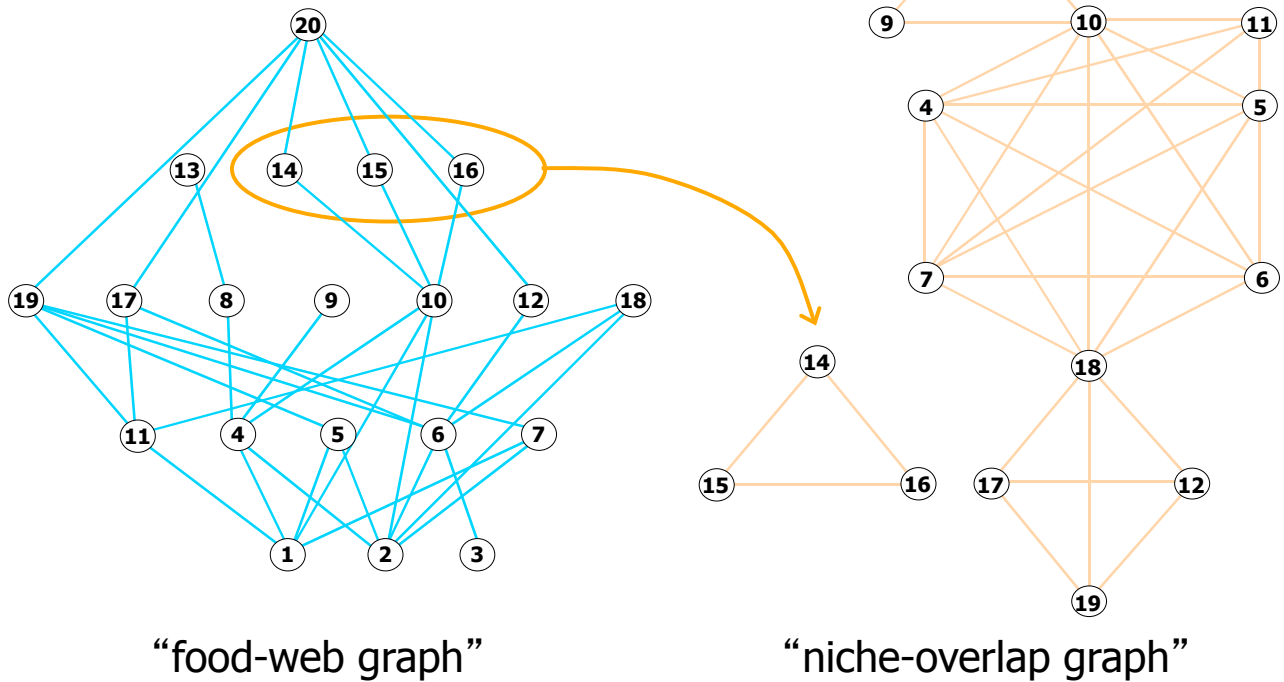


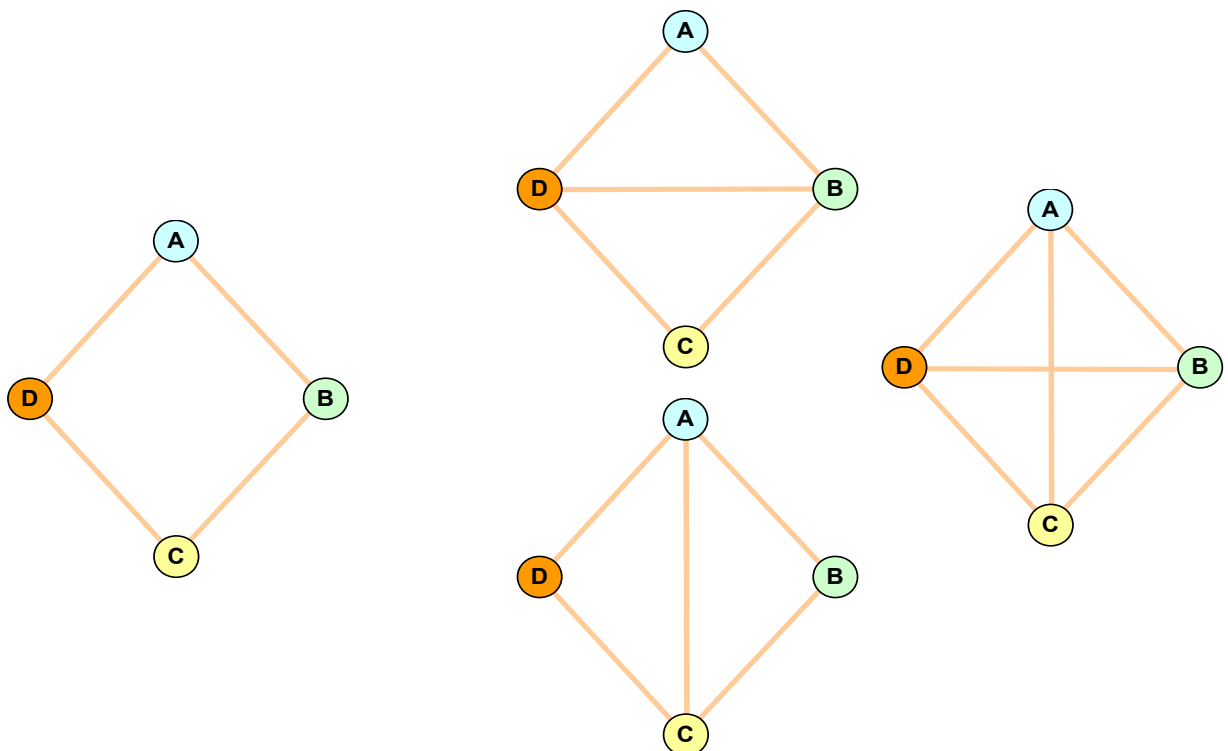
3. Models of food-web structure

Introduction: Food webs and derived graphs

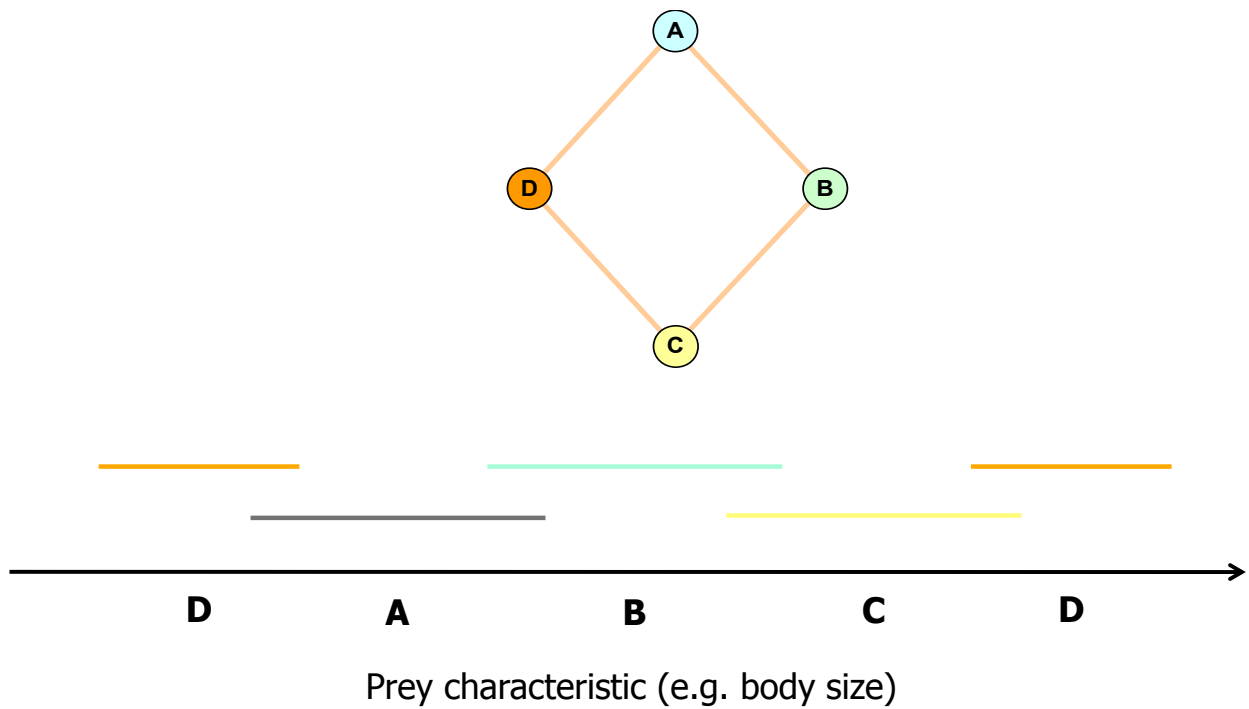
From trophic to competitive structure :



