The structure of ecological interaction networks: Which questions? What do we know?

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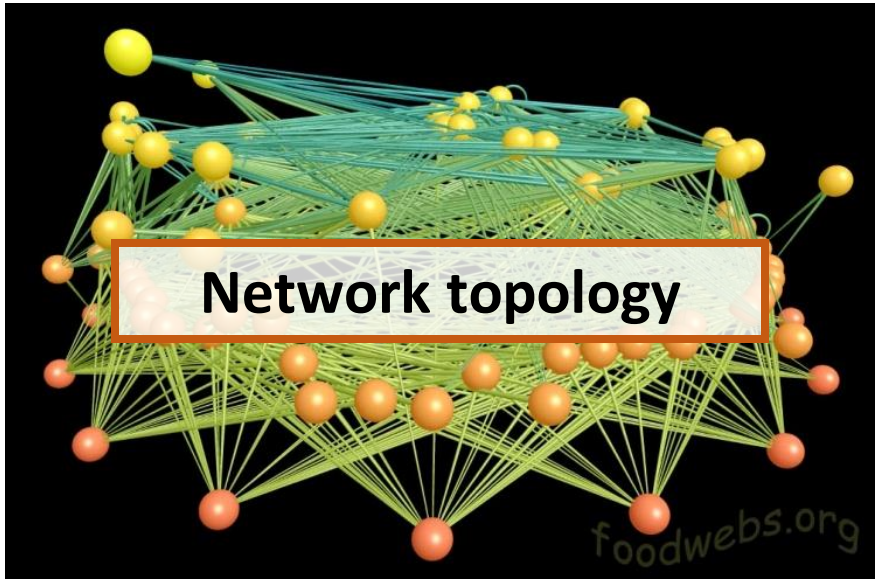
CESAB
CENTRE FOR THE SYNTHESIS AND ANALYSIS OF BIODIVERSITY

Why study ecological interaction networks?



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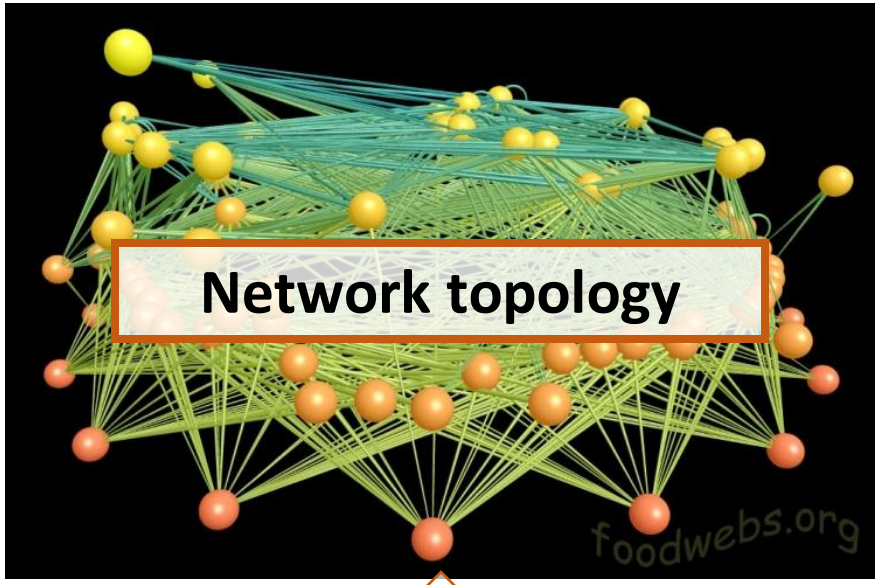
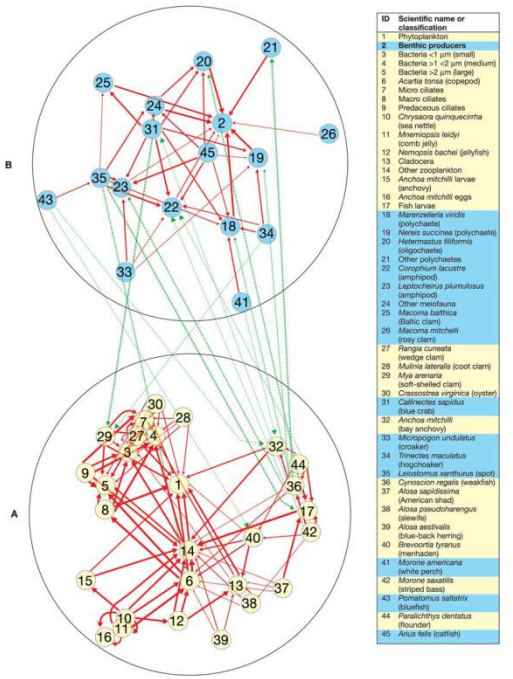
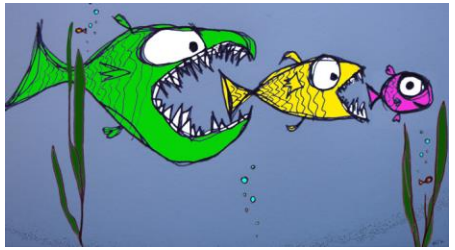
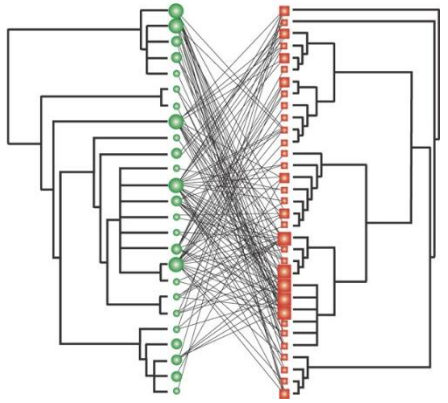


