adjacency_matrix(m,mode  
="directed")  
i_index <- seq(from = 0, to = 1,  
by =0.1)  
i_index <- head(i_index,-1)  
prob_exp<-exponent.removal(net,  
i_index)  
V(net)$name<-1:200  
iterate(fw_to_attack=net,  
prob_exp, alpha1=50, iter=10,  
i_index, plot = TRUE)
```

Examples based on a variety of datasets

Secondary extinction when a species loses all its prey items (except itself if cannibalistic)

Different scenarios based on how removed species are chosen

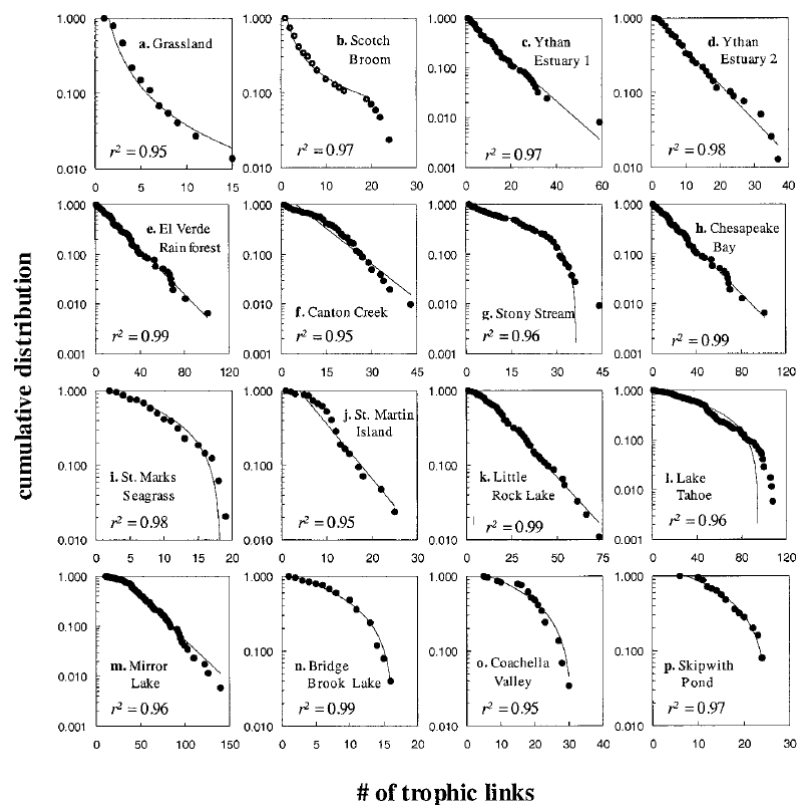


A quick primer on network stats

- Degree distributions
- Null models (randomizations) of networks
- Modularity and block models
- Nestedness

Degree distributions

1. Can be computed empirically (easily)
2. Networks can be generated from degree sequence (harder)
3. Can be compared to benchmark distributions (power law, Poisson, Erdős-Rényi...)



Degree distributions

1. Can be computed empirically (easily)
2. Networks can be generated from degree sequence (harder)
3. Can be compared to benchmark distributions (power law, Poisson, Erdős-Rényi...)

```
net<-  
graph_from_adjacency_matrix(  
m)  
hist(degree(net),breaks=0:ma  
x(degree(net)))  
plot(degree_distribution(net  
, cumulative = TRUE))  
  
net<-  
sample_degseq(degree(net),me  
thod = "vl")  
  