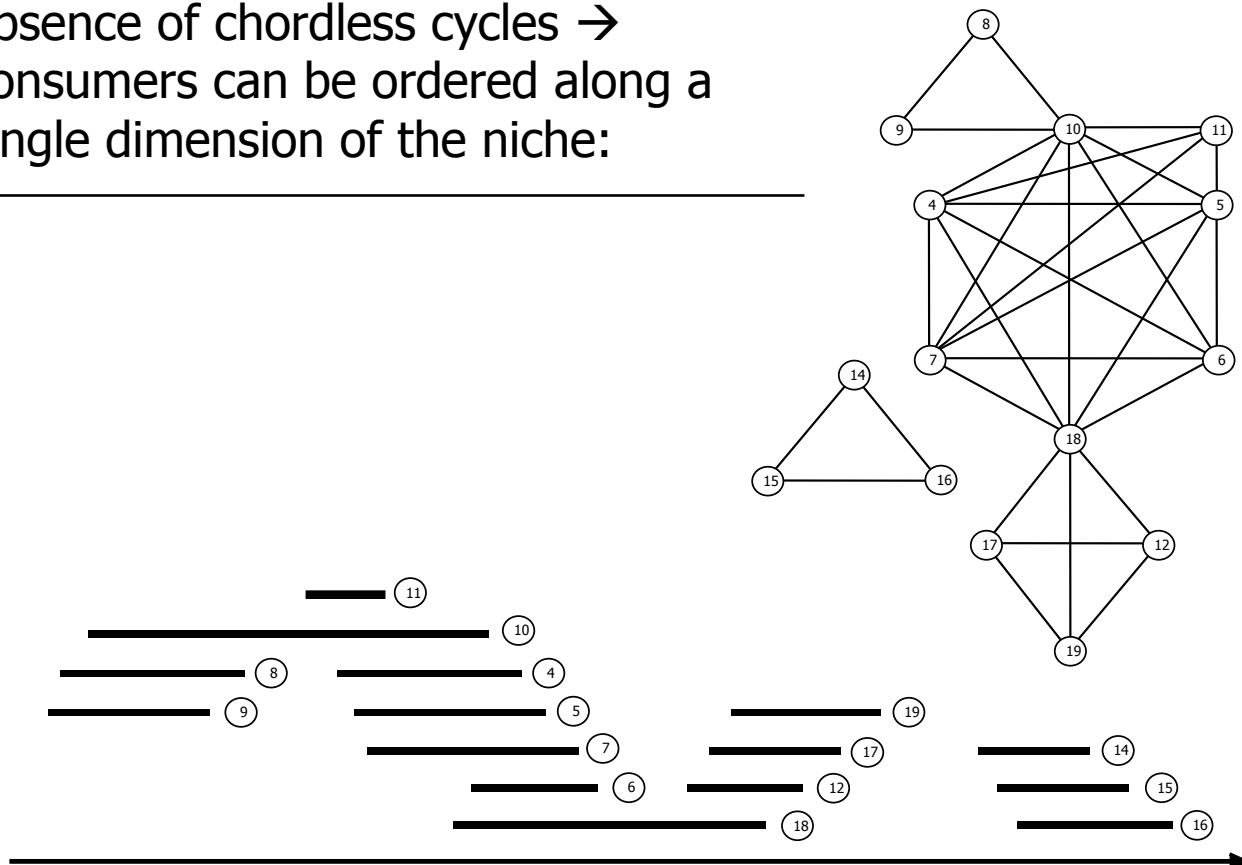
Chordless cycles



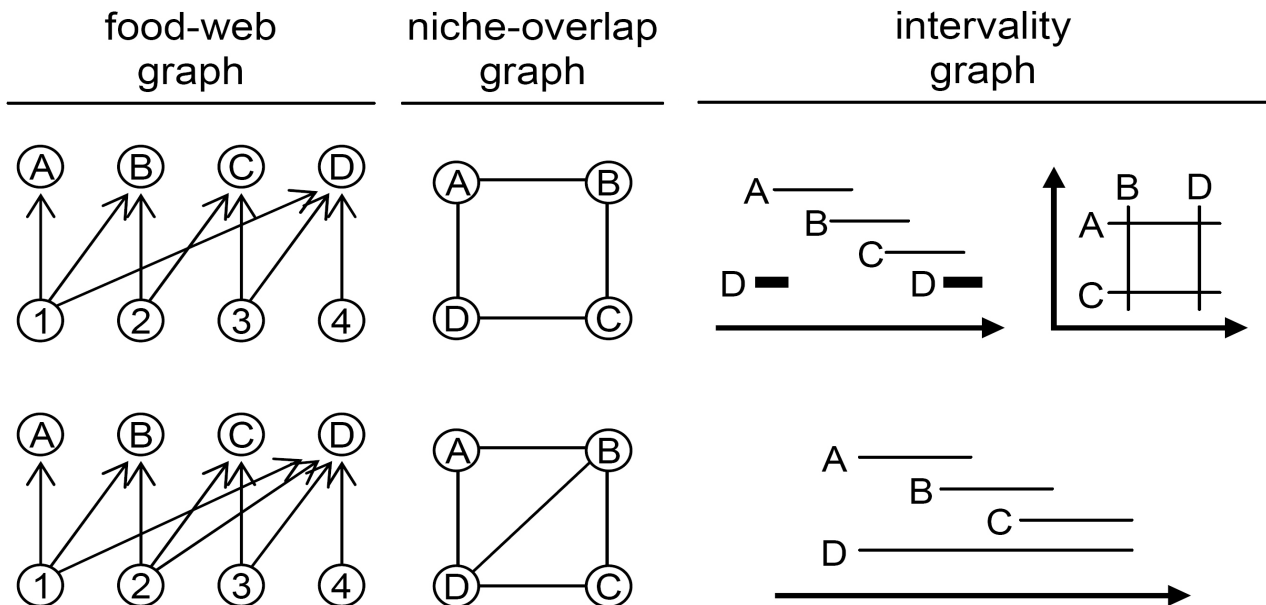
Chordless cycles, intervality, and niche theory



absence of chordless cycles →
consumers can be ordered along a
single dimension of the niche:

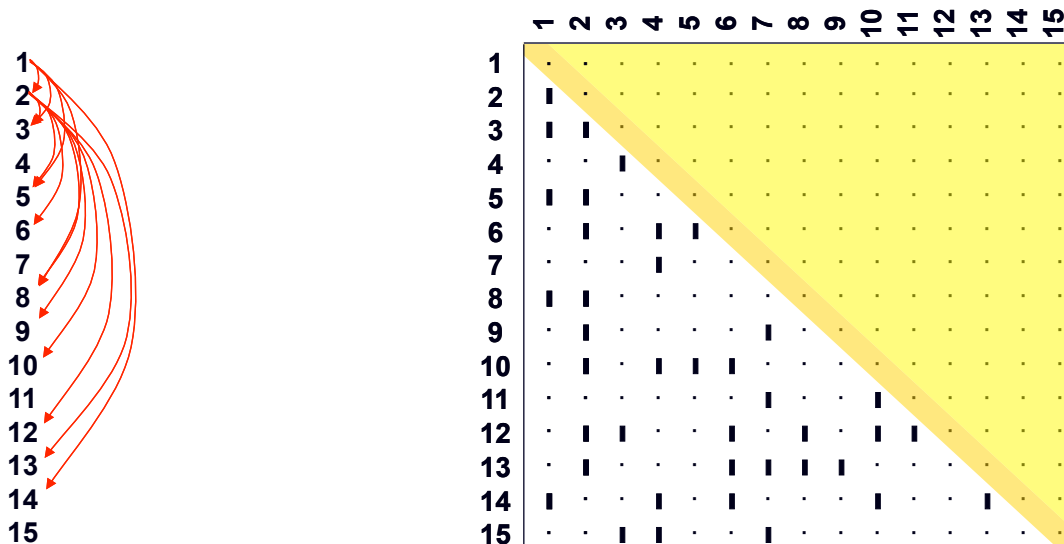


Niche overlap and intervality graphs



3.1. The cascade model [Cohen & Newman 1985]

Parameters : - number of species S
- number of trophic links L (or L/S , or L/S^2)



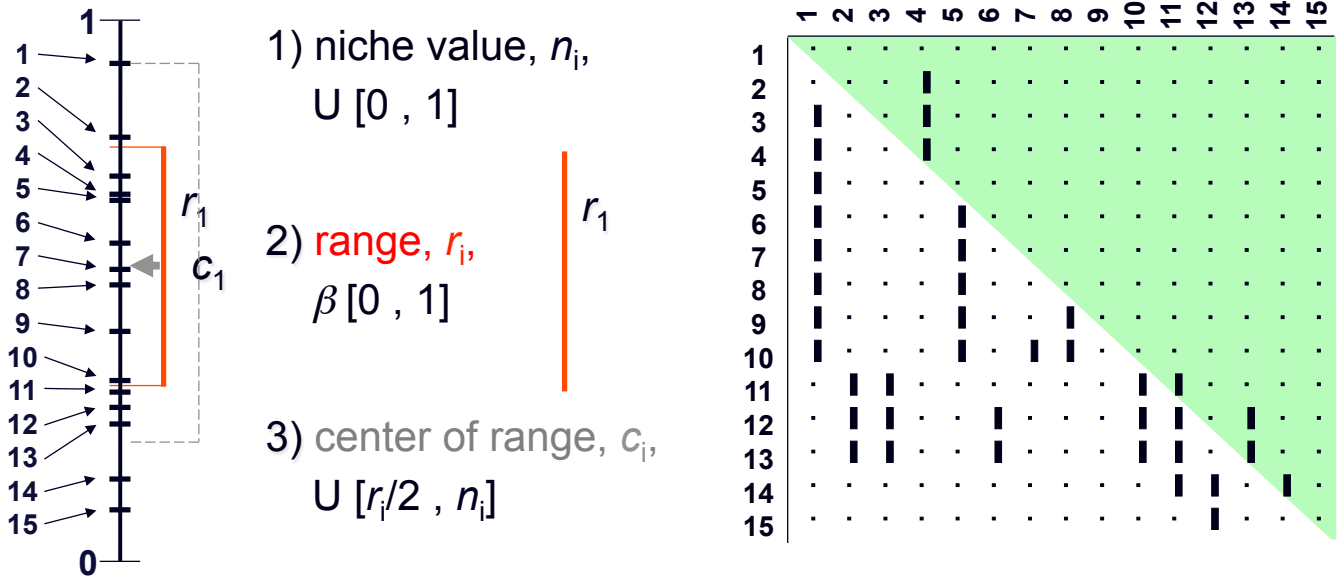
3.2. The niche model [Williams & Martinez 2000]