Mechanisms determining interactions between species



Chesapeake Bay food web
Krause et al. (2003)





Rezende et al. 2007

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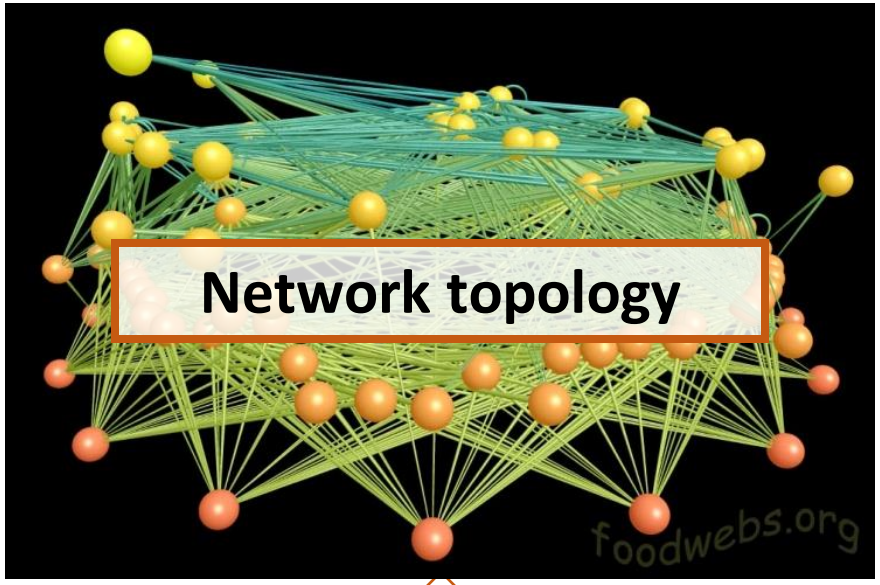
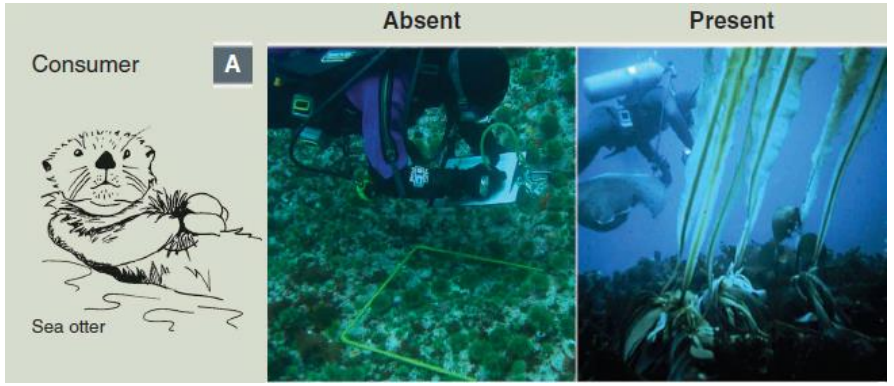
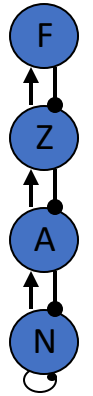