mean(degree(net))  
ks.test(degree(net),"pbinom"  
,length(V(net)),mean(degree(  
net))/length(V(net)))
```

Degree distributions

Usefulness of power laws in ecology?
few nodes in ecology => impossible to ascertain?

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Power-Law Distributions in Empirical Data*

Aaron Clauset[†]
Cosma Rohilla Shalizi[‡]
M. E. J. Newman[§]

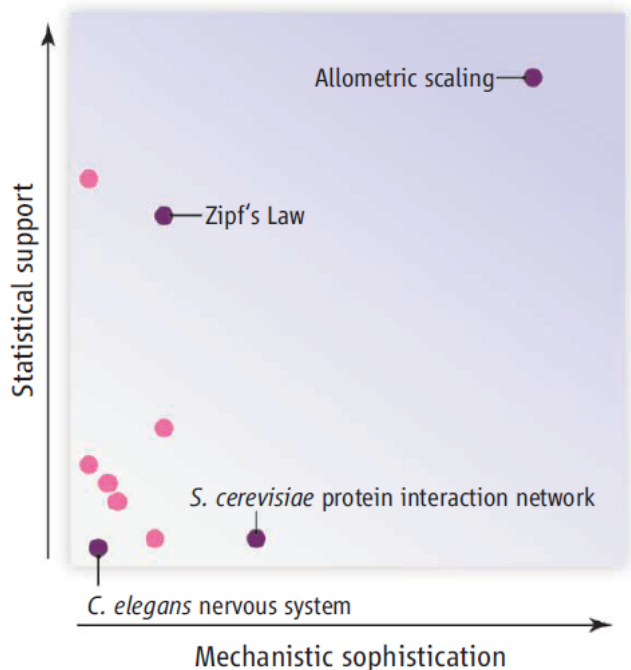
MATHEMATICS

Critical Truths About Power Laws

Most reported power laws lack statistical support and mechanistic backing.

Michael P. H. Stumpf¹ and Mason A. Porter²

Degree distributions



As a rule of thumb, a candidate power law should exhibit an approximately linear relationship on a log-log plot over at least two orders of magnitude in both the x and y axes. This criterion rules out many data sets, including just about all biological networks.

How good is your power law? The chart reflects the level of statistical support—as measured in (16, 21)—and our opinion about the mechanistic sophistication underlying hypothetical generative models for various reported power laws. Some relationships are identified by name; the others reflect the general characteristics of a wide range of reported power laws. Allometric scaling stands out from the other power laws reported for complex systems.

Null models / randomizations

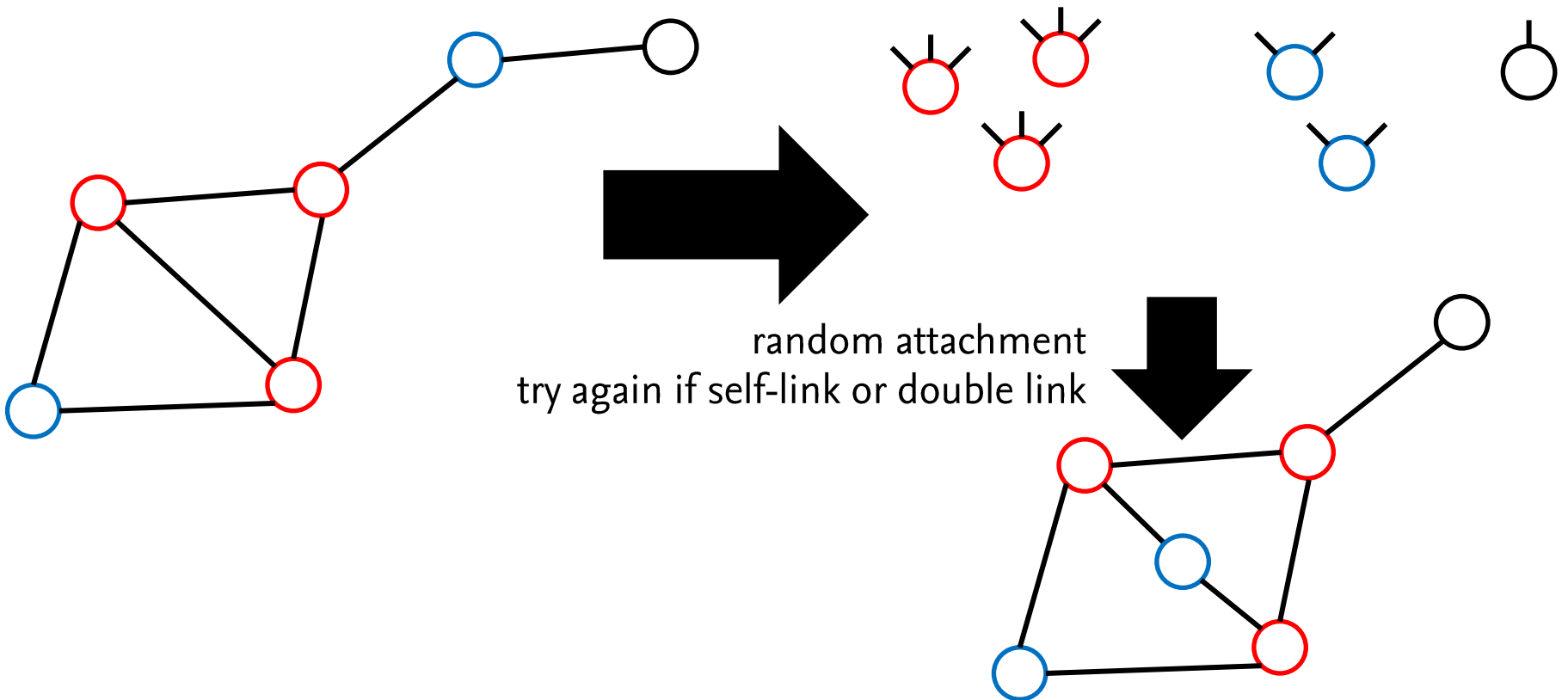
Statistics on networks are hard to test because...
everything is dependent on everything else

Two possibilities for statistical tests:

- define a probabilistic model to build H_0
- define a null model based on a randomization of data

Null models / randomizations

Configuration model: null model corresponding to randomization of edges with fixed degrees



Null models / randomizations

Algorithm for bipartite binary matrices 

ARTICLE

Received 27 Dec 2013 | Accepted 14 May 2014 | Published 11 Jun 2014

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A fast and unbiased procedure to randomize ecological binary matrices with fixed row and column totals

Giovanni Strona¹, Domenico Nappo¹, Francesco Boccacci¹, Simone Fattorini² & Jesus San-Miguel-Ayanz¹

