Mesoscopic analysis of ecological networks using Hill numbers

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Jackson Pollock

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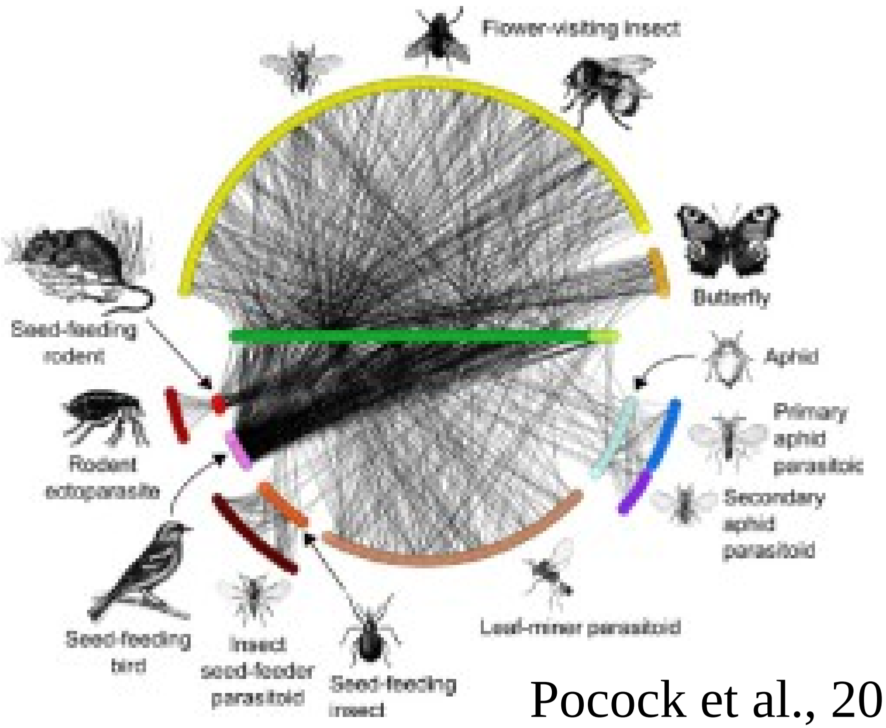
Aim : assess the diversity of one or several ecological communities that are interacting through an ecological network

α-diversity : *richness of a community*

β-diversity : “*the extent of change in community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments*” Whittaker 1960

Classic diversity index omit interactions



Pocock et al., 2012

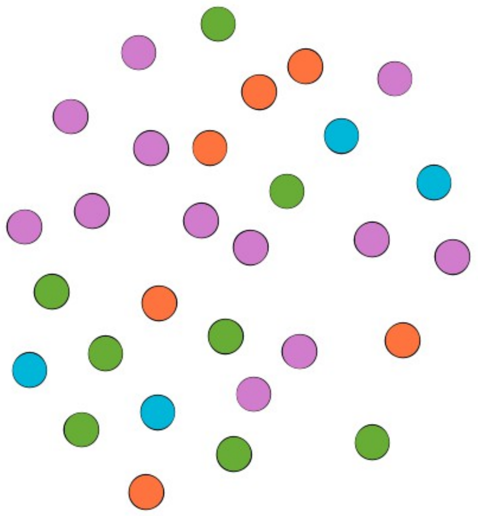
Measuring diversity of a community ?

A diversity of metrics

- Shannon entropy
- Simpson index

Unifying framework : True diversity (Hill numbers, 1973)

set of organisms
colours are species



Suppose that (E) is composed of N individuals, belonging to S distinct species, with relative abundances : $(p_1, ..., p_s)$

$$M_{q-1} = \sqrt[q-1]{\sum_{i=1}^{S} p_i p_i^{q-1}}$$

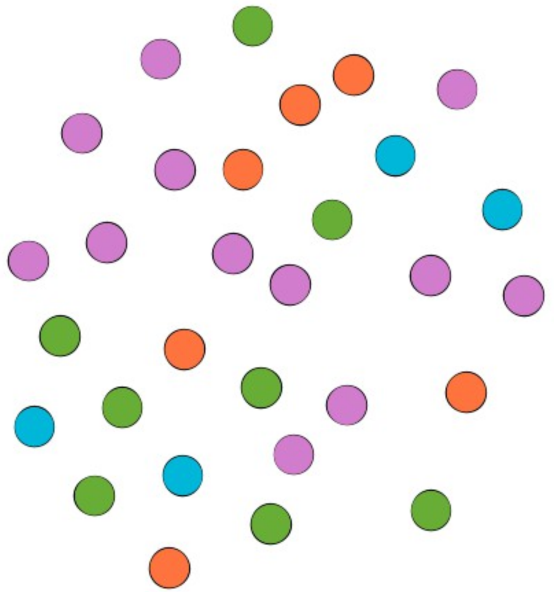
Generalized mean of order q-1

$$D_q = 1/M_{q-1} = (\sum_{i=1}^{S} p_i^q)^{1/(1-q)}$$

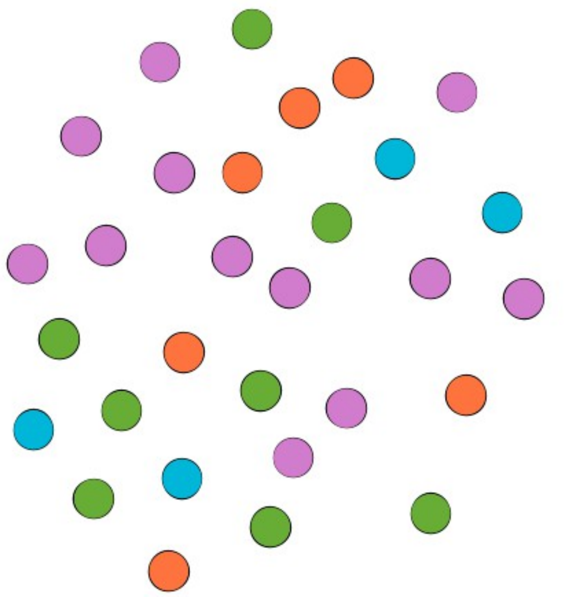
$$D_1 = exp(-\sum_{i=1}^{S} p_i log(p_i))$$

$$D_q = 1/M_{q-1} = (\sum_{i=1}^{S} p_i^q)^{1/(1-q)}$$

Hill number of order q



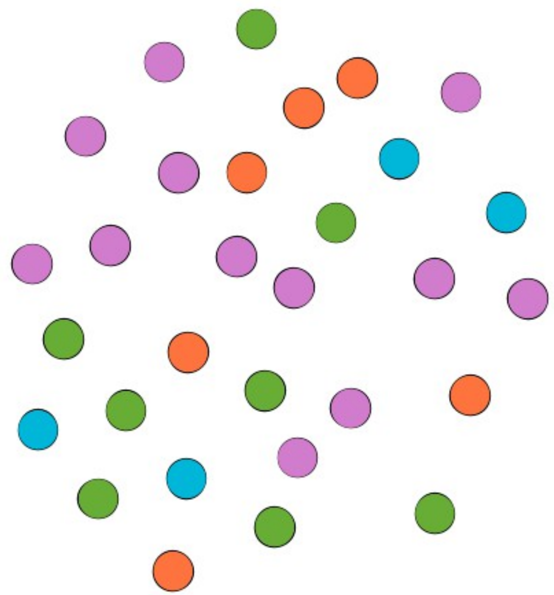
$$D_q = 1/M_{q-1} = (\sum_{i=1}^{S} p_i^q)^{1/(1-q)}$$ Hill number of order q



$$D_0 = S$$ Species richness

$$D_1 = exp(\sum_{i=1}^{S} p_i log(p_i))$$ Shannon entropy (exp)

$$D_2 = \frac{1}{\sum_{i=1}^{S} p_i^2}$$ Inverse of Simpson index



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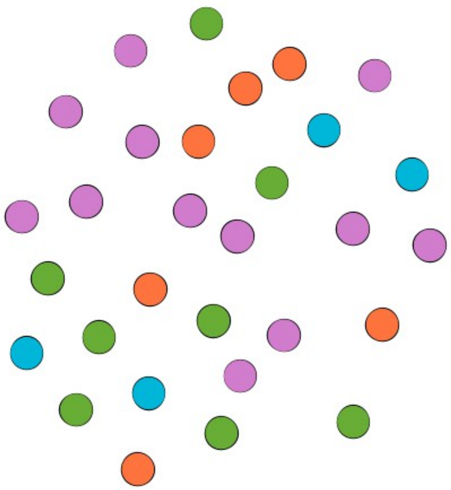
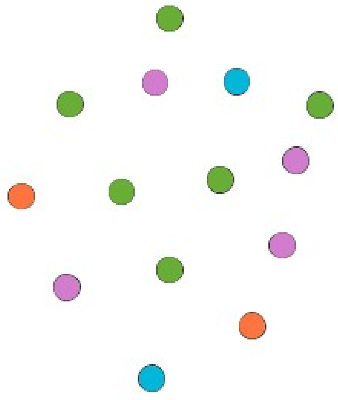
α-diversity

Comparing two communities

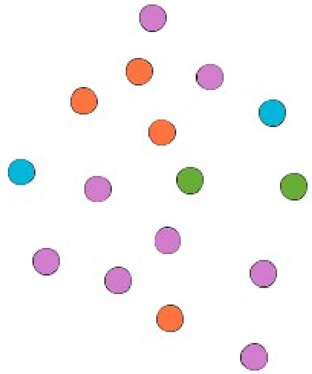
β-diversity concept :
"The extent of change in community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments' Whittaker, 1960



Meta-community



community 1



community 2

Comparing two communities

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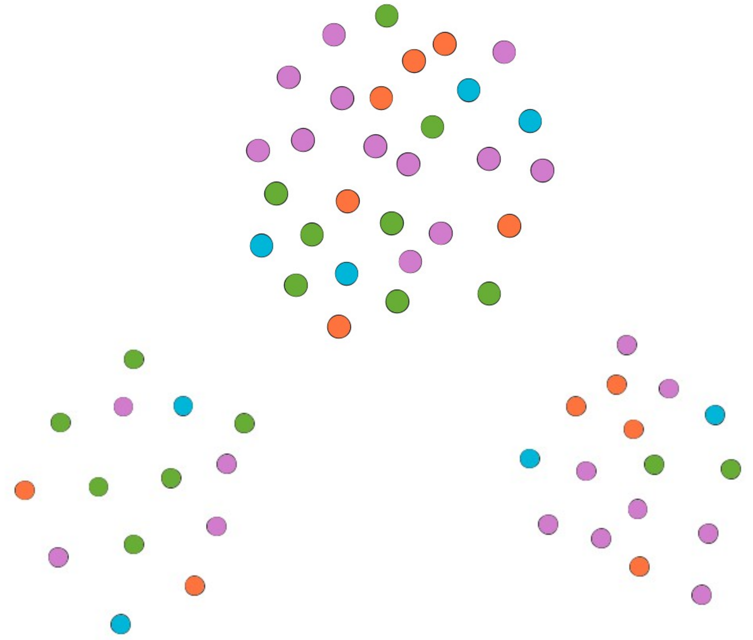