Parameters :

- number of species S

- number of trophic links L (or L/S , or L/S^2)

- constraints: species eat all prey in a range



Performance of the niche model

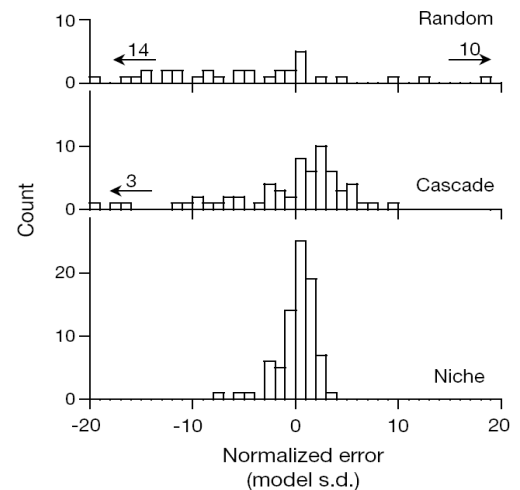


Table 2 Comparison of empirically observed properties with niche-model means

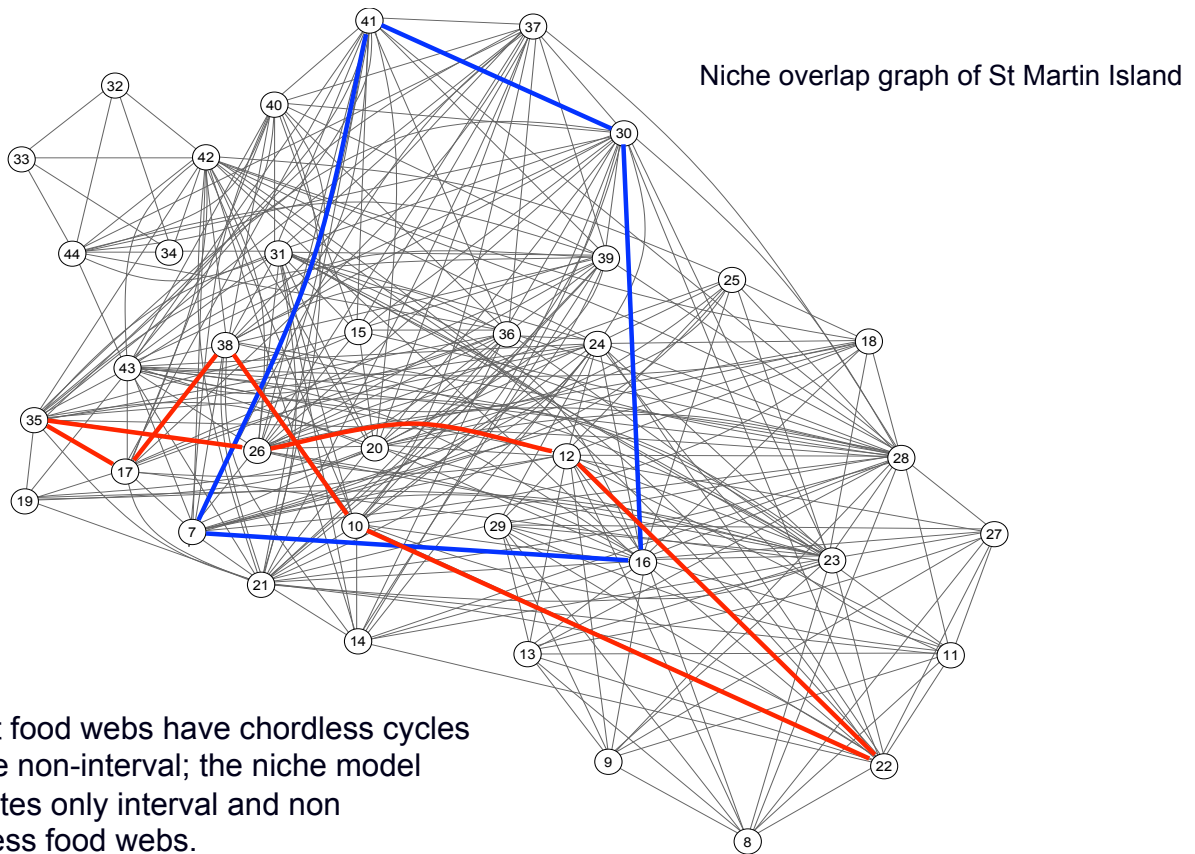
Property	Skipwith Pond	Little Rock Lake	Bridge Brook Lake	Chesapeake Bay	Ythan Estuary	Coachella Desert	St Martin Island
T	0.040 (0.030)	0.011 (0.043)	0 (0.081)	0.32* (0.14)	0.37† (0.073)	0 (0.029)	0.17 (0.078)
I	0.92 (0.88)	0.86 (0.85)	0.68 (0.75)	0.52 (0.59)	0.54† (0.74)	0.90 (0.88)	0.69 (0.75)
B	0.040 (0.095)	0.13 (0.11)	0.32* (0.17)	0.16 (0.27)	0.090* (0.19)	0.10 (0.089)	0.14 (0.17)
GenSD	0.92 (0.81)	1.42† (1.08)	1.09 (1.02)	0.78* (1.13)	1.14 (1.18)	0.73 (0.82)	1.02 (1.09)
VulSD	0.54 (0.51)	0.61 (0.58)	0.61 (0.61)	1.12* (0.72)	1.41† (0.65)	0.60 (0.51)	0.78 (0.62)
MxSim	0.76 (0.75)	0.75* (0.69)	0.74* (0.62)	0.50 (0.49)	0.52* (0.59)	0.72 (0.76)	0.54* (0.62)
ChnLg	6.22 (7.30)		4.04 (5.75)	3.99 (4.23)	5.91 (7.37)	6.69 (7.92)	5.20 (6.73)
ChnSD	1.43 (1.56)		0.93* (1.48)	1.20 (1.34)	1.46 (1.87)	1.45 (1.63)	1.30 (1.67)
ChnNo	3.71 (4.09)		2.85 (3.10)	2.37 (2.31)	4.03 (4.36)	4.31 (4.60)	3.52 (3.86)
Loop	0.40 (0.69)	0.33 (0.47)	0.32 (0.27)	0 (0.030)	0 (0.098)	0.62 (0.73)	0 (0.21)
Cannib	0.32 (0.46)	0.14 (0.14)	0.12 (0.21)	0.032 (0.082)	0.038 (0.069)	0.66* (0.45)	0* (0.13)
Omniv	0.60 (0.75)		0.40* (0.60)	0.52 (0.41)	0.54 (0.60)	0.76 (0.77)	0.60 (0.62)

Niche-model means are in parentheses. See text for property descriptions. See Supplementary Information for complete results for all three models.

* Normalized errors between 2 and 3 model s.d.

† Normalized errors >3 model s.d.

Chordless cycles in recent data



Chordless cycles are numerous in recent food-webs :

Food-web :	Number of taxa	Number of chordless cycles of size :			
		4	5	6	7
Coachella Desert	30	42	0	0	0
Chesapeake Bay	33	0	0	0	0
Skipwith Pond	35	0	0	0	0
St-Martin Island	44	230	91	29	0
Everglades graminoids	63	568	130	12	0
Cypress	64	0	0	0	0
Bridge Brook Lake	75	0	0	0	0
Mangrove Estuary	90	4231	8840	5424	6616
Ythan Estuary	92	213	156	10	0
Florida Bay	122	5769	15825	35824	21158
Little Rock Lake, North Basin, Winter	124	102	8	0	0
Little Rock Lake, Annual web	180	1210	3572	8888	5203
Little Rock Lake, South Basin, Summer	200	3689	8788	23340	13104