Consequences on community functioning and stability

- Understand cascading effects in networks



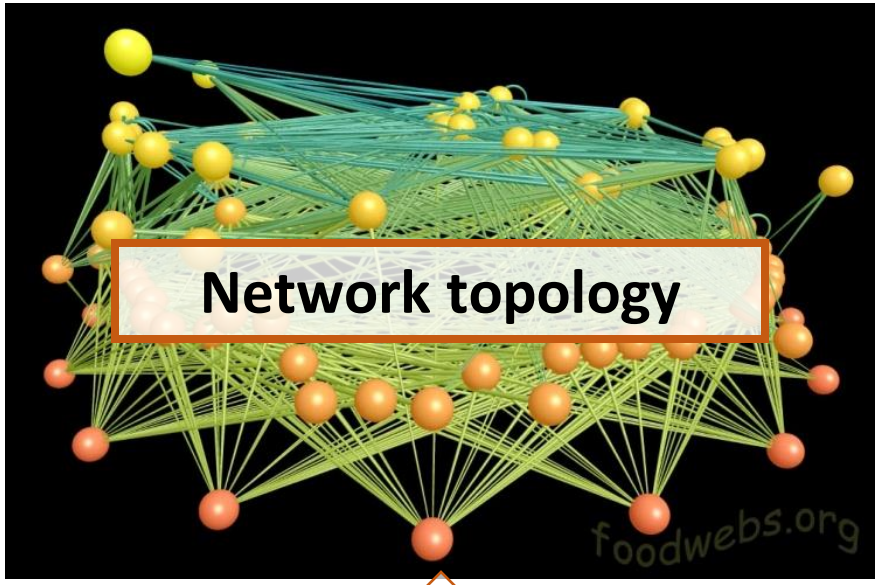
Estes et al. (2011)



Model population dynamics

$$dN_i/dt = N_i\left(r_i + \sum_j^n \alpha_{ij} N_j\right)$$

Why study ecological interaction networks?



Consequences on community functioning and stability

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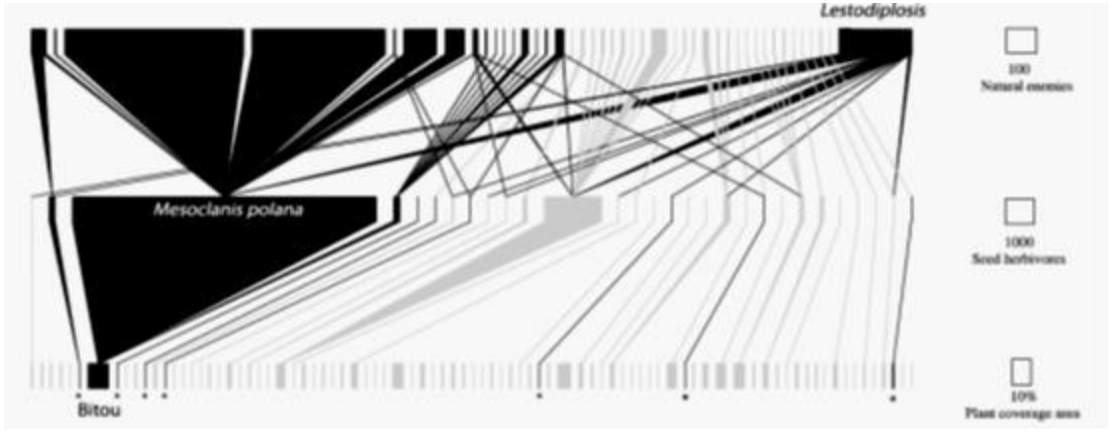
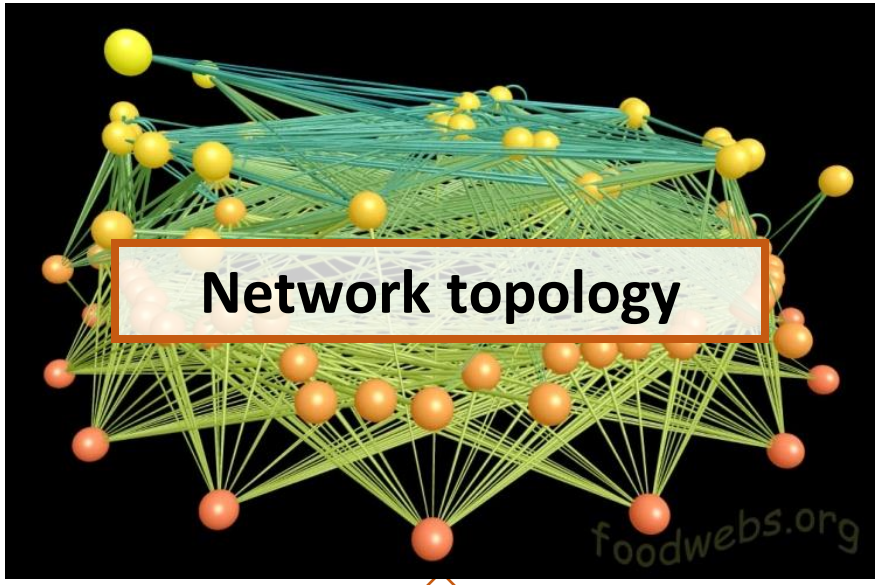