```
net<-sample_bipartite(50,50,"gnp",0.1)
sample.bip.config<-
simulate(nullmodel(as_incidence_matrix(net),"curveball"),nsim=
1000)
dim(sample.bip.config)
```

Null models / randomizations

For unipartite networks, slightly harder task

```
n<-1000
net<-sample_gnp(n,0.2, directed = FALSE)
sample.config.undirected<-lapply(1:100,function(x)
sample_degseq(degree(net), method = "vl"))
length(sample.config.undirected)
```

For directed networks, even worse (no control over uniformity)

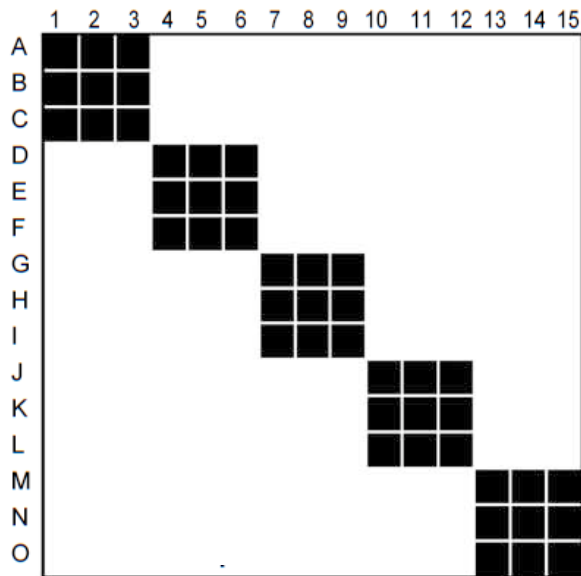
```
net<-sample_gnp(n,0.2, directed = TRUE)
sample.config.directed<-lapply(1:100,function(x)
sample_degseq(degree(net,mode="out"), degree(net,mode="in"),
method = "simple.no.multiple"))
length(sample.config.directed)
```

Null models for weighted networks are even more difficult to define...

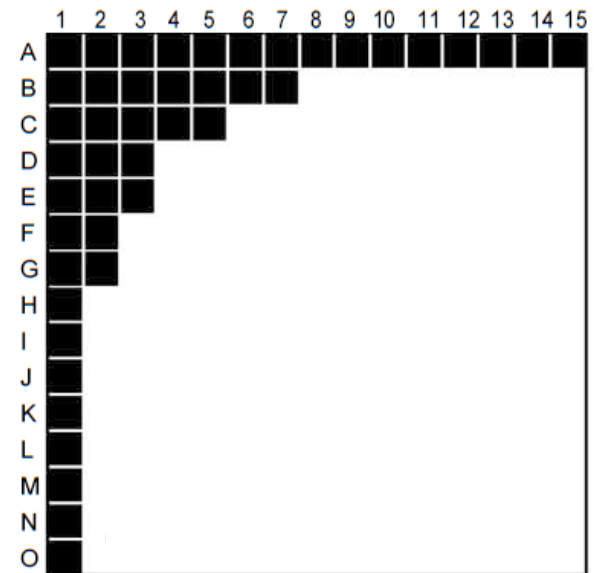
Network structure

Ecological interaction networks might have non-random structure

modular



nested



Modularity

Modularity

$$Q = \frac{1}{A} \sum_{i,j} \left[a_{ij} - \frac{d_i d_j}{A} \right] \delta_{ij}$$

where δ_{ij} equals 1 if nodes i and j belong to the same module

Principle : compare a_{ij} to its expectation given the degrees d_i , taking only edges within modules (= groups)

Modules = groups that maximize the value of Q

Modularity

Works for undirected networks

Several algorithms (edge-betweenness, leading eigenvector, fast greedy, multilevel/louvain...)