3.3. Phylogenetic constraints → nested-hierarchy model

Sylviidae

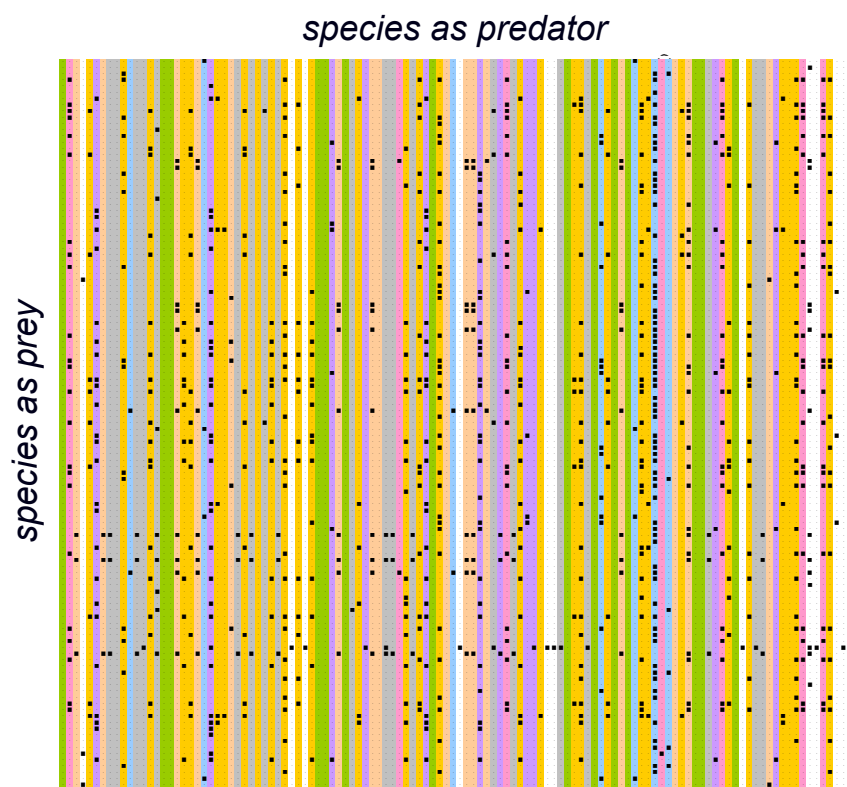


Fringillidae

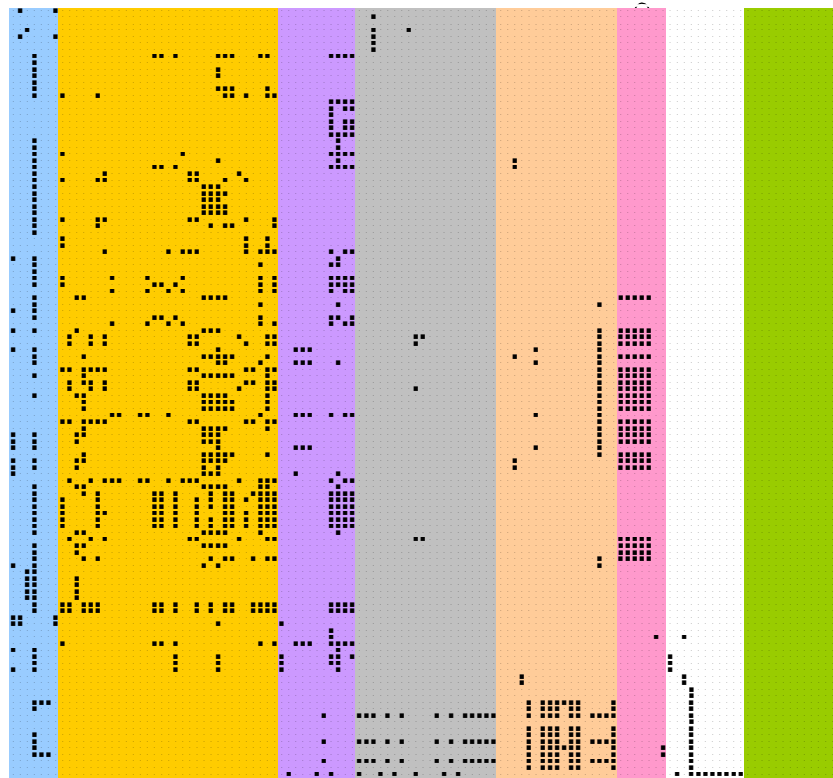


Species inherit the morphology and physiology of their ancestors, and are constrained to occupy similar trophic niches.

"Unordered" food web matrix (Grande Cariçaie):

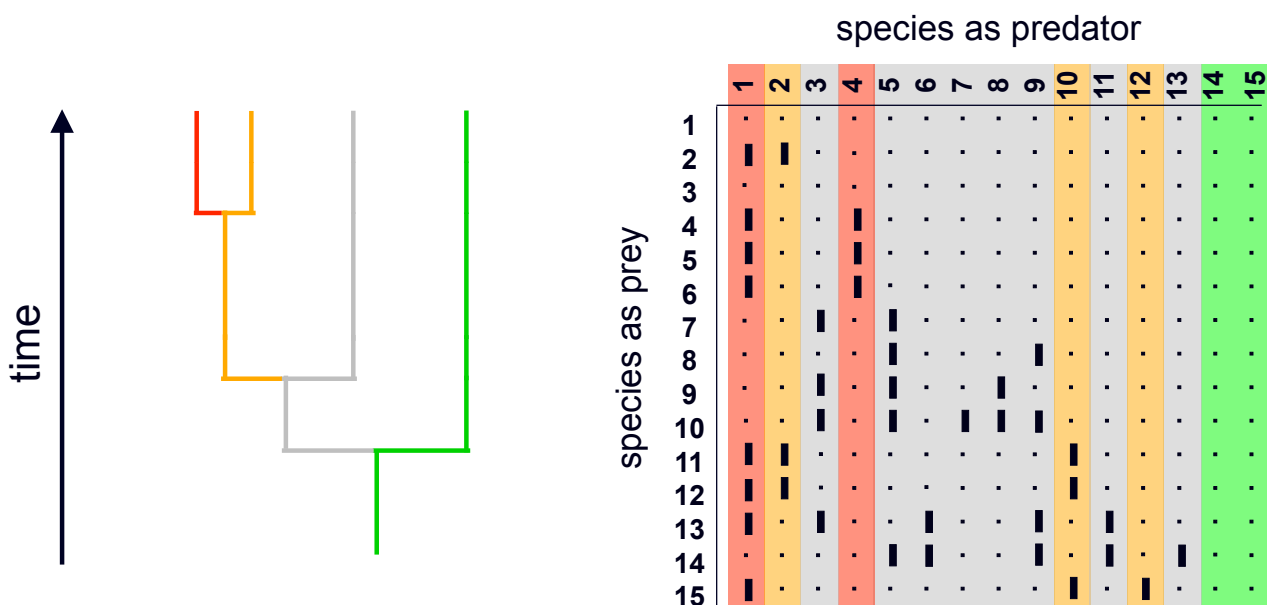


Food web matrix ordered by taxonomy



The nested-hierarchy model [Cattin et al. 2004]

Parameters : - number of species S & number of trophic links L
- sequential model