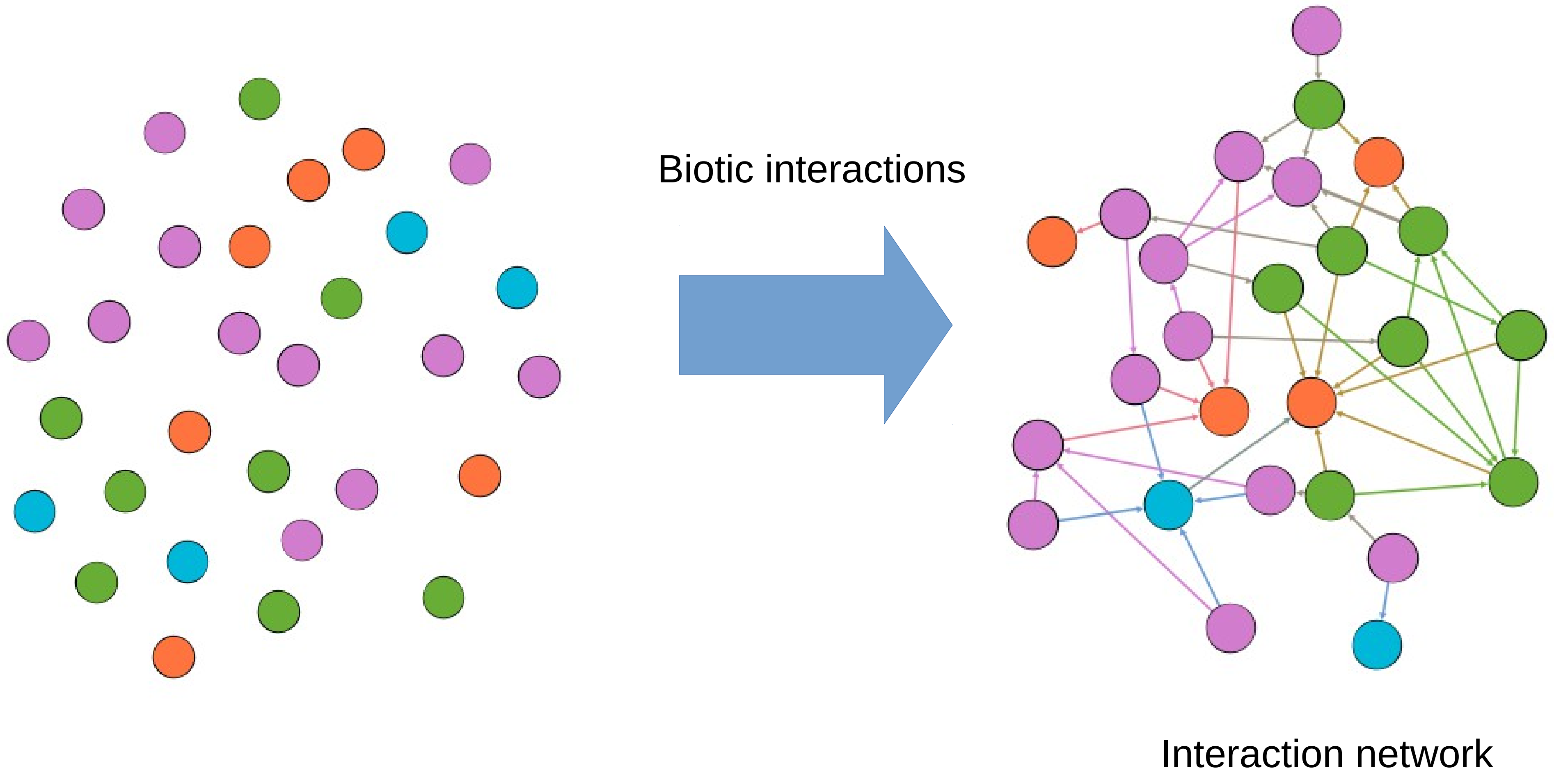
$$\beta(q) = \begin{cases} \dfrac{\gamma(q)}{\left(\omega(\alpha_1(q))^{1-q} + (1-\omega)(\alpha_2(q))^{1-q}\right)^{\frac{1}{1-q}}} & q \neq 1 \\ \dfrac{\gamma(q)}{exp(\omega log(\alpha_1(q)) + (1-\omega) log(\alpha_2(q)))} & q = 1 \end{cases}$$

$$\omega = \frac{n_1}{n_1+n}$$

$$1 \leq \beta(q) \leq 2$$
$$\beta(q) \leftarrow \beta(q) - 1$$
$$0 \leq \beta(q) \leq 1$$

ratio of generalised means in presence of two classifications (species and space)
cf Tuomisto, 2010, Ecography

β-diversity


Biotic interactions
Interaction network

G a network ,A its adjacency matrix,
V(G) set of nodes, $|V(G)| = n$
$E(G)$ *set of edges*, $|E(G)| = L$
Q *set of classes*(*e.g. species, functional groups*)

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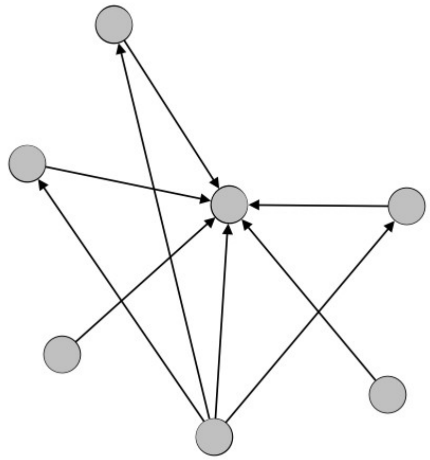
Connectance

Q=$\{q\}$
$\pi = Pr(i \rightarrow j | i, j \in q)$
$C = \hat{\pi} = L/S^2$

Connectance does not take into account species identity

Not a measure of diversity, since there is only one group



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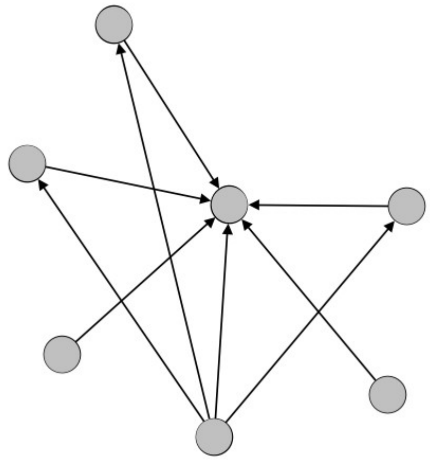
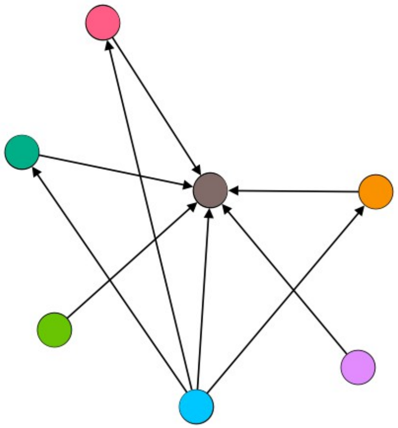
Link number

Q=$\{S_1, ..., S_n\}$
$\pi_{i,j} = Pr(i \to j|, i \in S_i, j \in S_j)$
$\hat{\pi}_{i,j} = A_{i,j} \in \{0, 1\}$
$L = \sum_{1 \leq i,j \leq n} A_{i,j}$

Measure of α-diversity





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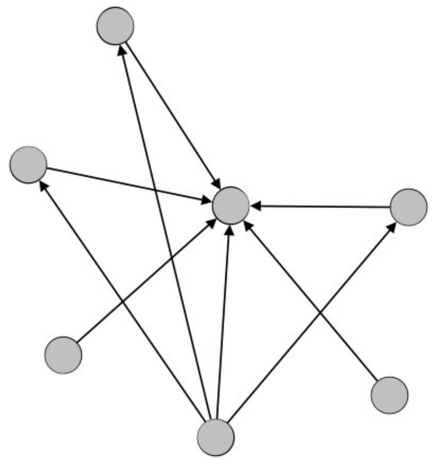
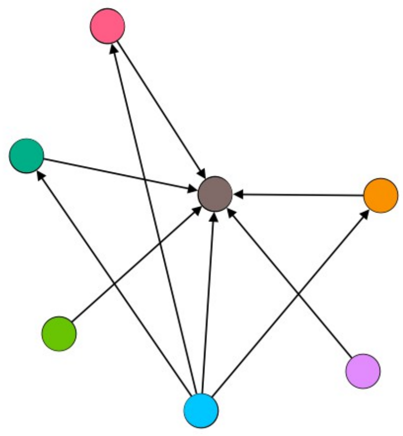
scale (size of Q)

Macroscopic scale

Microscopic scale





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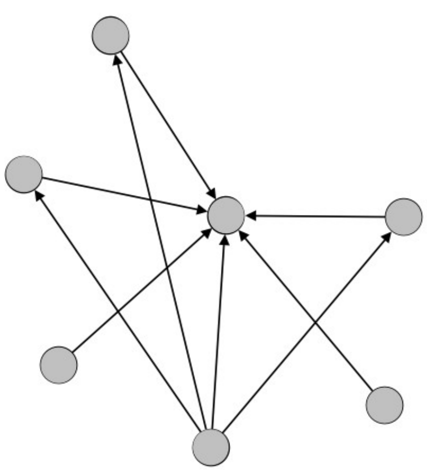
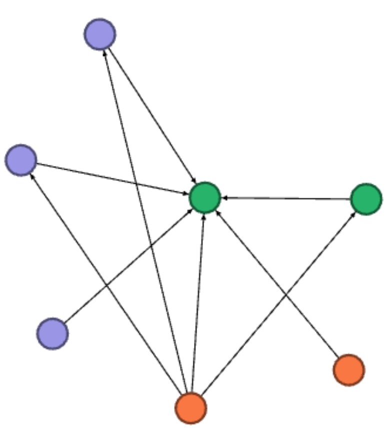
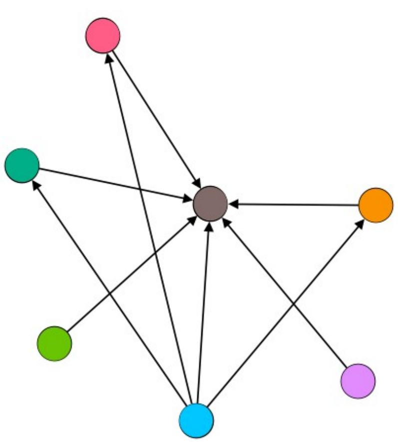
scale (size of Q)

Macroscopic scale

Microscopic scale

Mesoscopic scale ?