```
net<-sample_gnp(100,0.2, directed = FALSE)
EB.mod<-cluster_edge_betweenness(net)
LE.mod<-cluster_leading_eigen(net)
ML.mod<-cluster_louvain(net)

plot(EB.mod,net,layout = layout_with_mds)
plot(LE.mod,net,layout = layout_with_mds)
plot(ML.mod,net,layout = layout_with_mds)
```

Modularity

Works for undirected networks

Several algorithms (edge-betweenness, leading eigenvector, fast greedy, multilevel/louvain...)

Not adapted to directed networks:

- make the network symmetric or
- use another definition of modularity for directed networks

Modularity of the empirical FW

Is the empirical FW less modular (or more modular) than the niche model food webs?

Compute the modularity score (using Louvain) of the 100 matrices created with the niche model (noted ms) as a list (with `lapply`)

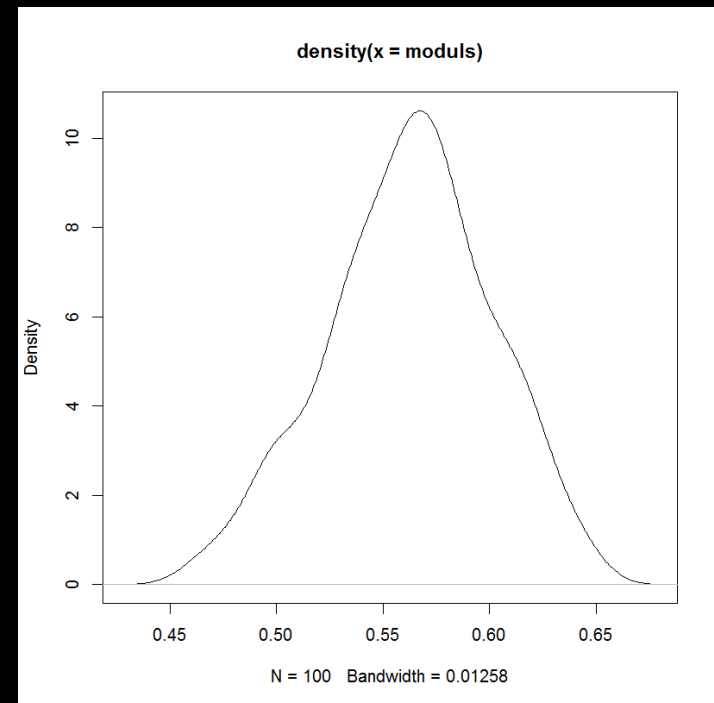
Plot their density

Compute the p-value (“higher tail”) using this collection of simulated modularities and the `ecdf` function

Modularity of the empirical FW

```
#### Is the empirical FW less modular (or more modular)
than the niche model food webs?
moduls<-lapply(1:100,function(x)
  cluster_louvain(graph_from_adjacency_matrix(ms[[x]],mo
de="undirected"))$modularity[2])
plot(density(moduls))
```

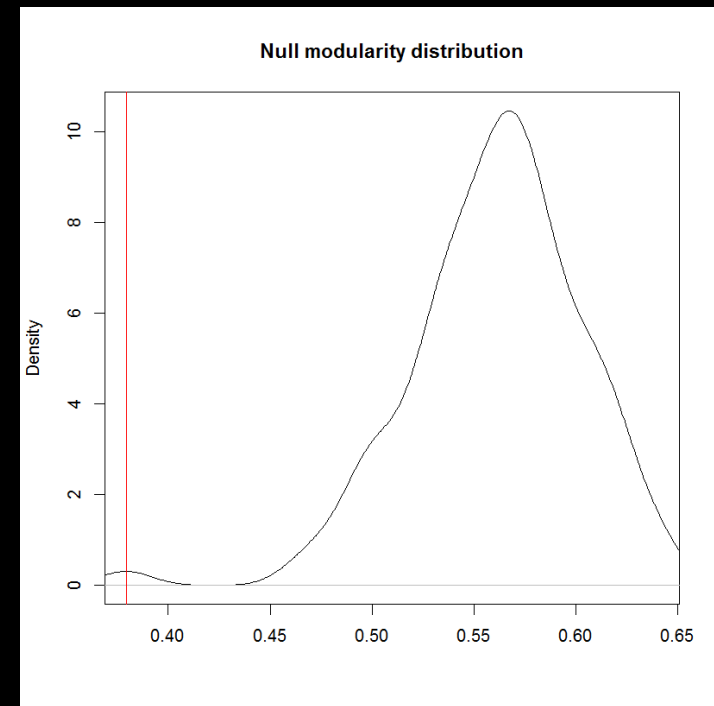
```
modul.ecdf<-ecdf(moduls)
1-modul.ecdf(modul$modularity[2])
```



Modularity of the empirical FW