Performance of the nested-hierarchy model

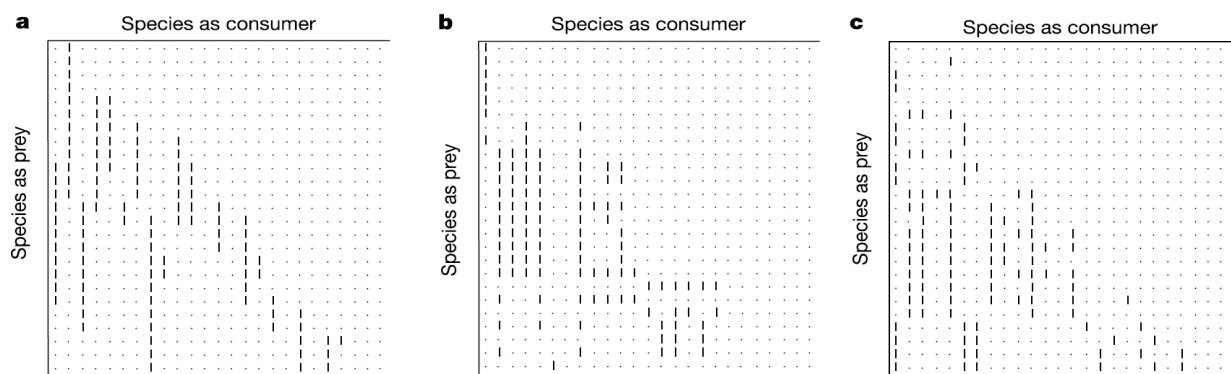


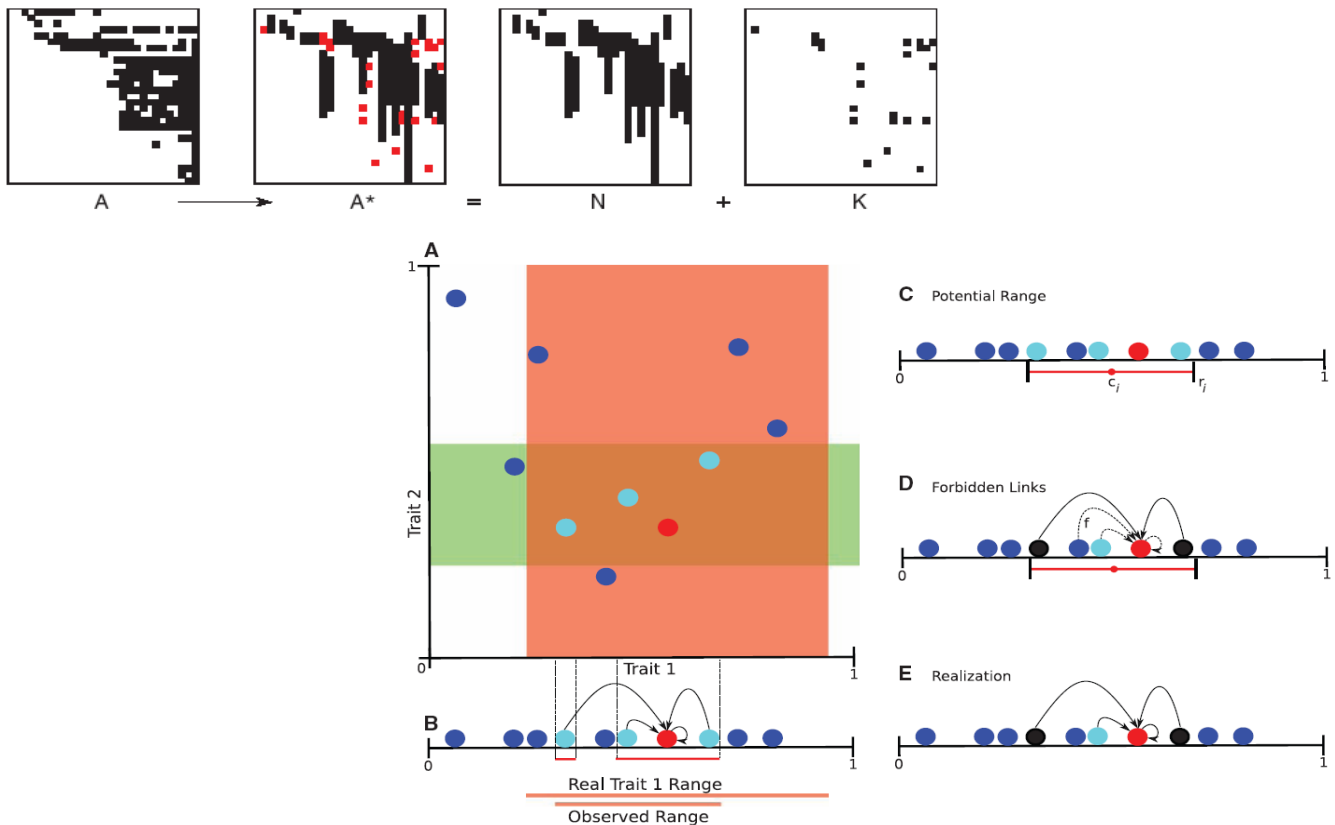
Figure 1 Comparison of one simulation of the niche model (a) and of the nested hierarchy model (c), with respect to a real food web (b); Bridge Brook Lake⁴. The food-web matrix depicts the trophic relationships, where a vertical mark indicates that the species in the column consumes the species in the row (columns and rows contain the same species).

Performance of the nested-hierarchy model

Table 1 Comparison of properties for seven food webs																													
Property	Skipwith Pond				Little Rock Lake				Bridge Brook Lake				Chesapeake Bay				Ythan Estuary				Coachella Desert				St Martin Island				
T	0.06	[0.04]	0.08	0.05	[0]	0.03	0.10	[0]	0.10	0.14	[0.28]	0.15	0.08	[0.38]	0.07	0.06	[0]	0.08	0.09	[0.17]	0.08	0.06	[0.04]	0.08	0.09	[0.17]	0.08	0.09	[0.17]
I	0.85	[0.92]	0.82	0.85	[0.87]	0.88	0.73	[0.68]	0.74	0.60	[0.62]	0.59	0.74	[0.53]	0.77	0.86	[0.90]	0.83	0.75	[0.69]	0.77	0.86	[0.90]	0.83	0.75	[0.69]	0.77	0.86	[0.90]
B	0.09	[0.04]	0.10	0.10	[0.13]	0.08	0.17	[0.32]	0.16	0.26	[0.10]	0.26	0.18	[0.09]	0.17	0.09	[0.10]	0.08	0.17	[0.14]	0.15	0.09	[0.04]	0.10	0.10	[0.13]	0.08	0.17	[0.32]
Gen_{sd}	0.76	[0.92]	0.83	1.06	[1.40]	1.08	0.98	[1.09]	1.03	1.12	[0.71]	1.17	1.17	[1.16]	1.18	0.81	[0.73]	0.83	1.06	[1.02]	1.09	0.76	[0.92]	0.83	1.06	[1.40]	1.08	0.98	[1.09]
Vul_{sd}	0.55	[0.54]	0.59	0.59	[0.57]	0.59	0.63	[0.61]	0.72	0.73	[1.03]	0.80	0.66	[1.40]	0.71	0.53	[0.60]	0.60	0.64	[0.78]	0.71	0.55	[0.54]	0.59	0.59	[0.57]	0.59	0.63	[0.61]
M_{sim}	0.73	[0.76]	0.67	0.69	[0.76]	0.54	0.61	[0.71]	0.56	0.48	[0.34]	0.48	0.58	[0.50]	0.50	0.74	[0.72]	0.67	0.62	[0.54]	0.53	0.73	[0.76]	0.67	0.69	[0.76]	0.54	0.61	[0.71]
Ch_{mean}	6.23	[4.81]	5.38	—	—	—	4.86	[2.55]	4.30	3.28	[2.77]	3.30	6.39	[4.89]	6.94	6.95	[7.18]	5.78	5.76	[4.20]	5.62	6.23	[4.81]	5.38	—	—	—	4.86	[2.55]
Ch_{sd}	1.56	[1.32]	1.58	—	—	—	1.51	[0.76]	1.52	1.36	[1.14]	1.42	1.89	[1.50]	2.17	1.68	[1.89]	1.64	1.65	[1.30]	1.82	1.56	[1.32]	1.58	—	—	—	1.51	[0.76]
Ch_{log}	4.21	[3.52]	3.70	—	—	—	3.20	[2.62]	2.90	2.35	[2.11]	2.32	4.39	[3.99]	4.38	4.62	[4.90]	4.04	3.96	[3.52]	3.71	4.21	[3.52]	3.70	—	—	—	3.20	[2.62]
Lo	0.25	[0.12]	0.40	—	—	—	0.05	[0]	0.13	0.00	[0.24]	0.02	0.01	[0]	0.06	0.26	[0]	0.42	0.03	[0]	0.11	0.25	[0.12]	0.40	—	—	—	0.05	[0]
Can_{sp}	0.43	[0.32]	0.10	0.14	[0.15]	0.03	0.21	[0.12]	0.03	0.08	[0]	0.00	0.07	[0.04]	0.01	0.44	[0.66]	0.09	0.13	[0]	0.02	0.43	[0.32]	0.10	0.14	[0.15]	0.03	0.21	[0.12]
O	0.77	[0.6]	0.76	—	—	—	0.61	[0.36]	0.60	0.42	[0.38]	0.41	0.61	[0.53]	0.61	0.75	[0.79]	0.78	0.63	[0.60]	0.63	0.77	[0.6]	0.76	—	—	—	0.61	[0.36]
Cy_4	0	[0]	0	0	[639]	626	0	[0]	0	0	[0]	0	0	[206]	18	0	[36]	1	0	[226]	6	0	[0]	0	0	0	0	0	[0]
D_{diet}	0	[0.35]	0.16	0	[0.08]	0.09	0	[0.004]	0.09	0	[0.08]	0.02	0	[0.32]	0.02	0	[0.28]	0.17	0	[0.17]	0.07	0	[0]	0	0	0	0	0	[0]

For each food web, empirical values are in brackets, means (medians for Cy_4) for the niche model are on the left, and those for the nested hierarchy model on the right. See Methods for a description of the properties of the food webs. Little Rock Lake food web is too large for Ch_{mean} , Ch_{sd} , Ch_{log} , Lo and O to be computed in a reasonable length of time.

3.4. The minimum potential niche model [Allessina et al. 2008]



4. Statistical models to study network structure

Other recent "stochastic" models of food web structure :

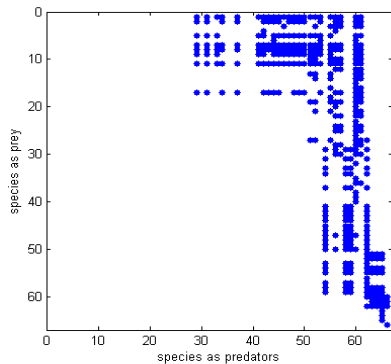
- The **generalized cascade model** [Stouffer et al. 2005]
Model encompassing cascade and niche models as extremes
- The **matching model** [Rossberg et al. 2006]
Trophic interactions depend body-size and abstract traits, which are subjected to evolution. Model of evolution on a long time scale..
- The **extended generalized cascade model** [Capitán et al. 2013]
Non contiguous prey above the diagonal.