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$Q = \{1, ..., |Q|\} \quad 1 \leq |Q| \leq n$

$$\alpha_k = \frac{\sum_{i=1}^{n} \mathbb{1}(i \in k)}{n}$$

group proportion

$$l_{k,l} = \frac{\sum_{i=1}^{n} \mathbb{1}(i \to j, i \in k, j \in l)}{L}$$

link proportion (connecting group k and l)

$$\pi_{k,l} = Pr(i \to j | i \in k, j \in l)$$

$$\hat{\pi}_{k,l} = \frac{\sum_{i=1}^{n} \mathbb{1}(i \to j, i \in k, j \in l)}{\sum_{i=1}^{n} \mathbb{1}(i \in k) \sum_{j=1}^{n} \mathbb{1}(j \in l)}$$

connectance between class k and l

If there is only one class, then it's a scalar equal to connectance

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$$\mathrm{D}_{q,\alpha} = (\textstyle\sum_{k=1}^{|Q|} \alpha_k^q)^{\frac{1}{1-q}}$$ → Hill number on group proportion

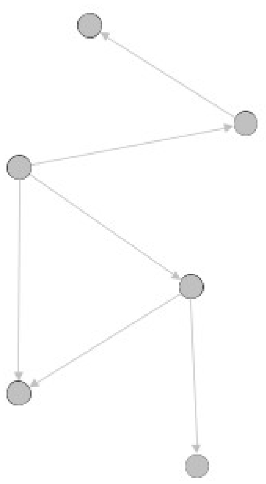
$$D_{q,l} = (\textstyle\sum_{1 \leq k,l \leq |Q|} l_{k,l}^q)^{\frac{1}{1-q}}$$ → Hill number on links proportion

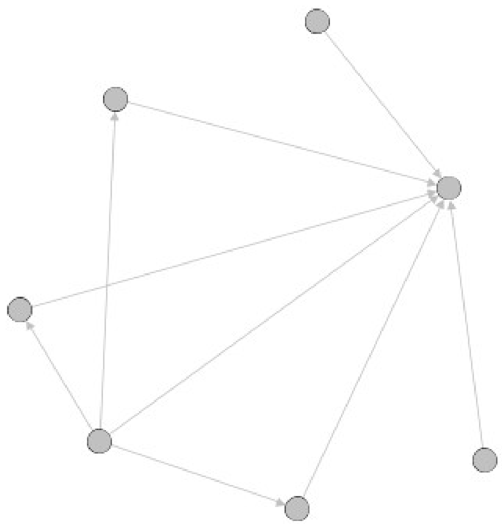
$$D_{q,\pi} = (\textstyle\sum_{1 \leq k,l \leq |Q|} (\frac{\pi_{k,l}}{\sum_{k,l} \pi_{k,l}})^q)^{\frac{1}{1-q}}$$ → Hill number on connectance matrix

The network dissimilarity problem

G_1 $a\ network, A_1\ its\ adjacency\ matrix$
$V(G_1)\ set\ of\ nodes, |V(G_1)| = n_1$
$E(G_1)\ set\ of\ edges, |E(G_1)| = L_1$

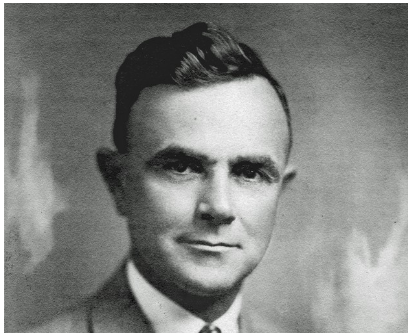
G_2 $a\ network, A_2\ its\ adjacency\ matrix$
$V(G_2)\ set\ of\ nodes, |V(G_2)| = n_2$
$E(G_2)\ set\ of\ edges, |E(G_2)| = L_2$





Macroscopic comparison

Q : set of groups of the metaweb
Elton niches= species that have a similar position in the network
Q={q}
Compare connectance of the two networks



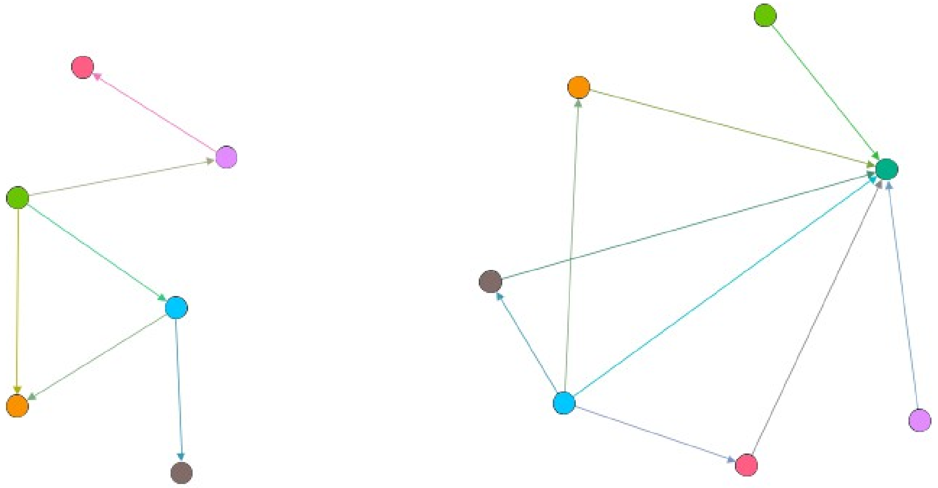
Charles Elton (1900-1991)

Microscopic comparison

$$Q_1 = \{S_1, ..., S_{n_1}\}$$
$$Q_2 = \{S_1, ..., S_{n_2}\}$$
$$Q_{meta} = Q_1 \cup Q_2$$
$$Q_{inter} = Q_1 \cap Q_2$$

What already exists : Poisot, 2012

$$\beta_{WN} = 1 - \frac{A_1 \odot A_2}{(|A_1| + |A_2|)/2}$$



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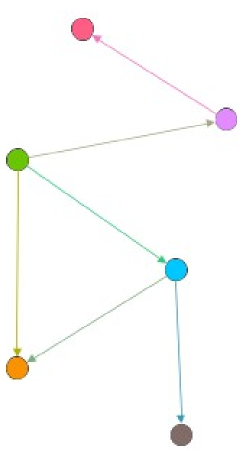
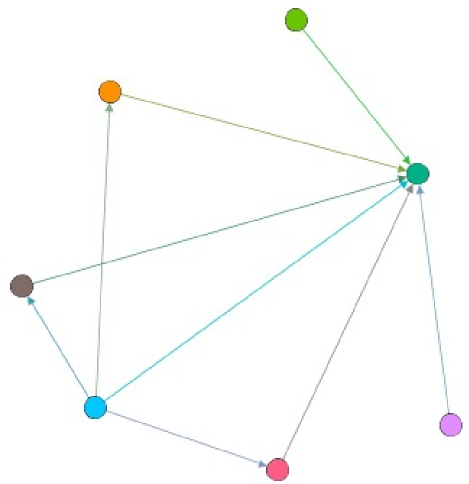




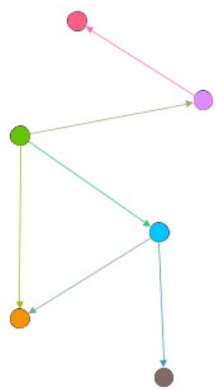
What already exists : Poisot, 2012

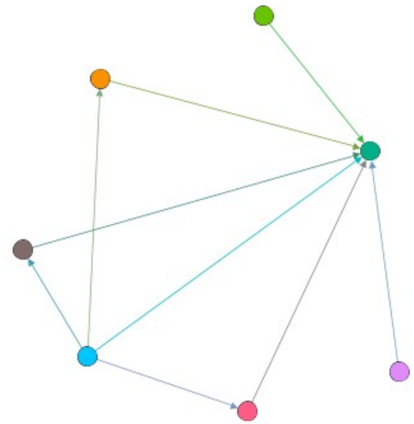
$$\beta_{WN} = 1 - \frac{A_1 \odot A_2}{(|A_1| + |A_2|)/2}$$

Both species turnover and plasticity of interactions (at a species level) contribute to β_{WN}

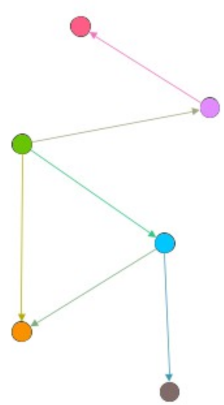
Aim : seperate these two effects

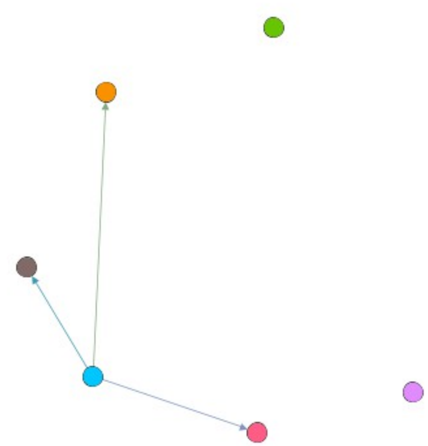
Microscopic comparison





$$G_1^{inter} = induced.subgraph(G_1, Q_{inter})$$
$$A_1^{inter} : adjacency\, matrix$$
$$G_2^{inter} = induced.subgraph(G_2, Q_{inter})$$
$$A_2^{inter} : adjacency\, matrix$$





$$\beta_{WN} = 1 - \frac{A_1 \odot A_2}{(|A_1| + |A_2|)/2}$$

Total dissimilarity

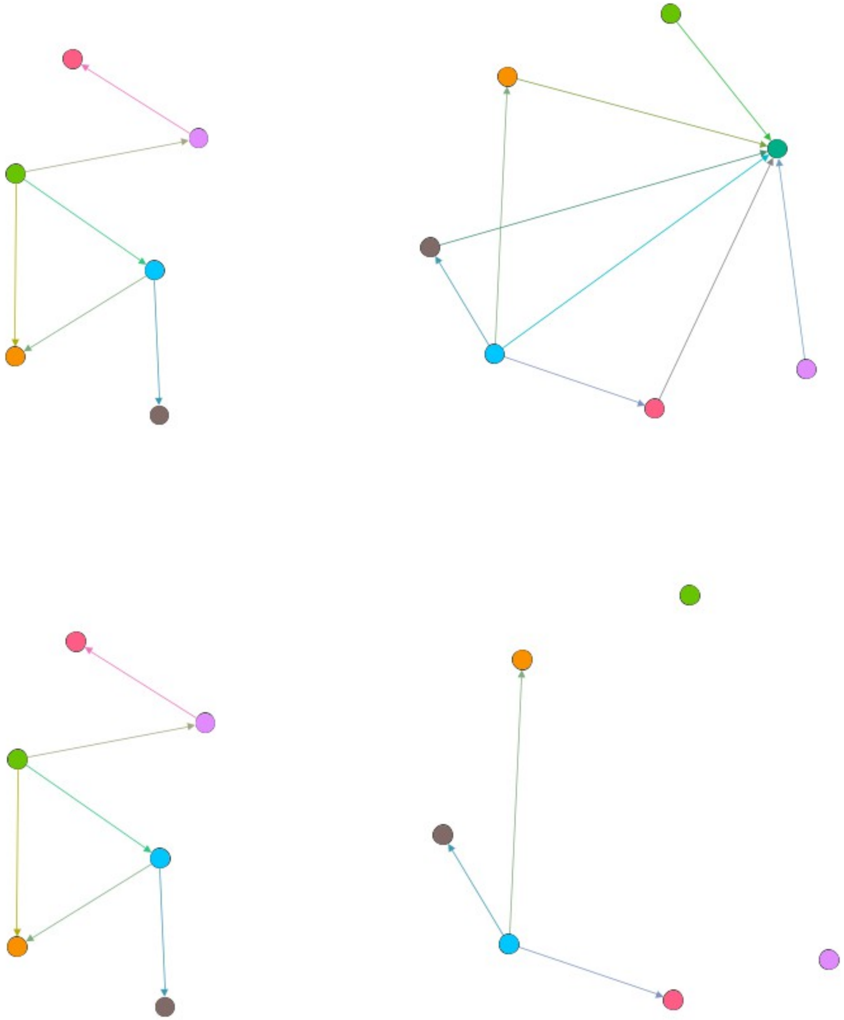
$$\beta_{OS} = 1 - \frac{A_1^{inter} \odot A_2^{inter}}{(|A_1^{inter}| + |A_2^{inter}|)/2}$$