```
####Is the empirical FW less modular (or more modular)
than the niche model food webs?
```

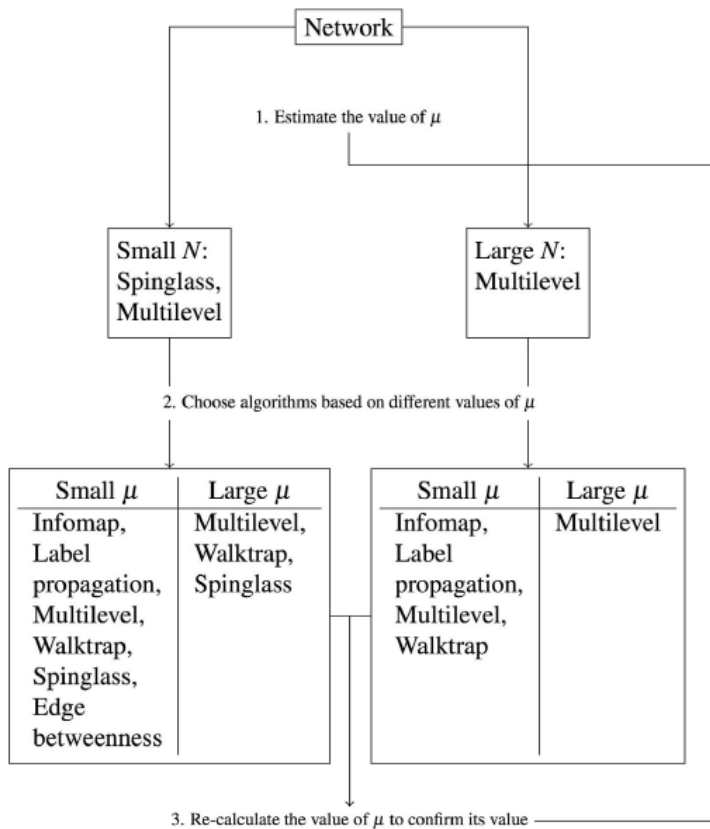
```
p.val(modul$modularity[2],moduls,"larger","Null
modularity distribution")
```



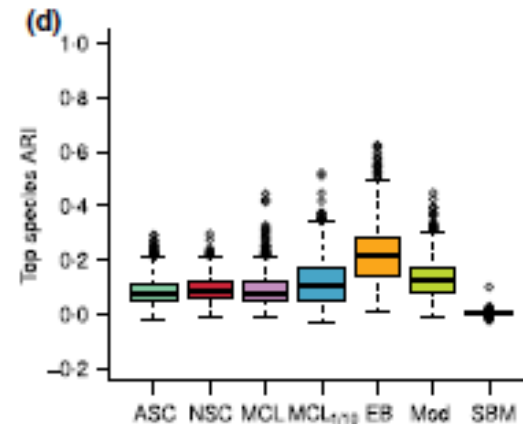
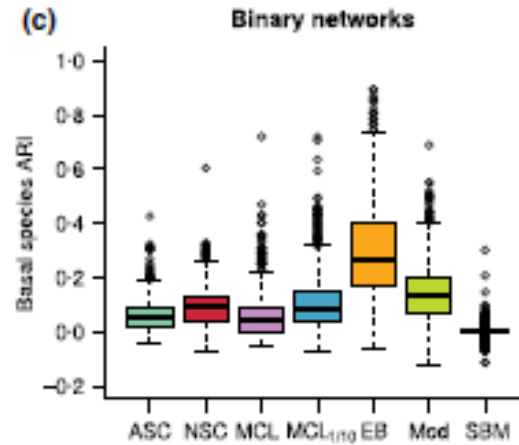
Which algorithm?

Unipartite networks

Bipartite networks



Yang et al. (2016) *SciRep*



Leger et al. (2015) *MethEcolEvol*

Block models

Idea: find blocks of nodes that “behave” similarly



Figure 6 Incidence matrix generated according to a LBM with three blocks of crops, two blocks of farms and $\pi = (0.5 \ 0.1 \ 0.6 \ 0.5 \ 0.6 \ 0.1)$. (A) Observed incidence matrix and (B) same incidence matrix re-organized and clustered in homogeneous blocks obtained by LBM inference.

Block models

Idea: find blocks of nodes that “behave” similarly

Different distributions for elements (Bernoulli, Poisson, ...)

Infer one parameter by block + group proportions