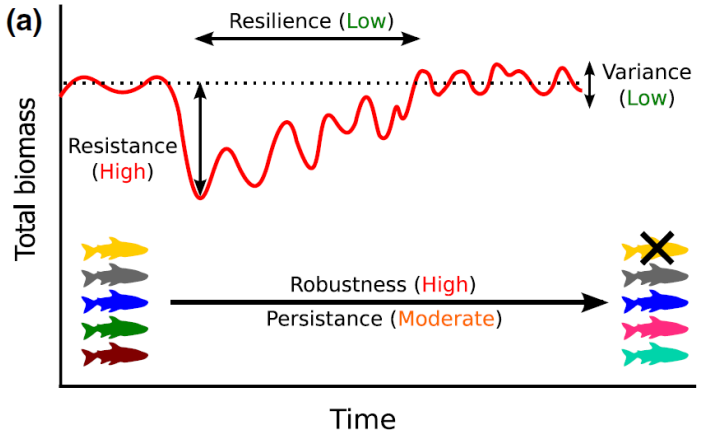
Cavalheiro et al. (2008)

Why study ecological interaction networks?



Consequences on community functioning and stability

➢ Study the links between network structure and ecosystem responses to perturbations



Donohue et al. (2016)

Questions

I. Mechanisms determining interactions between species

- What is the structure of ecological networks? Are there structural generalities?
- Can we predict interactions from species traits?
- How do networks change with environmental conditions?
- What is the role of interaction type?

TODAY

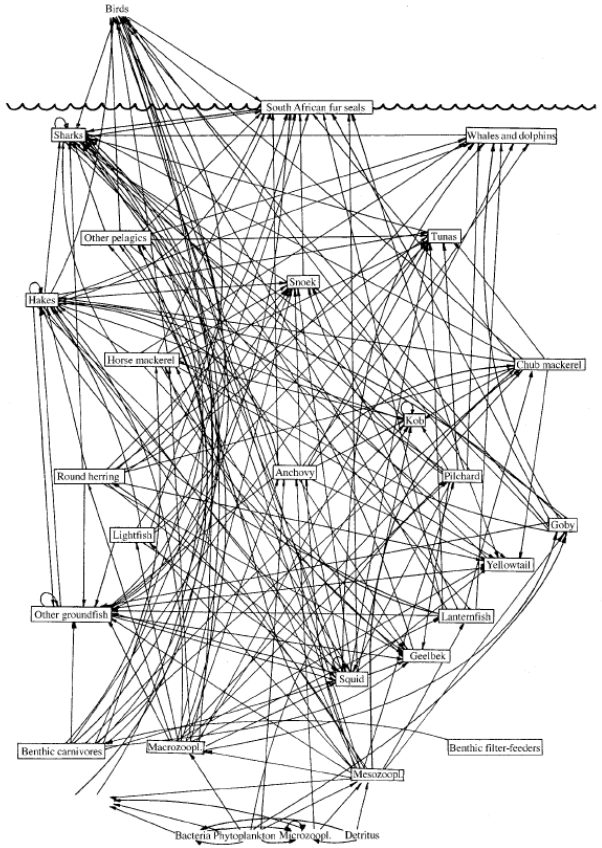
WEDNESDAY?