Dissimilarity due to **plasticity of interactions**

$$\beta_{ST} = \beta_{WN} - \beta_{OS}$$

Dissimilarity due to **species turnover**

Microscopic comparison



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Total dissimilarity

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Dissimilarity due to **plasticity of interactions**

$$\beta_{ST} = \beta_{WN} - \beta_{OS}$$

Dissimilarity due to **species turnover**

Mesoscopic comparison ?

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$$Q_1 = \{1, ..., |Q_1|\} \qquad 1 \leq |Q_1| \leq n$$

$$G_2\ a\ network, A_2\ its\ adjacency\ matrix,$$
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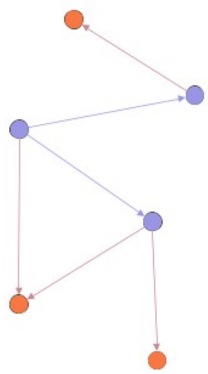
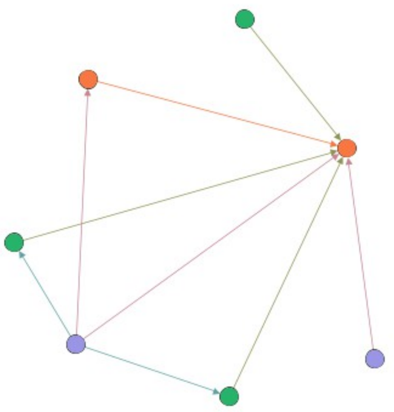
$$Q_{inter} = Q_1 \cap Q_2$$



G1



G2

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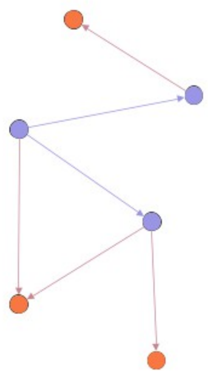

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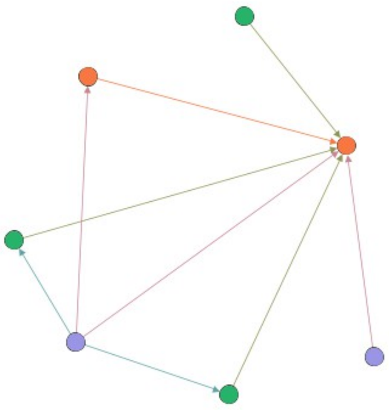

G2

$$\alpha_{G_{meta},k} = \omega \alpha_{G_2,k} + (1-\omega)\alpha_{G_1,k}$$
$$\omega = \frac{n_1}{n_1+n_2}$$

$$l_{G_{meta},k} = \omega l_{G_2,k} + (1-\omega) l_{G_1,k}$$
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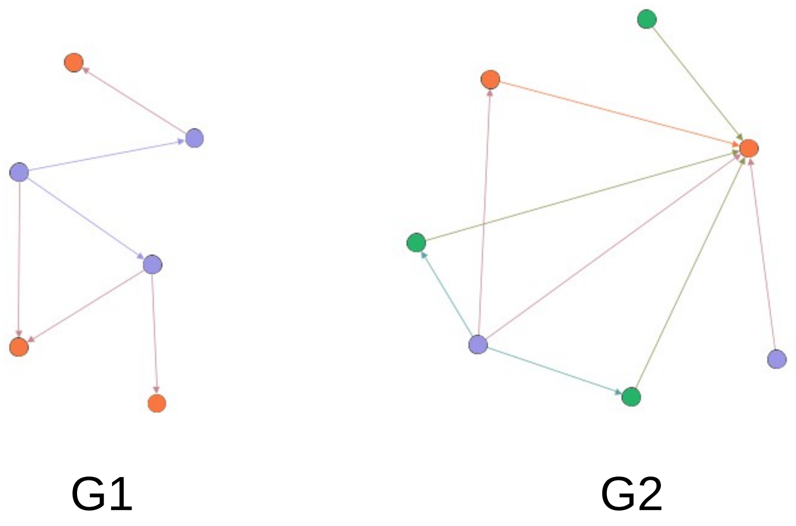

$$\beta_\alpha(q) = \frac{D_\alpha^{G_{meta}}(q)}{(\omega(D_\alpha^{G_1}(q))^{1-q}+(1-\omega)(D_\alpha^{G_2}(q)^{1-q})^{\frac{1}{1-q}}}$$
$$\beta_L(q) = \frac{D_L^{G_{meta}}(q)}{(\omega(D_L^{G_1}(q))^{1-q}+(1-\omega)(D_L^{G_2}(q)^{1-q})^{\frac{1}{1-q}}}$$

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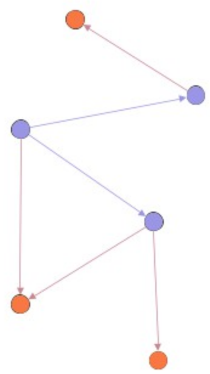
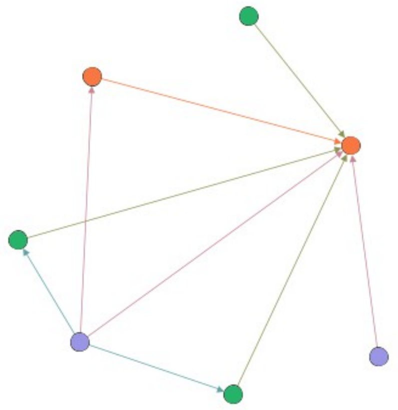


G1

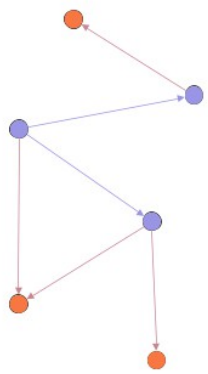


G2

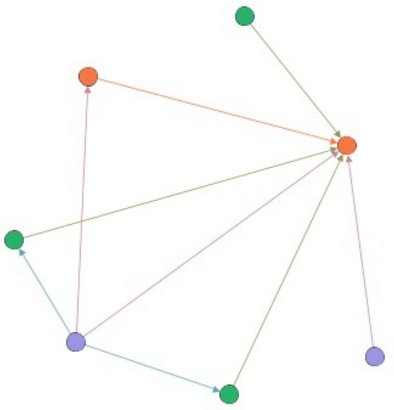
$$1 \leq \beta_{\alpha,L}(q) \leq 2$$
$$\beta_{\alpha,L}(q) \leftarrow \beta_{\alpha,L}(q) - 1$$
$$0 \leq \beta_{\alpha,L}(q) \leq 1$$

$$\beta_\alpha(q) = \frac{D_\alpha^{G_{meta}}(q)}{\left(\omega(D_\alpha^{G_1}(q))^{1-q} + (1-\omega)(D_\alpha^{G_2}(q))^{1-q}\right)^{\frac{1}{1-q}}}$$

$$\beta_L(q) = \frac{D_L^{G_{meta}}(q)}{\left(\omega(D_L^{G_1}(q))^{1-q} + (1-\omega)(D_L^{G_2}(q))^{1-q}\right)^{\frac{1}{1-q}}}$$



G1



G2

A particular case : Tim Poisot case (microscopic turnover)

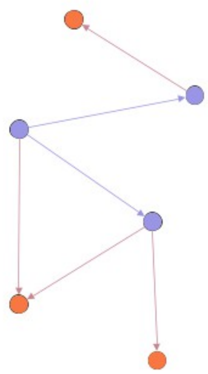
$$Q_1 = \{1, ..., n_1\}$$
$$Q_2 = \{1, ..., n_2\}$$
$$\omega = 1/2$$

Easy to show that :

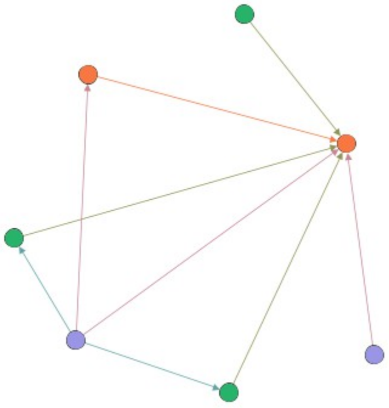
$$\beta_\alpha(0) = \beta_S$$
$$\beta_L(0) = \beta_{WN}$$

$$\beta_\alpha(q) = \frac{D_\alpha^{G_{meta}}(q)}{(\omega(D_\alpha^{G_1}(q))^{1-q}+(1-\omega)(D_\alpha^{G_2}(q)^{1-q})^{\frac{1}{1-q}}}$$

$$\beta_L(q) = \frac{D_L^{G_{meta}}(q)}{(\omega(D_L^{G_1}(q))^{1-q}+(1-\omega)(D_L^{G_2}(q)^{1-q})^{\frac{1}{1-q}}}$$



G1



G2

A particular case : Tim Poisot case (microscopic turnover)

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$$\omega = 1/2$$

Easy to show that :

$$\beta_\alpha(0) = \beta_S$$
$$\beta_L(0) = \beta_{WN}$$

Do change of link diversity reflect change in connectivity ?
Yes, but there is a group size effect too !