```
sbmnet <- sampleSimpleSBM(100, c(.5, .25, .25), list(mean =  
diag(.4, 3) + 0.05), model = 'bernoulli')  
sbmnet$networkData  
net.SBM <- estimateSimpleSBM(as.matrix(sbmnet$networkData))  
plot(net.SBM, 'expected')  
plot(net.SBM, 'data')
```

Modularity and blocks

Components of a network = species sets that can be linked by a series of edges

`count.components()`, `components()`, `largest_component()`

```
#### is the empirical food web structured by modules or blocks?
```

```
Find blocks for mat
```

```
Find modules for mat using the Louvain algorithm
```

```
Compare the two classifications using the function make_alluvial_2
```

```
#### are blocks/modules related to trophic levels?
```

```
Count the components of net.mat
```

```
Determine the trophic levels of net.mat
```

```
Plot the network net.mat using the layout layout_as_food_web
```

```
Plot the relationships between trophic levels, block memberships and module memberships
```

Modularity and blocks

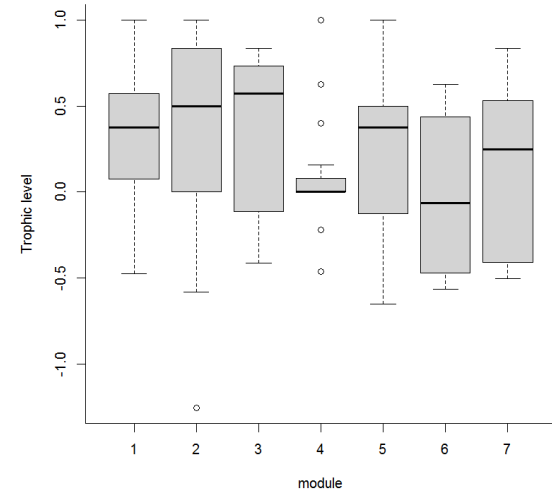
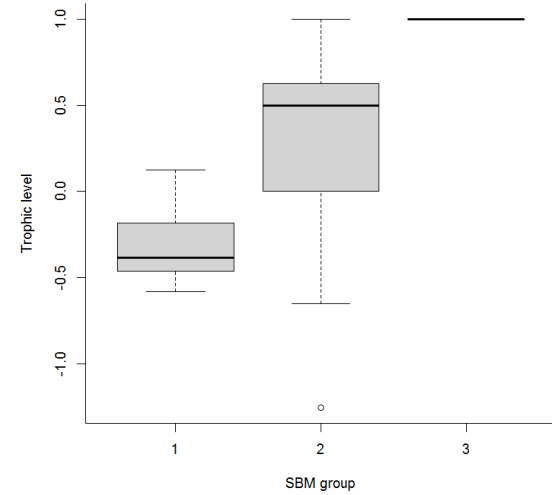
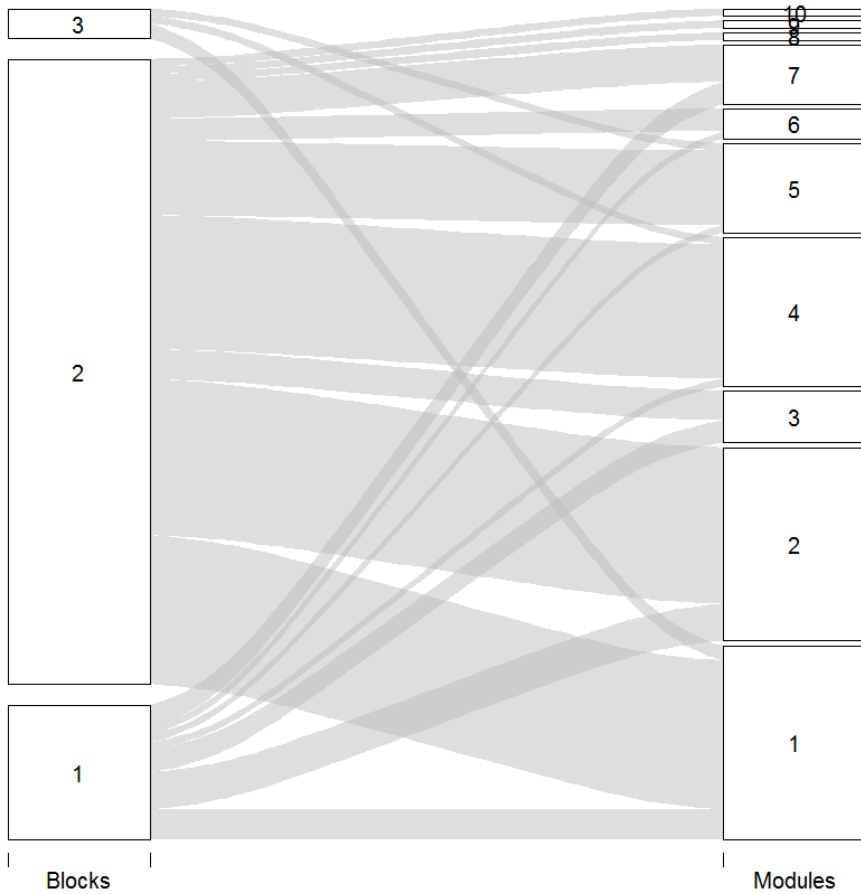
Components of a network = species sets that can be linked by a series of edges

`count.components()`, `components()`, `largest_component()`