First mechanistic model of food-web structure :

- The **ADBM (allometric diet breadth model)** [Petchey et al. 2008]
First **mechanistic** model using allometric rules and optimal foraging theory to infer the trophic network. Uses Body-Size as an explanatory variable.
→ the model predicts a single matrix configuration for a given observed food-web

Statistical model for networks : 1st steps (GLM context)

The **response variable** is the **adjacency matrix** of the network :
for food web the predation matrix



The **explanatory variable** is the **body size** of species (length or mass) :

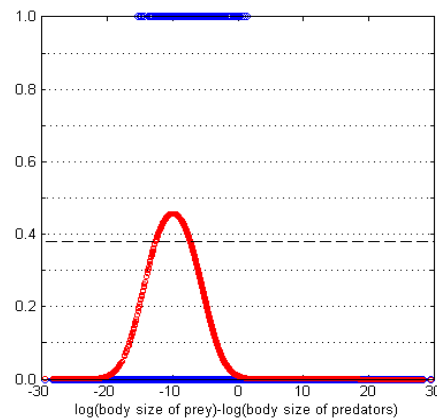
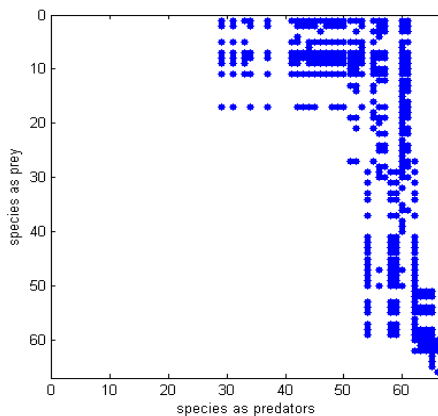
$\log(\text{body size of prey}) - \log(\text{body size of predator})$

$$P(a_{ij} = 1)$$

We model the probability that there is a trophic link

From this we can infer a fitted adjacency matrix

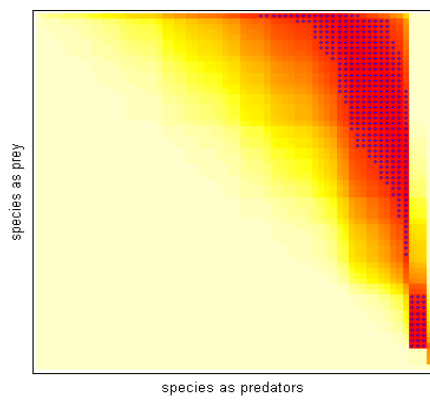
4.1. The body size model [Data: Tuesday Lake]



$$\log \frac{P(a_{ij} = 1)}{P(a_{ij} = 0)} = \alpha + \beta \log \frac{m_i}{m_j} + \gamma \log^2 \frac{m_i}{m_j}$$

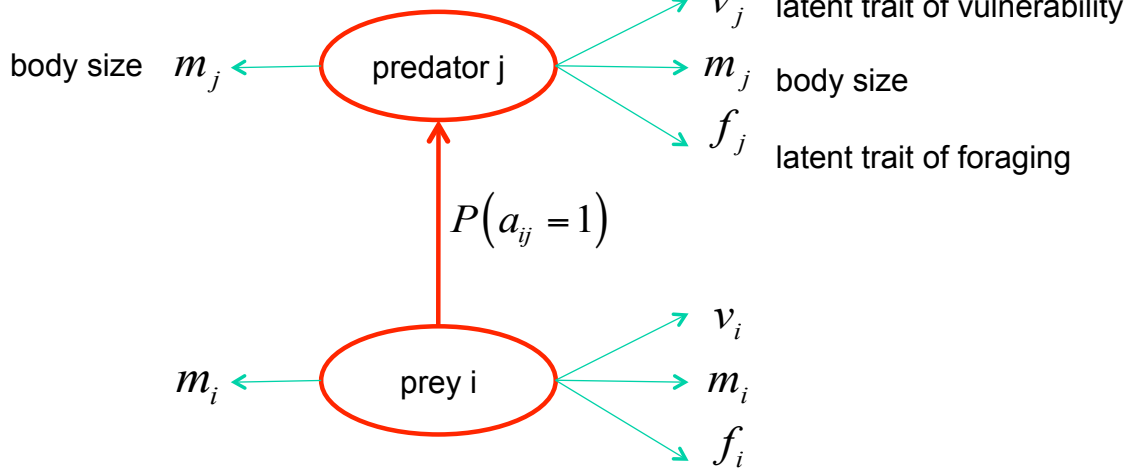
the parameters are : α , β and γ

→ Proportion of correct trophic links: 46%



From body size model to latent traits model

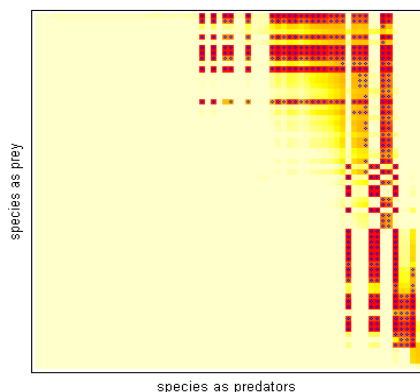
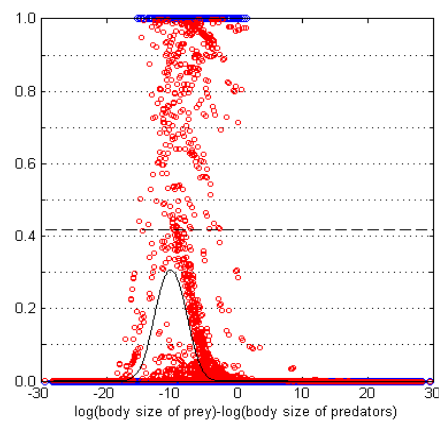
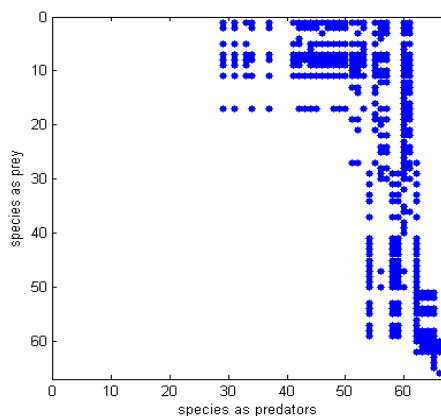
Body size model