Here, we work on : G_1^{inter} G_2^{inter}

$$\left(\pi_{k,l}^{G_1^{inter}}\right)_{1\leqslant k,l\leqslant |Q_{inter}|}$$
$$\left(\pi_{k,l}^{G_2^{inter}}\right)_{1\leqslant k,l\leqslant |Q_{inter}|}$$

$$\pi_{k,l}^{G_{meta}^{inter}} = \omega\pi_{k,l}^{G_1^{inter}} + (1-\omega)\pi_{k,l}^{G_2^{inter}}$$

Here, we work on : G_1^{inter}
G_2^{inter}

$$\left(\pi_{k,l}^{G_1^{inter}}\right)_{1\leqslant k,l\leqslant |Q_{inter}|}$$
$$\left(\pi_{k,l}^{G_2^{inter}}\right)_{1\leqslant k,l\leqslant |Q_{inter}|}$$

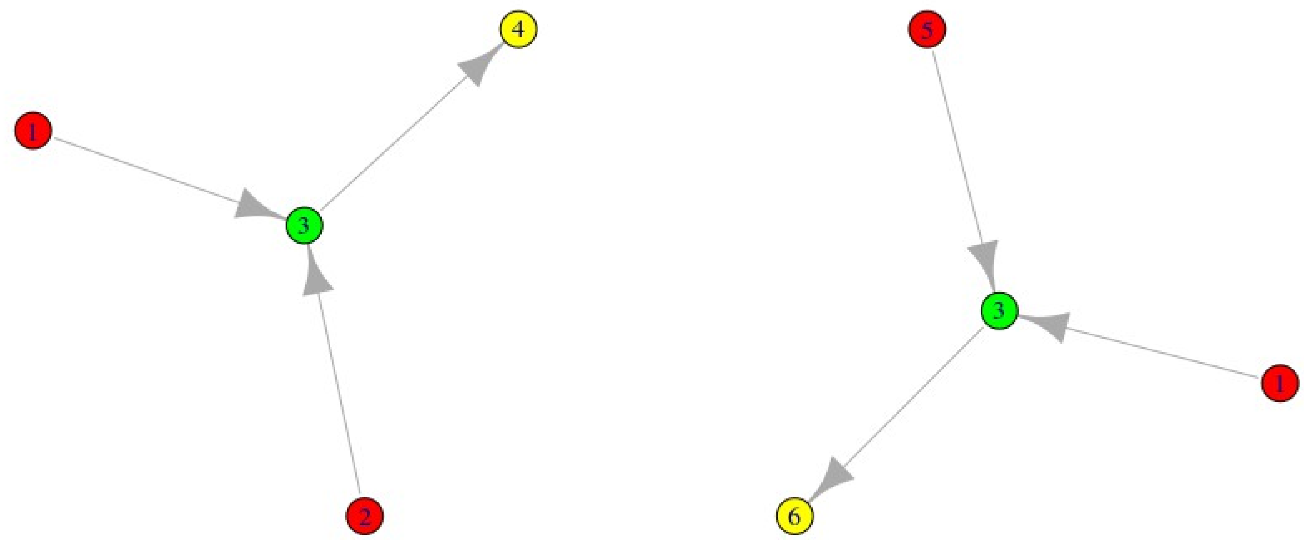
$$\pi_{k,l}^{G_{meta}^{inter}} = \omega\pi_{k,l}^{G_1^{inter}} + (1-\omega)\pi_{k,l}^{G_2^{inter}}$$

$$\beta_\pi(q) = \frac{D_\pi^{G_{meta}^{inter}}(q)}{\left(\omega(D_\pi^{G_1^{inter}}(q))^{1-q}+(1-\omega)(D_\pi^{G_2^{inter}}(q)^{1-q}\right)^{\frac{1}{1-q}}}$$

A particular case : Tim Poisot case (microscopic scale)

$Q_1 = \{1, ..., n_1\}$
$Q_2 = \{1, ..., n_2\}$
$\omega = 1/2$

$$\beta_\pi(0) = \beta_{OS}$$



Macroscopic scale

C=0.19

Mesoscopic scale

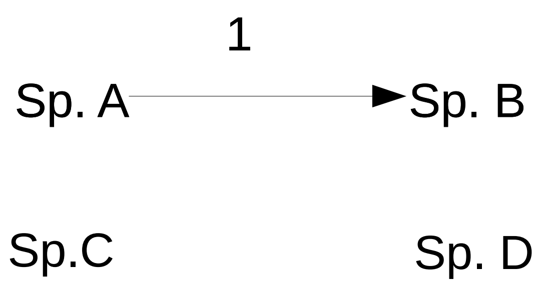
$\beta_{\alpha}=0$
$\beta_{L}=0$
$\beta_{\pi}=0$

Microsocopic scale

$\beta_{S}=0.5$
$\beta_{WN}=2/3$
$\beta_{OS}=0$
$\beta_{ST}=2/3$

A trait perspective

Forbidden links between species ?



At individual level :

$$\mathrm{Pr}(\mathrm{i}\rightarrow j|i \in A, j \in B) = 1$$

$$Pr(i \rightarrow j|i \in C, j \in D) = 0$$

A trait perspective

Forbidden links between species ?

$$\text{Sp. A} \xrightarrow{1} \text{Sp. B}$$

Sp.C   Sp. D

$$\mathrm{Pr}(\mathrm{i} \rightarrow j | i \in A, j \in B) = 1$$
$$Pr(i \rightarrow j | i \in C, j \in D) = 0$$

These binary relations neglect the intraspecific trait variability compared to interspecific trait variability

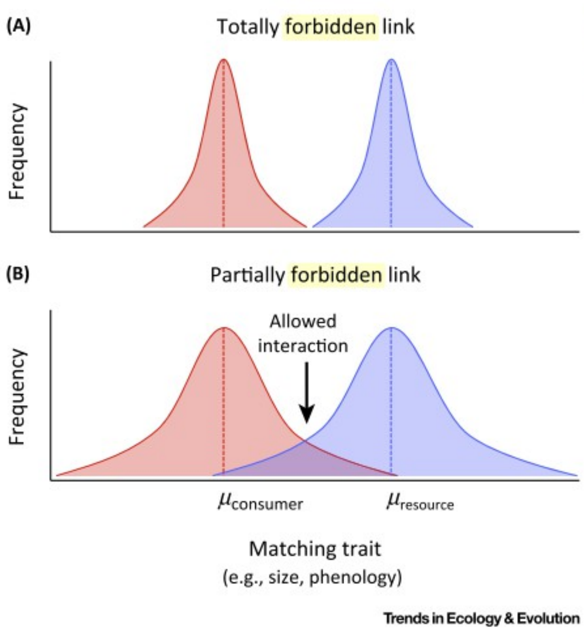


Figure 1. Frequency Distribution of Matching Traits (e.g., Body Size or Phenology) in a Consumer and a Resource Species. Interaction is possible whenever $x_{consumer} \geq x_{resource}$. (A) Mismatching between both trait means and intraspecific variability prevent interaction, leading to a totally forbidden link. (B) Mismatching occurs between trait means but intraspecific variability allows interaction, leading to a partially forbidden link. The difference between (A) and (B) – thus, our ability to infer interactions – may depend on how broadly intraspecific trait variability has been assessed in space and time (Box 1).

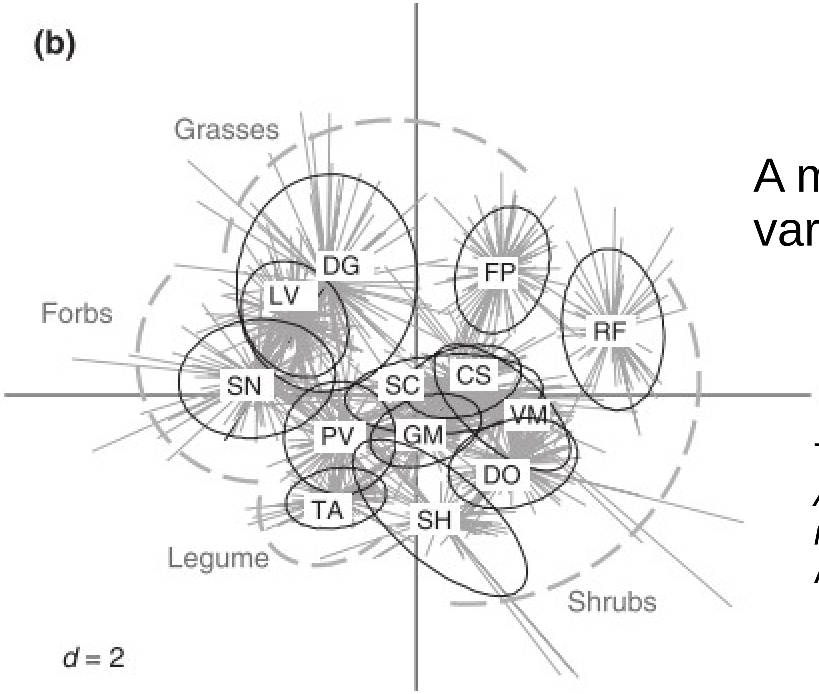
Taken from :
The labile limit of forbidden interactions
Gonzalez-Varo
Trends in Ecology and Evolution, 2016

$$\text{Sp. A} \xrightarrow{\pi} \text{Sp. B}$$

$$Pr(i \rightarrow j | i \in A, j \in B) = \pi$$

A trait perspective

Can we neglect intra-specific traits variability ?

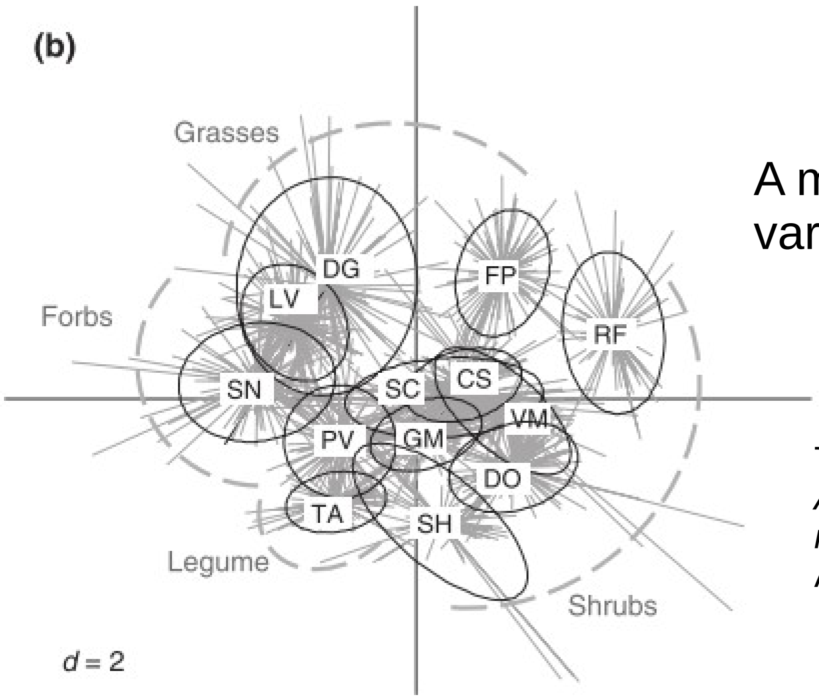


A mono-trophic view of traits intra/interspecific variability

Taken from :
A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits
Albert et al., Functionnal Ecology, 2010

A trait perspective

Can we neglect intra-specific traits variability ?