```
#### is the empirical food web structured by modules or blocks?  
m.SBM <- estimateSimpleSBM(mat)  
modul <-  
  cluster_louvain(graph_from_adjacency_matrix(mat, mode="undirected"))  
make_alluvial_2(m.SBM$memberships, modul$membership, "Blocks", "Modules")
```

```
#### are blocks/modules related to trophic levels?  
count_components(net.mat)  
net.comp <- components(net.mat)  
tl.1 <- trophic_levels(largest_component(net.mat))  
plot(largest_component(net.mat), layout = layout_as_food_web)  
plot(tl.1 ~ as.factor(m.SBM$indMemberships[which(net.comp$membership==1)  
  , ] %*% (1:3)), xlab="SBM group", ylab="Trophic level")  
plot(tl.1 ~ as.factor(modul$membership[which(net.comp$membership==1)]), x  
  lab="module", ylab="Trophic level")
```

Modularity and blocks



Spectral clustering

Idea: the Laplacian matrix of the graph, given by

$$L = D - A$$

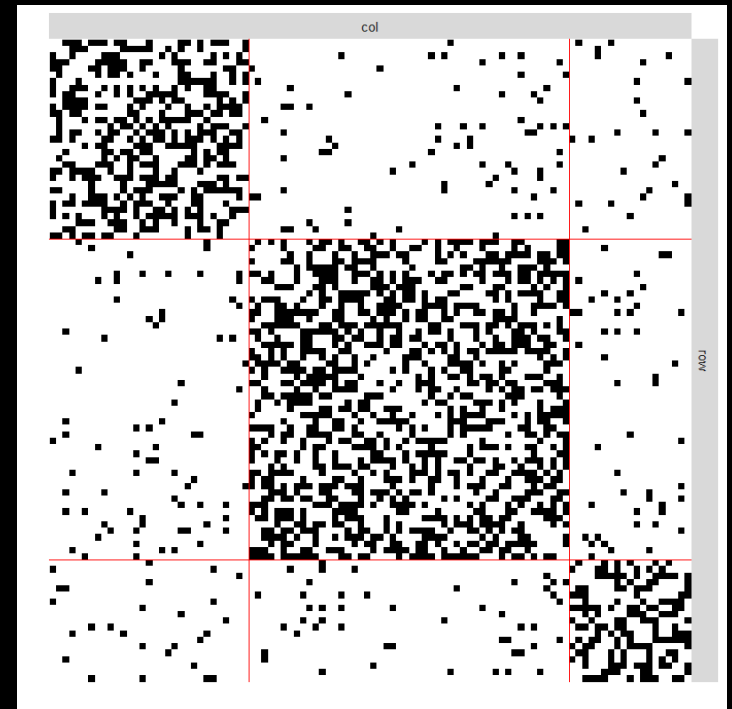
where D is the diagonal matrix with node degrees and A is the adjacency matrix,

is able to find components of the graph (= parts that are disconnected from one another) as the eigenvectors of eigenvalue 0

Heuristics: the eigenvectors associated with the low eigenvalues of L characterize the membership of nodes to “clusters” (through K-means algo)

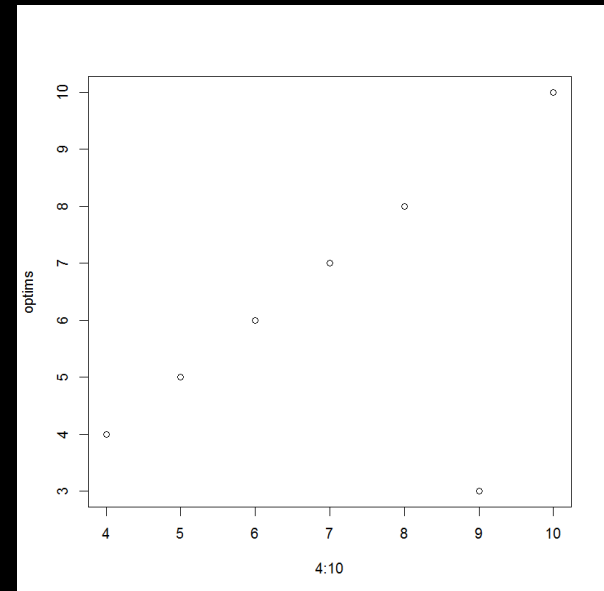
Spectral clustering