The linking probability depends only on the body size ratio

Now the linking probability depends on the body size ratio and the latent traits

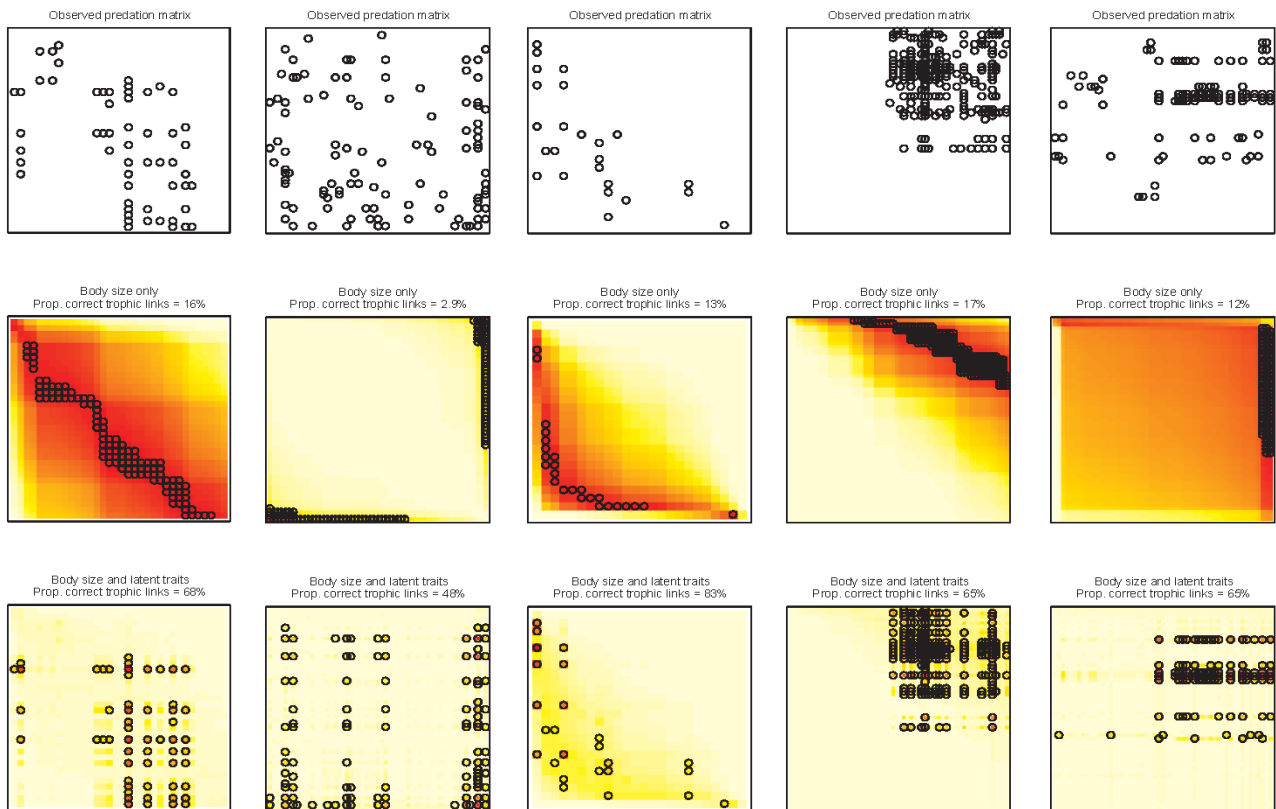
4.2. The latent traits model



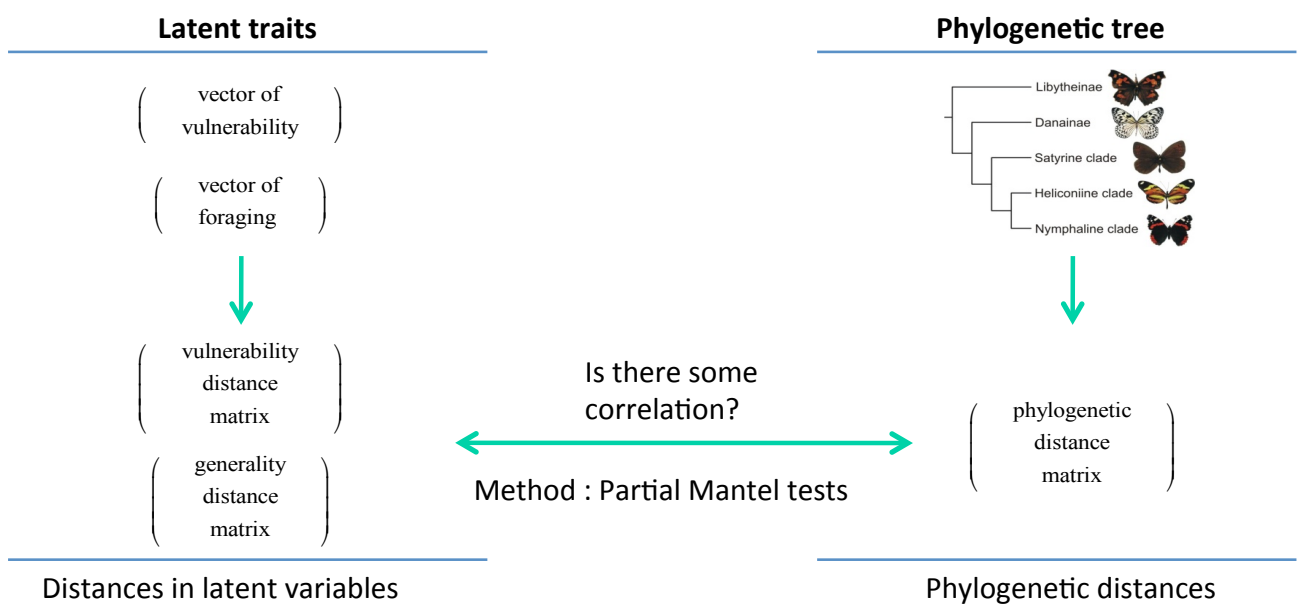
$$\log \frac{P(a_{ij} = 1)}{P(a_{ij} = 0)} = \alpha + \beta \log \frac{m_i}{m_j} + \gamma \log^2 \frac{m_i}{m_j} + v_i \delta f_j$$

the parameters are : α , β , γ , δ and for each species v_i and f_i

→ Proportion of correct trophic links : 87%



Biological interpretation of latent traits



Results of Mantel tests

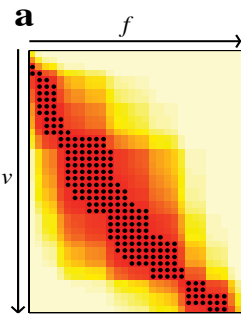
Food web	Body size versus latent vulnerability		Body size versus latent foraging		Phylogeny versus latent vulnerability		Phylogeny versus latent foraging	
	Correlation coefficient	<i>P</i>	Correlation coefficient	<i>P</i>	Correlation coefficient	<i>P</i>	Correlation coefficient	<i>P</i>
1	.092	.075	.132	.014	.484	< .001	.660	< .001
2	.178	.007	.052	.143	−.043	.830	.222	< .001
3	.139	.078	.324	< .001	.224	< .001	−.018	.583
4	.124	.052	.409	< .001	.358	< .001	.399	< .001
5	.020	.340	.243	< .001	.75	.037	.289	< .001
6	.222	< .001	−.154	.974	−.094	.890	.153	.001
7	−.115	.974	.373	< .001	.012	.403	−.084	.967
8	.030	.285	.291	< .001	.225	< .001	.374	< .001
9	.221	.089	−.015	.522	.214	.015	−.095	.839
10	.000	.473	.168	.002	.042	.174	.076	.019
11	.033	.107	.021	.261	−.036	.700	.025	.338
12	.093	.116	−.181	.960	.005	.455	−.056	.790

4.3. The matching-centrality model

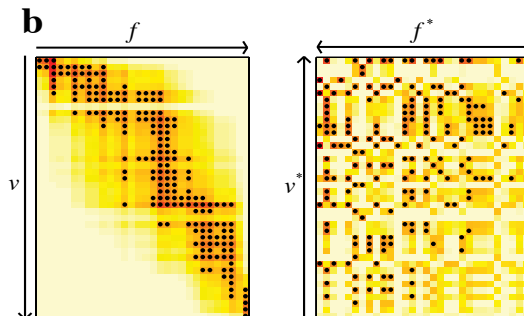
$$\text{logit}\left(P(a_{ij} = 1)\right) = \underbrace{\text{linking probability}}_{\text{matching term}} + \underbrace{\text{centrality term}}_{\text{centrality term}}$$

$$= -\lambda(v_i - f_j)^2 + \delta_1 v_i^* + \delta_2 f_j^*$$

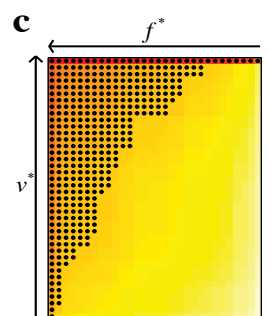
matching term only
 $\delta_1 = \delta_2 = 0$



matching and centrality terms
 $\delta_1, \delta_2, \lambda > 0$

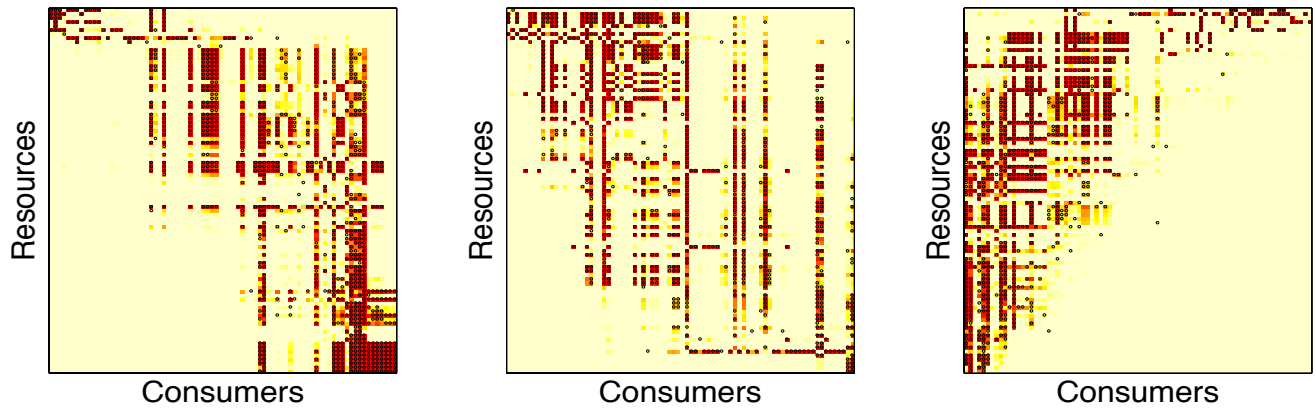


centrality term only
 $\lambda = 0$

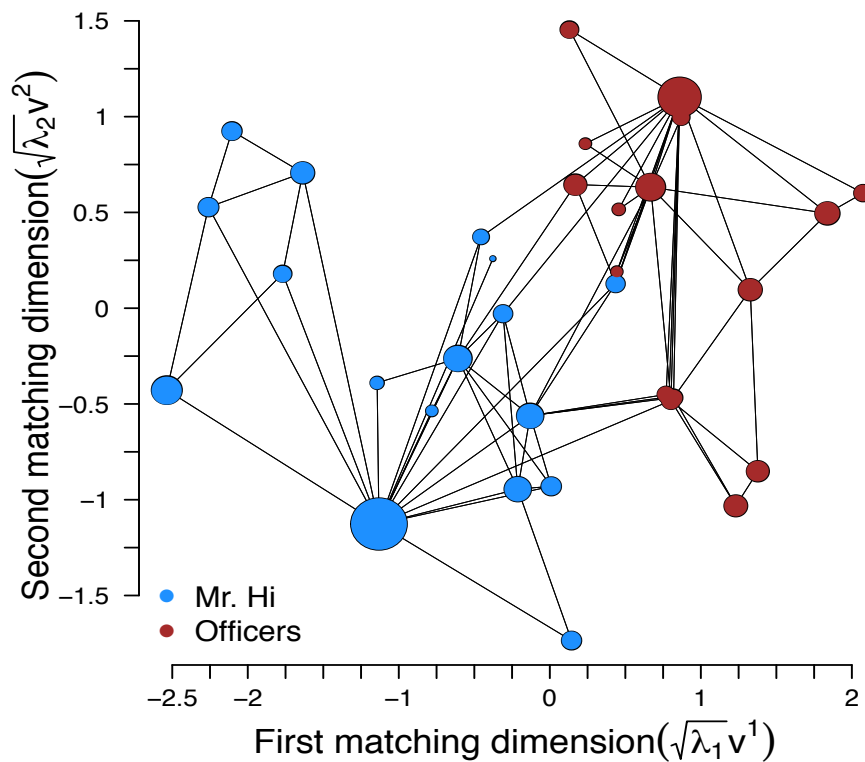


$$\log\left(\frac{P(a_{ij} = 1)}{1 - P(a_{ij} = 1)}\right) = -\underbrace{\sum_{k=1}^d \lambda_k (v_i^k - f_j^k)^2}_{\text{matching term}} + \underbrace{\delta_1 v_i^* + \delta_2 f_j^*}_{\text{centrality term}} + m$$