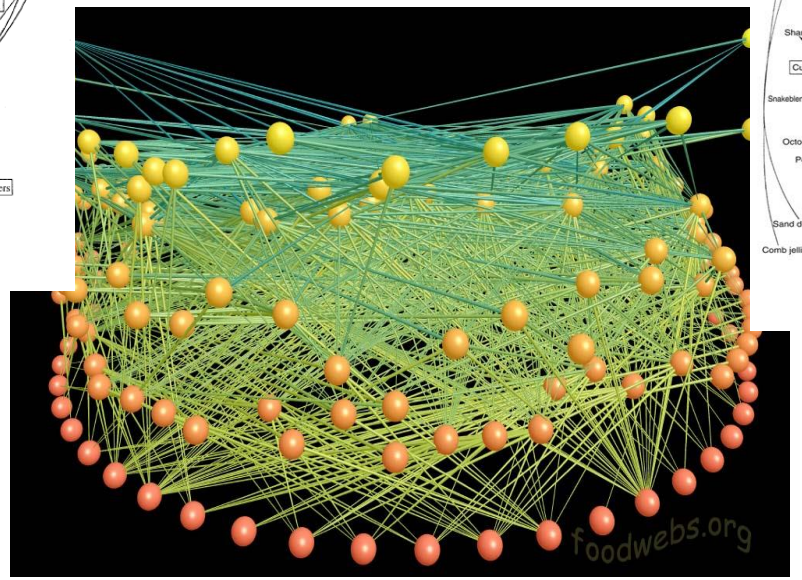
II. Consequences on community functioning and stability

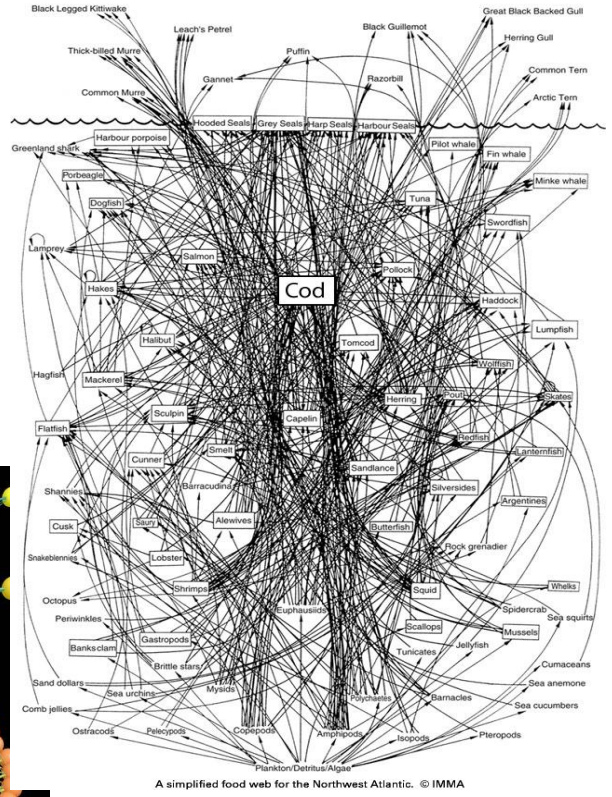
- What are the links between structure and stability?
- What are the links between structure and function?

TOMORROW

Analysing the structure of ecological networks: looking for general patterns?







A simplified food web for the Northwest Atlantic. © IMMA

Analysing the structure of ecological networks: looking for general patterns?

Part 1: examples of two historical patterns studied in food webs:

- The relationship between species diversity and the number of links/connectance
- The maximum food chain length

Analysing the structure of ecological networks: looking for general patterns?

Part 1: examples of two historical patterns studied in food webs:

- **The relationship between species diversity and the number of links/connectance**

- The maximum food chain length

The diversity – connectance relationship

- *S* – number of species
- *L* – number of links
- Linkage density – average number of feeding links per species: *L*/*S*
- Connectance (*C*)*:* proportion of possible links that is realised (a function of *S* and *L*)

$$C = \frac{\text{Number of realised links } (L)}{\text{Number of possible links}}$$

What is the number of possible links?
Depends on

1. whether links are directed
2. whether cannibalism is included
3. Whether the network is bipartite or not

The diversity – connectance relationship

Link species scaling law (constant link density)

vs.