```
SC<-  
  spectral_clustering(graph_from_adjacency_matrix(sbmnet  
    $networkData),3)  
plotMyMatrix(sbmnet$networkData,clustering=list("row"=SC  
  ,"col"=SC))
```



Spectral clustering

```
laplacian_spectral_gap(graph_from_adjacency_matrix(sbmnet$networkData))
optims<-sapply(4:10,function(n)
  laplacian_spectral_gap(graph_from_adjacency_matrix(sampleSimpleSBM(100, rep(1/n, n), list(mean = diag(.4, n) + 0.05), model = 'bernoulli')$networkData))$optim_n)
par(mfrow=c(1,1))
plot(4:10,optims)
```



Nestedness

- **Idea:** measure the tendency for specialists to only interact with a subsample of interactors of generalists
- Several indices

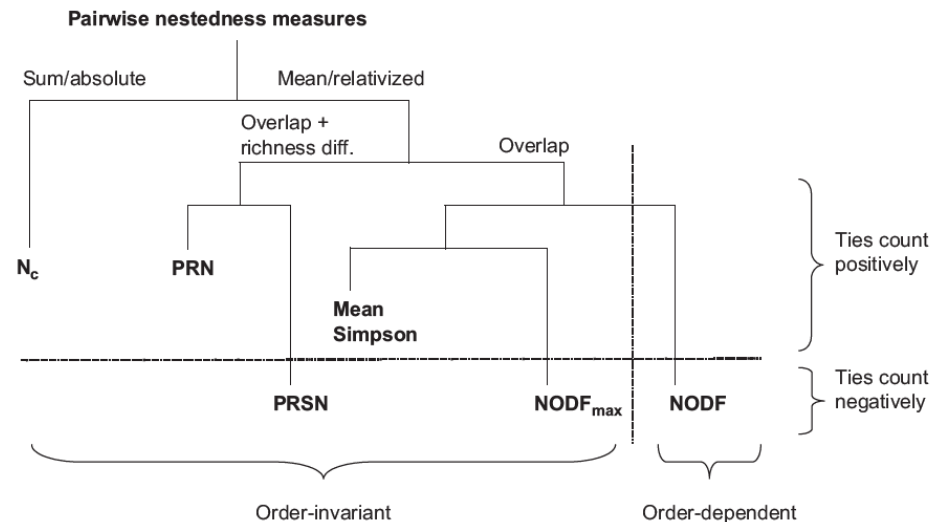


Figure 4. A tree-like summary of conceptual and technical issues to be considered when selecting pairwise measures of nestedness.

Nestedness

- Not necessarily a fruitful concept because...
 - theoretically questioned (James et al. 2012 = connectance)
 - choosing the good index is hard (Podani & Schmera 2012)
 - different indices give different results (Thomas et al. 2015)
 - for power law degree distribution, nestedness is completely determined by the exponent (Astegiano et al. 2015)
 - nestedness of common datasets is natural when sampling from the right matrix ensemble (Payrató-Borràs et al. 2019)

Last words

- Ecological interaction networks can be used to study community/ecosystem properties
- Random network models can help gauge generalities (invariants) and specificities
- All network patterns do not have a mechanistic model-based explanation (yet), but some do
- Interaction networks data of different types (interaction occurrences vs. interaction strengths) lend themselves to different analyses

Literature

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