A mono-trophic view of traits intra/interspecific variability

Taken from :
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For trophic networks :
Interaction is the resultant of a match between a vulnerability trait (prey) and a foraging trait (predator)
see : Gravel et al., 2016

A trait perspective

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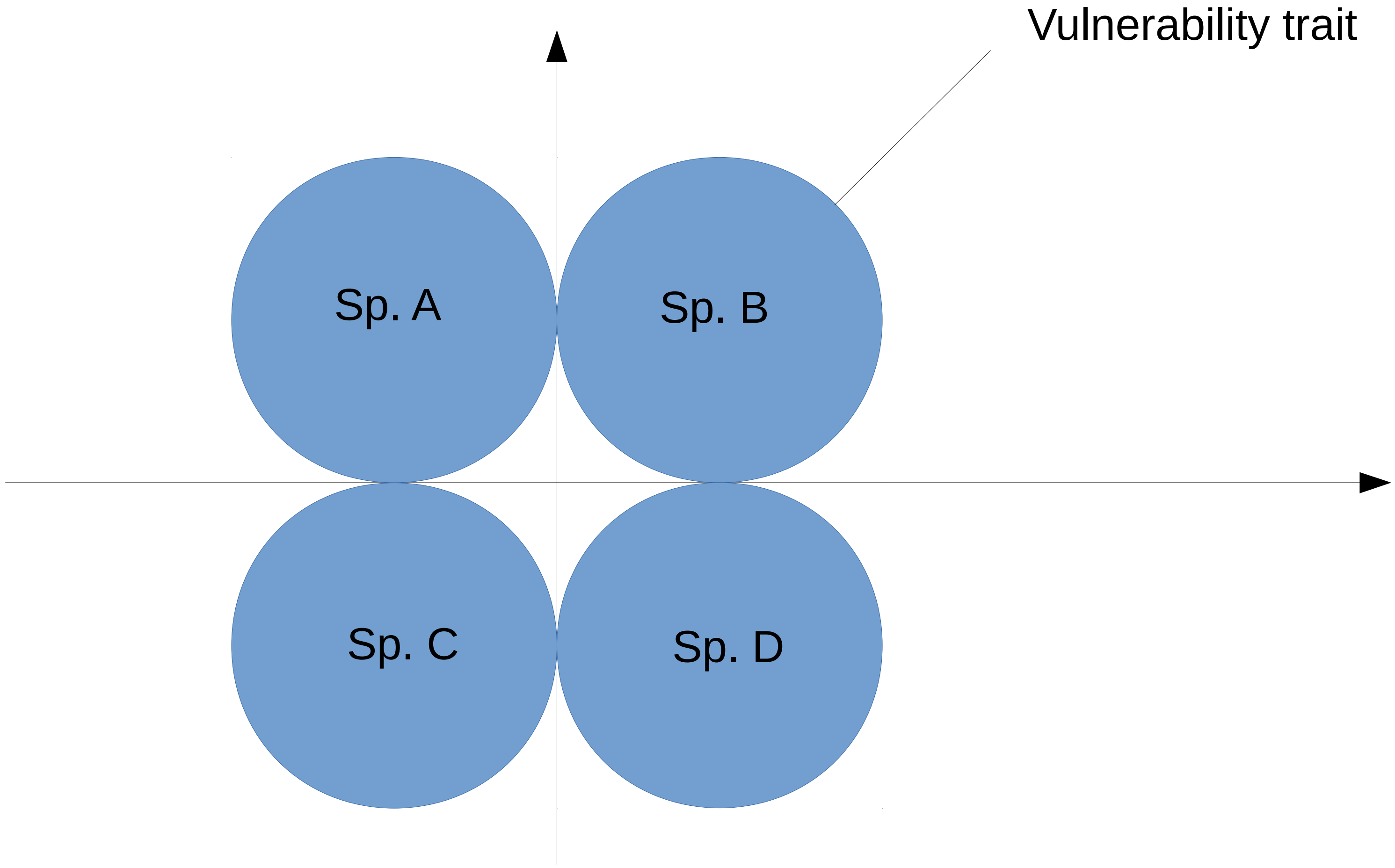

A trait perspective

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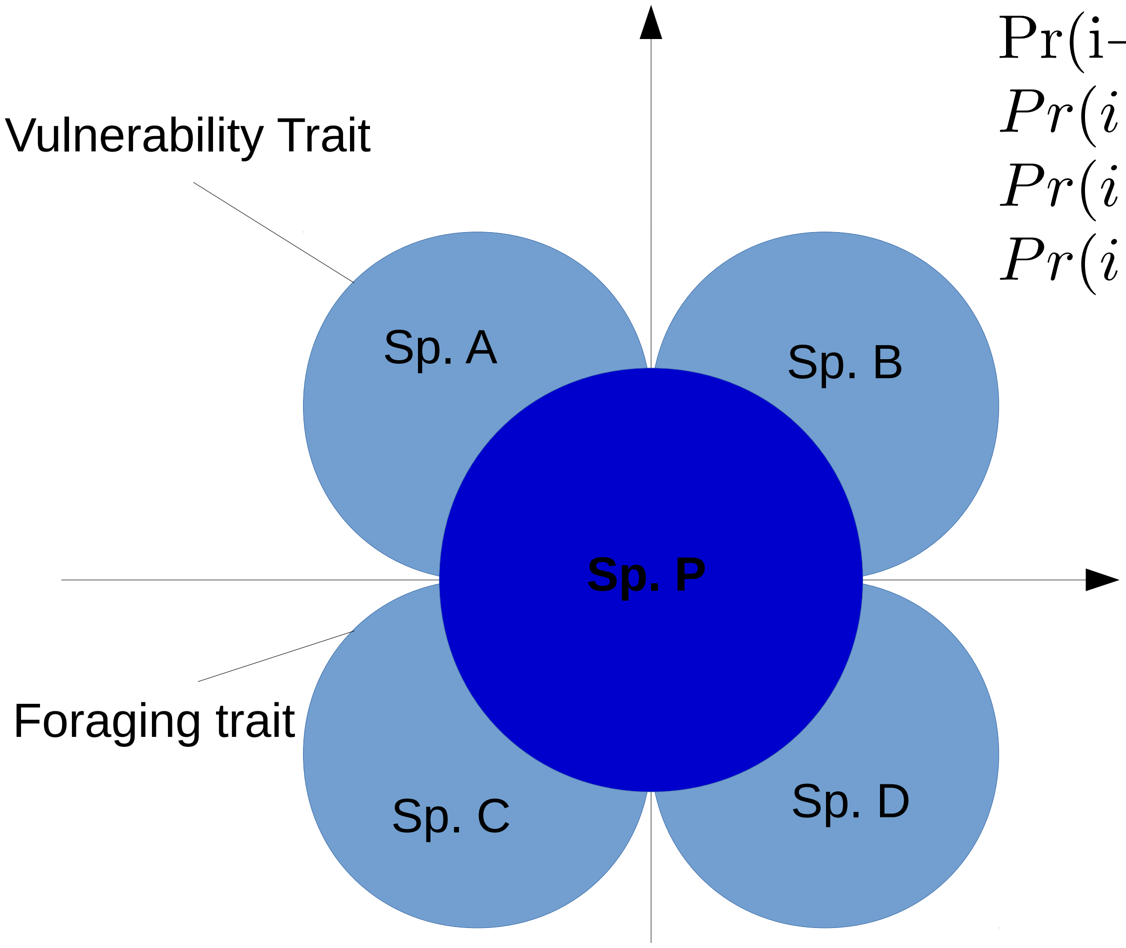
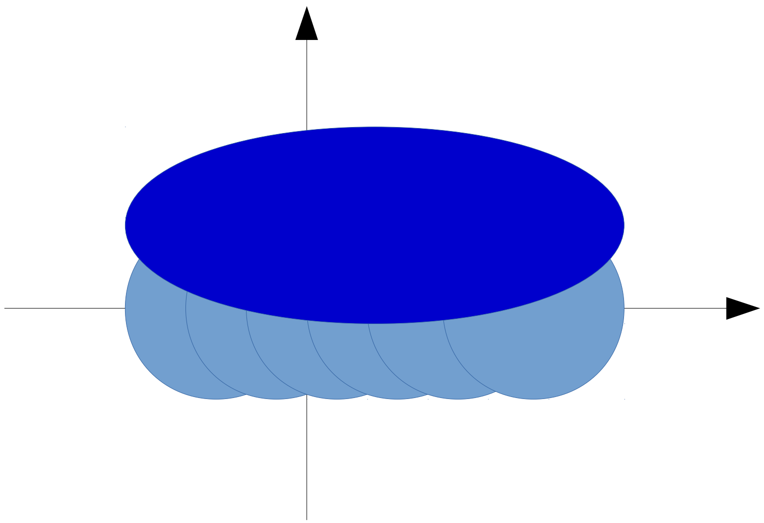
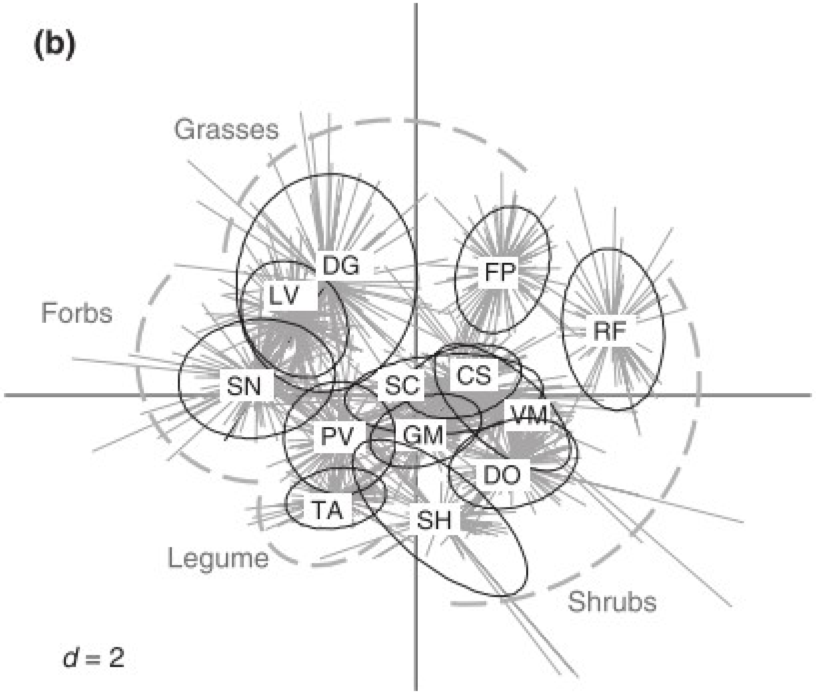


$$\mathrm{Pr}(\mathrm{i} \rightarrow j | i \in A, j \in P) = \pi$$
$$Pr(i \rightarrow j | i \in B, j \in P) = \pi$$
$$Pr(i \rightarrow j | i \in C, j \in P) = \pi$$
$$Pr(i \rightarrow j | i \in D, j \in P) = \pi$$