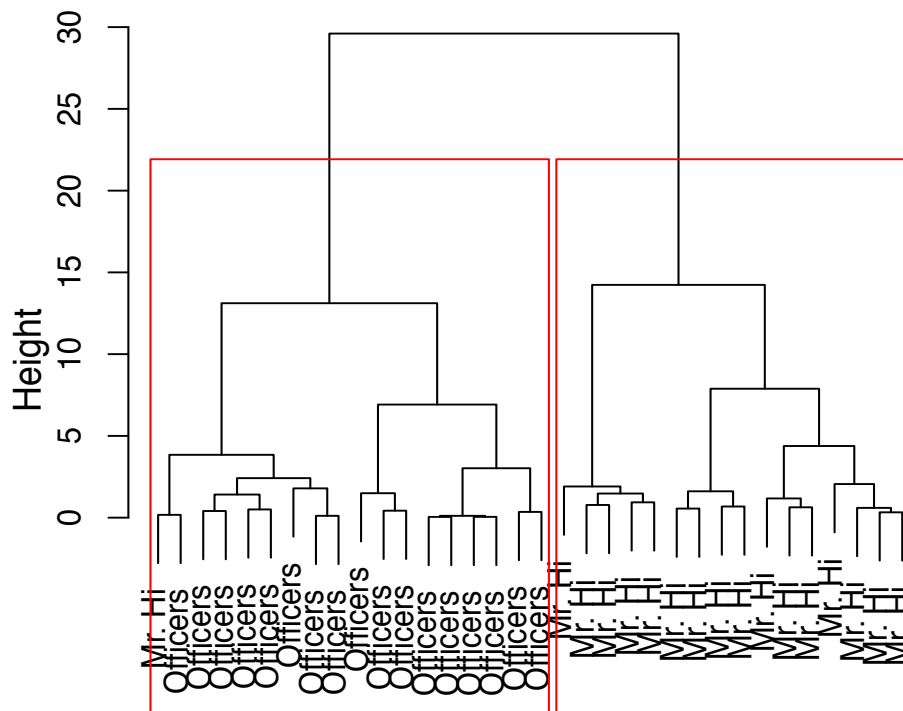
Matching-centrality representation of Little Rock Lake



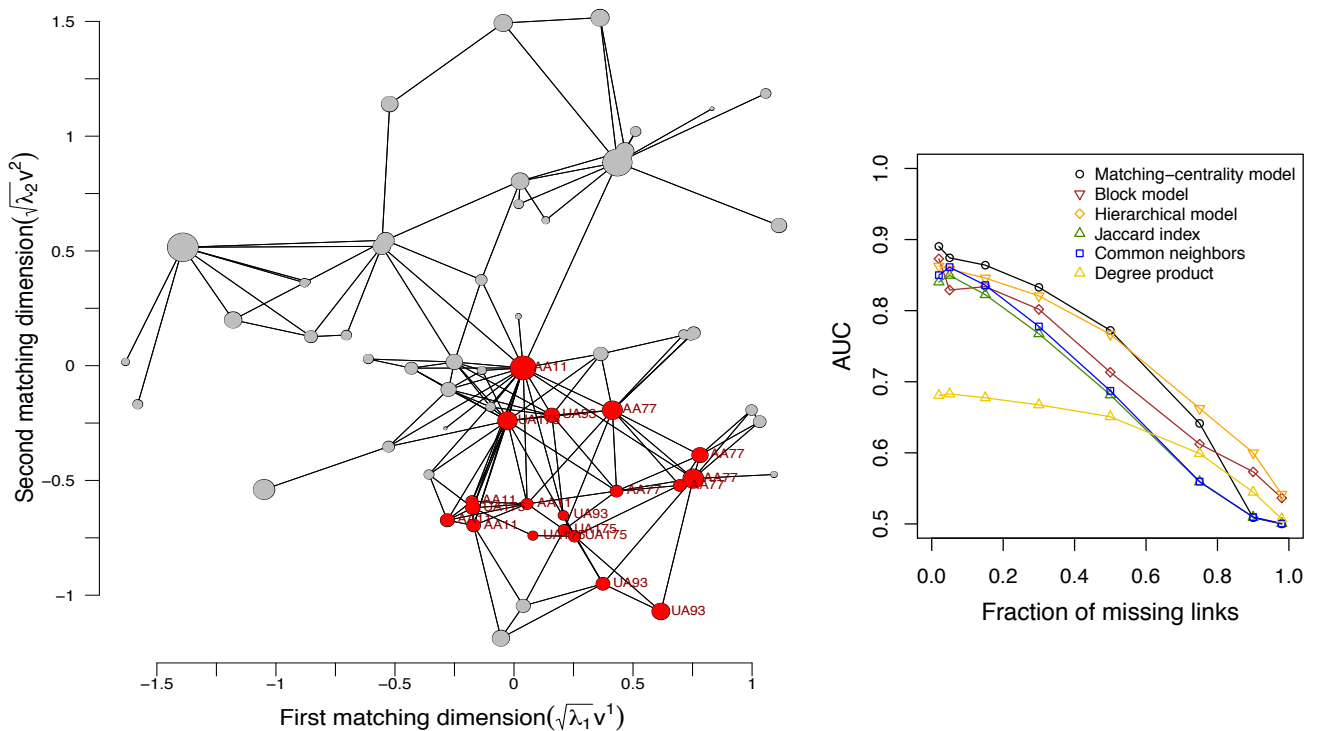
The Zachary Karate club social network



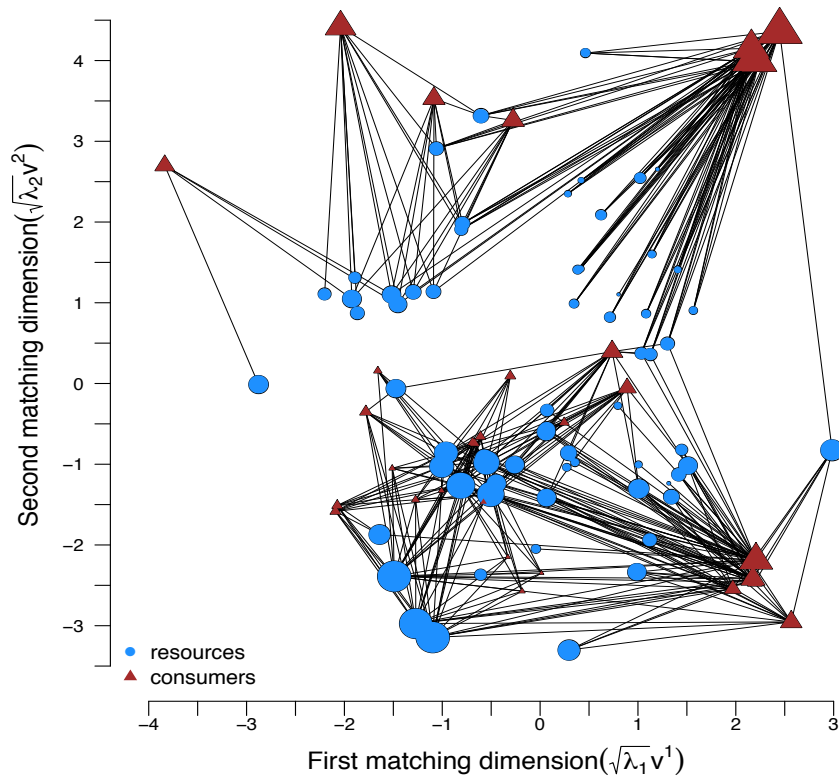
The Zachary Karate club social network



Reconstruction of the 9.11 terrorist network



Forecasting the behaviour of new nodes



Forecasting the behaviour of new nodes

$$\log \left(\frac{P(a_{ij} = 1)}{1 - P(a_{ij} = 1)} \right) = - \underbrace{\sum_{k=1}^d \lambda_k (v_i^k - f_j^k)^2}_{\text{matching term}} + \underbrace{\delta_1 v_i^* + \delta_2 f_j^*}_{\text{centrality term}} + m$$

$$\vec{v}^1, \vec{v}^2, \vec{f}^1, \vec{f}^2, \vec{v}^*, \vec{f}^* \sim MVN \left(\alpha + \beta \log(\vec{bs}), \Sigma(\rho) \right)$$

$$\Sigma(\rho)_{ij} = \begin{cases} \sigma^2 \cdot (1 - (1 - t_{ij})^\rho) & \text{if } i \neq j \\ \sigma^2 & \text{if } i = j \end{cases}$$

$$\hat{v}_k = \hat{\alpha} + \hat{\beta} \log(bs_k) + \Sigma(\hat{\rho})_{-kk} \Sigma(\hat{\rho})_{kk}^{-1} (\vec{v}_{-k} - \hat{v}_{-k})$$

Forecasting the behaviour of new nodes