A trait perspective



relevant in that case



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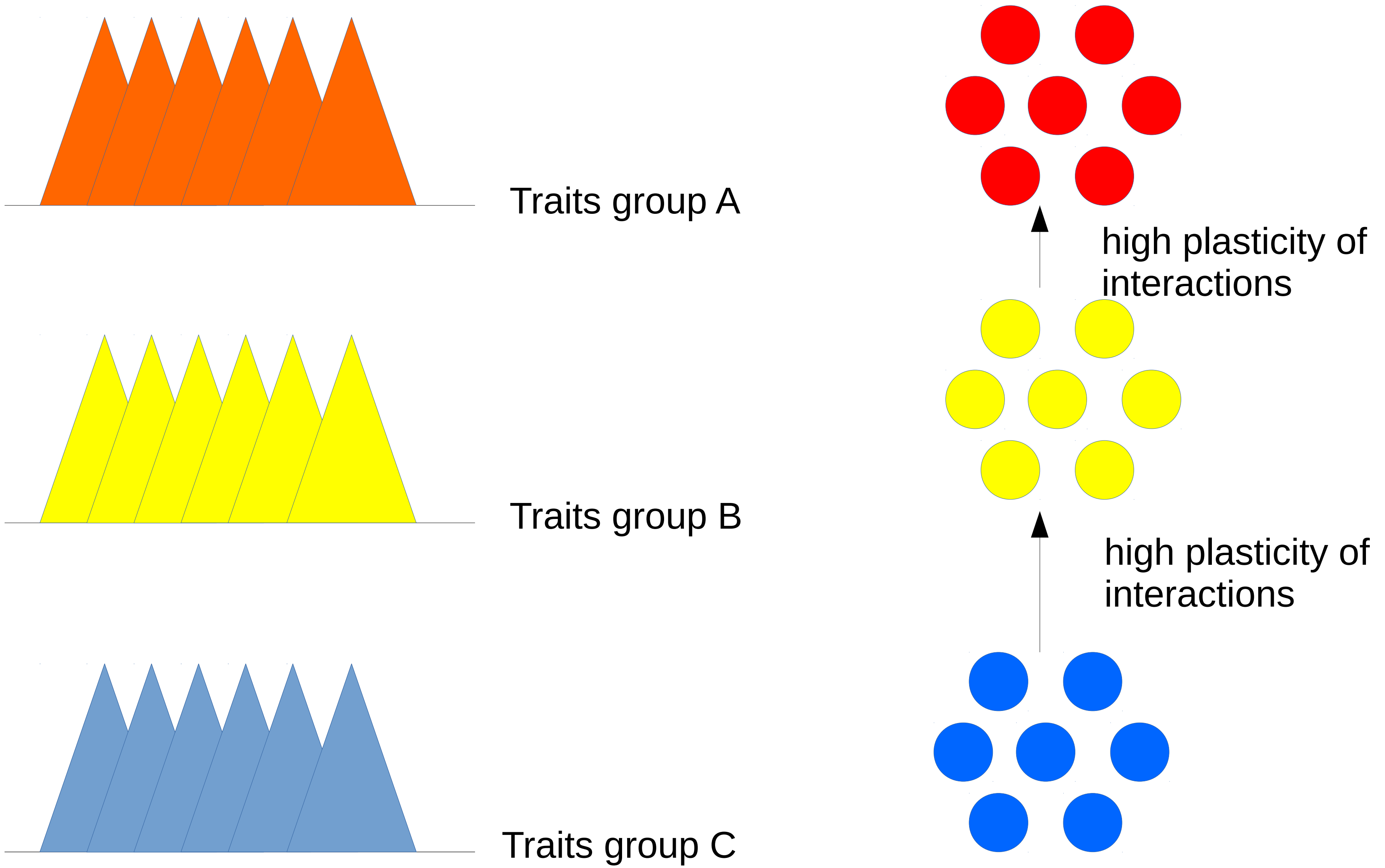
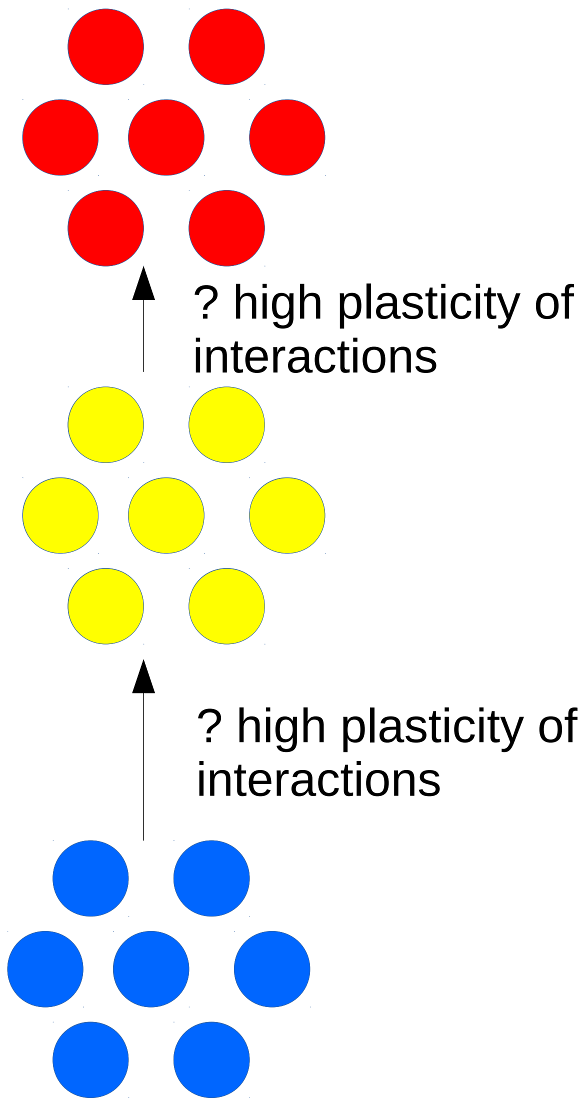
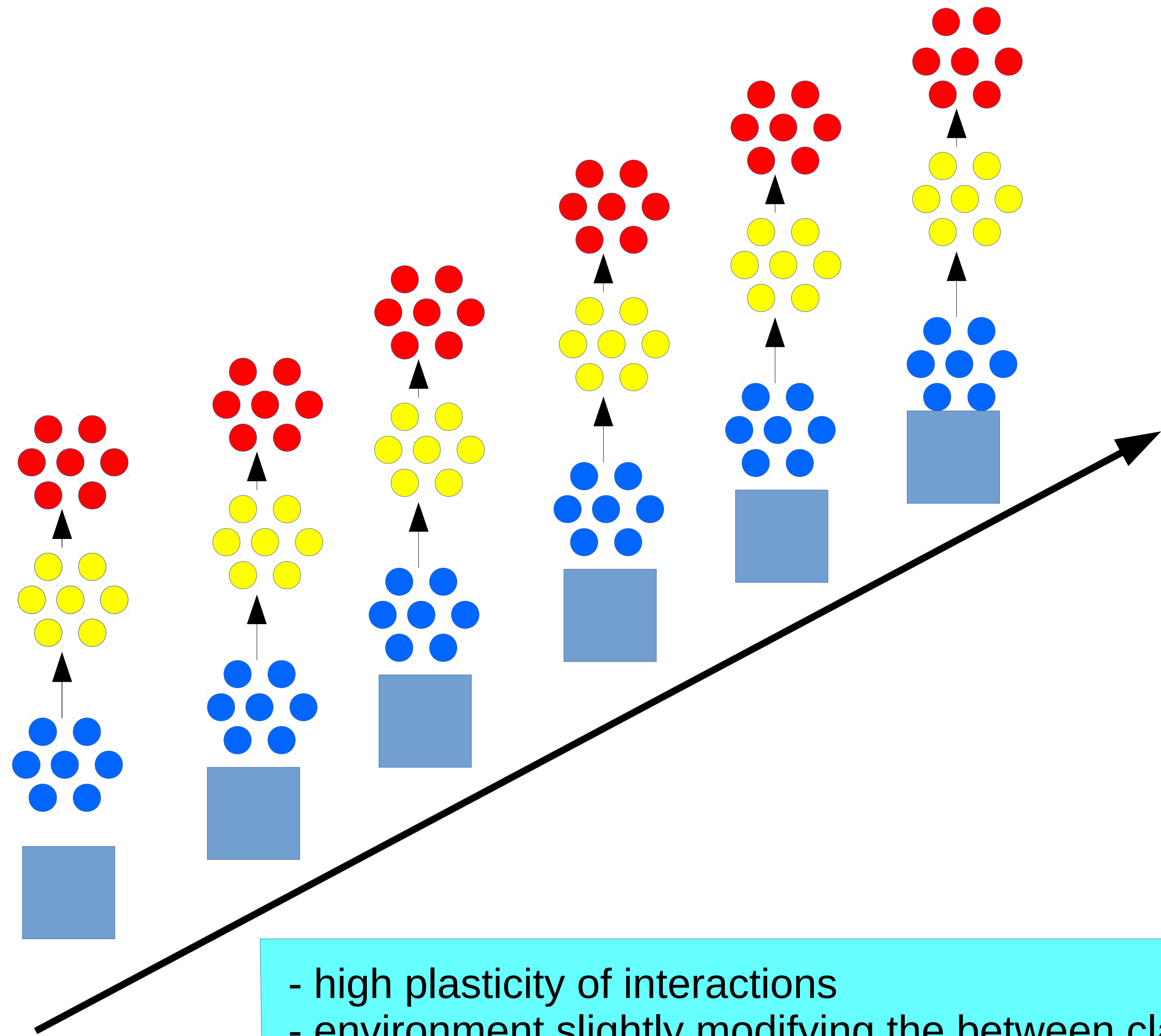
A trait perspective



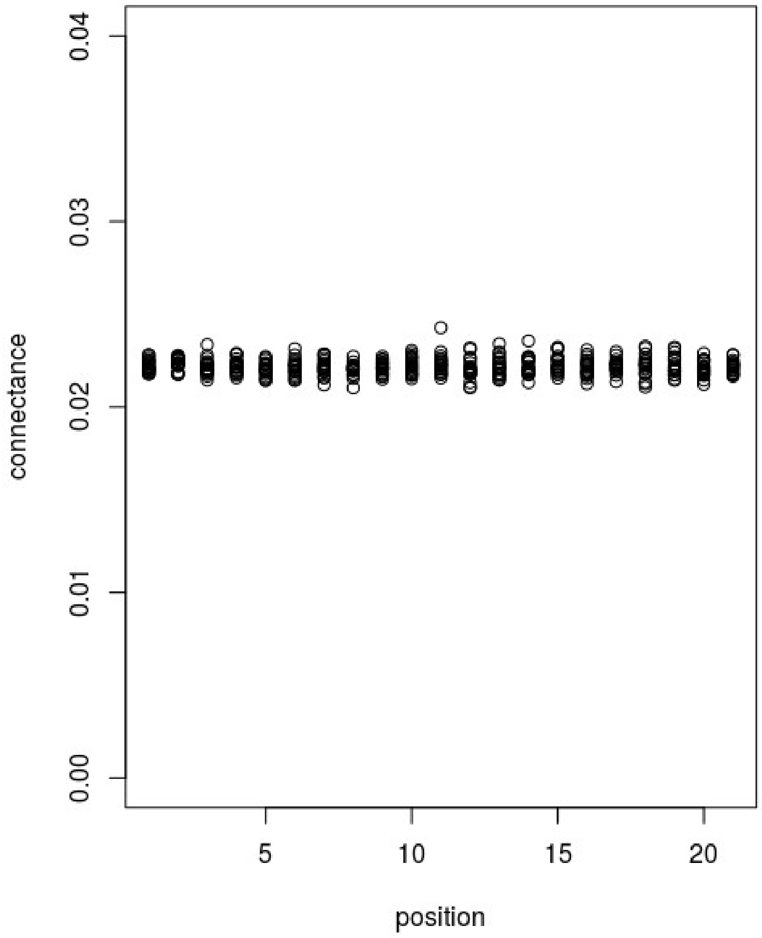
A trait perspective

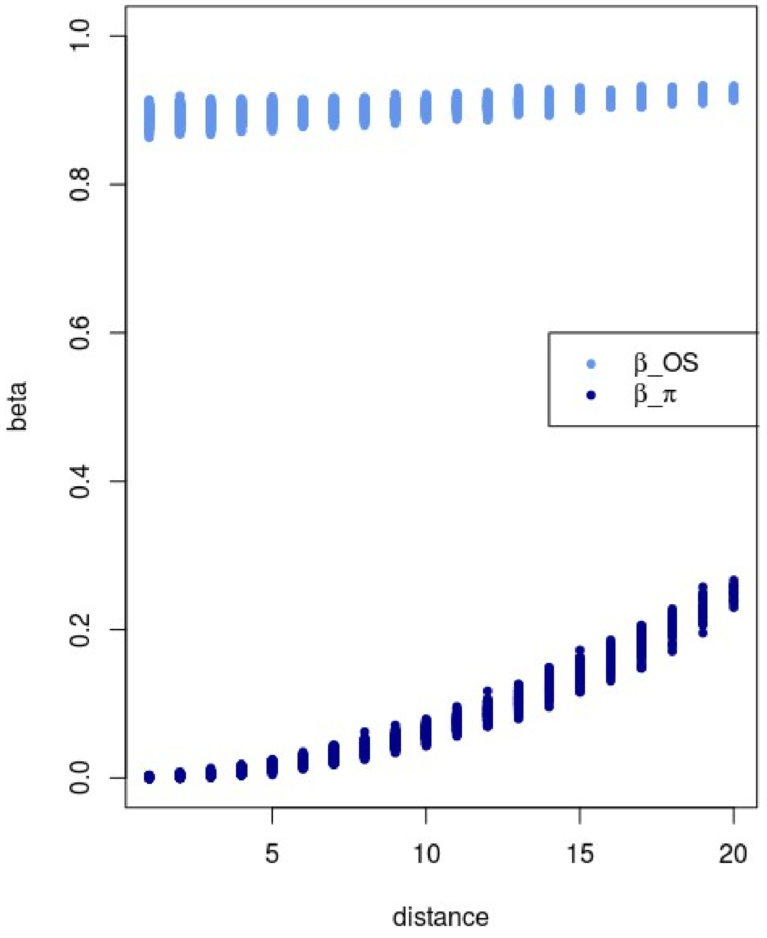




- high plasticity of interactions
- environment slightly modifying the between class connectivity but not the global connectance

A trait perspective





Macroscopic scale : no variations

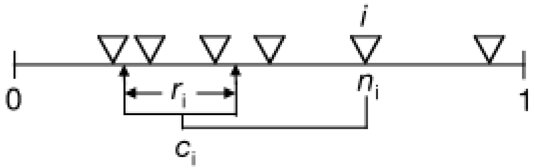
Microscopic scale : too much variations

Mesoscopic scale : strong pattern

Rarefactions curves

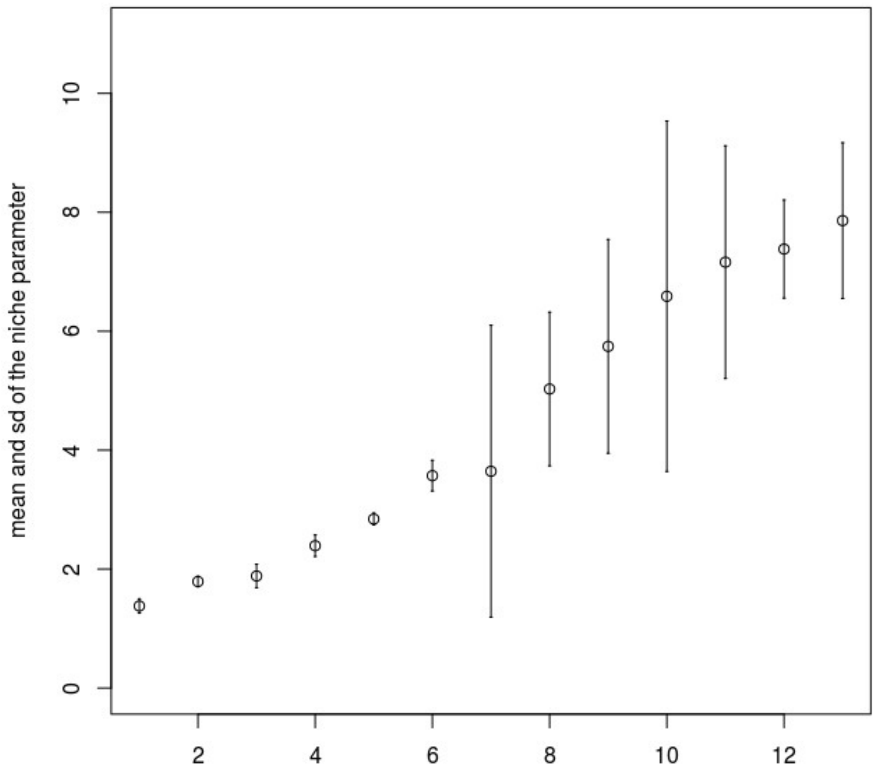
Aim : Test the robustness of mesoscopic metrics to incomplete sampling

Using a model of food web :
the niche model (Williams and Martinez, 2000)



Taken from :
Simple rules yield complex food webs,
Williams and Martinez, 2000, Nature

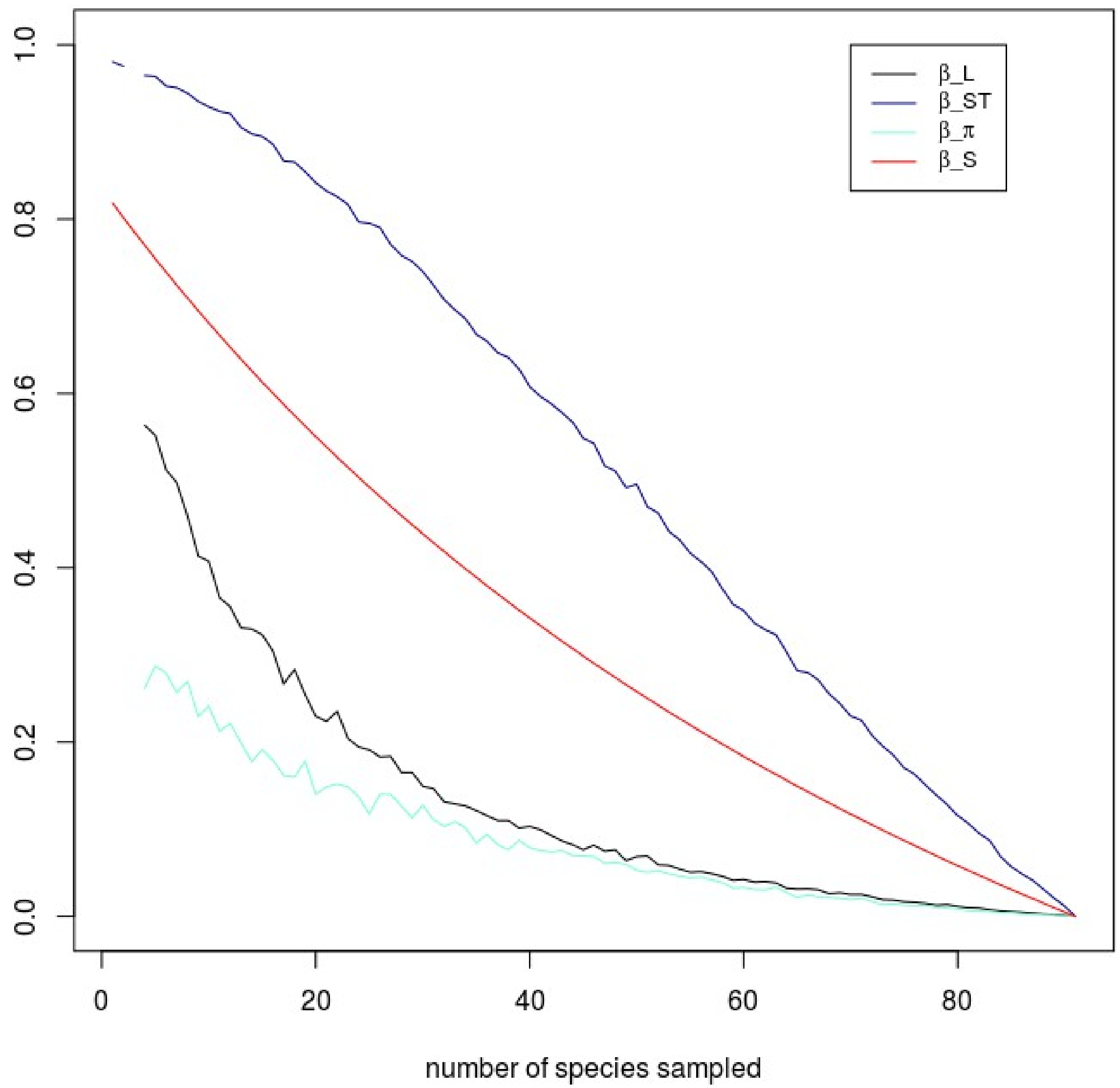
Inferring classes of nodes using Stochastic Block Model
(a model of community detection)



Groups inferred using SBM are almost functionnal groups

Rarefactions curves

Rarefaction curves : how robust are our metrics to incomplete species sampling ?



A framework using Hill numbers that allows network comparison at different scales, from macroscopic scale to microscopic scale

Ecological networks might evolve at different Elton niches scales, especially if you're interested in microbial/soil ecology

Mesoscopic analysis is more robust to incomplete sampling

Key question : *how to determine Elton niches* ?
Using network topology ?
Traits ?