Constant connectance hypothesis

?

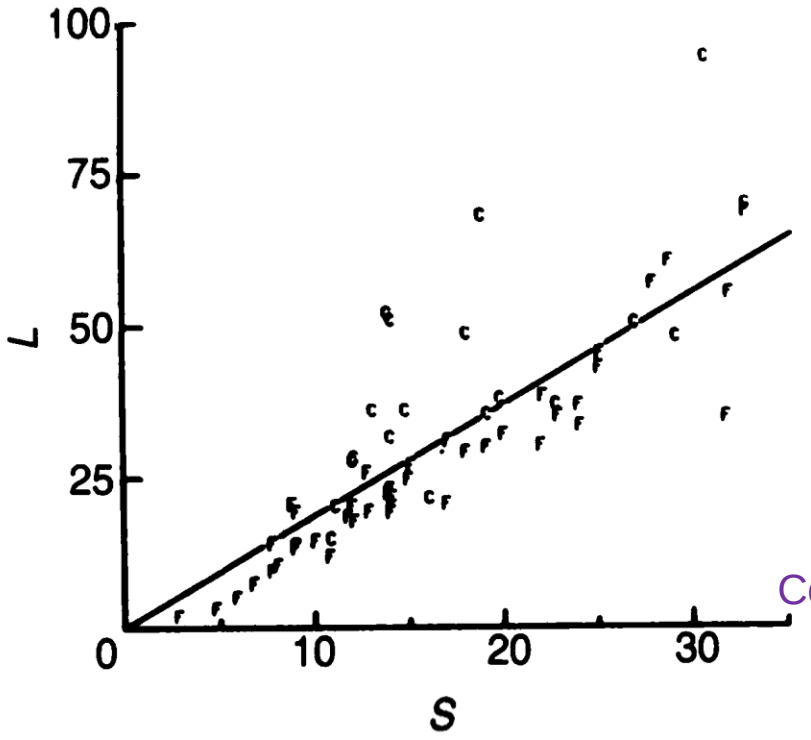
Cohen and Briand 1984

Martinez 1992

$$L = aS^b$$

L/S = constant

b = 1



Cohen and Briand 1984

The diversity – connectance relationship

Link species scaling law (constant link density)

vs.

Constant connectance hypothesis

?

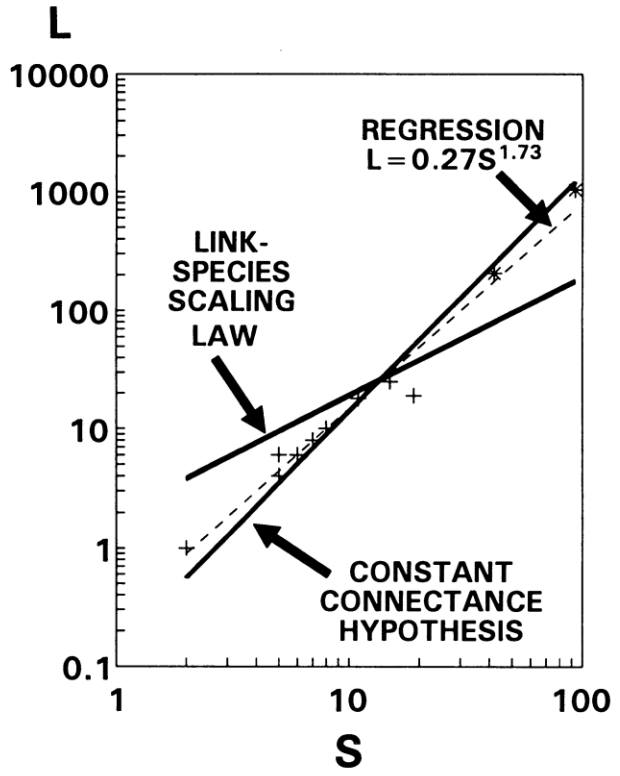
Cohen and Briand 1984

Martinez 1992

$$L = aS^b$$

C = constant

b = 2



Martinez 1992

The diversity – connectance relationship

A matter of data resolution?

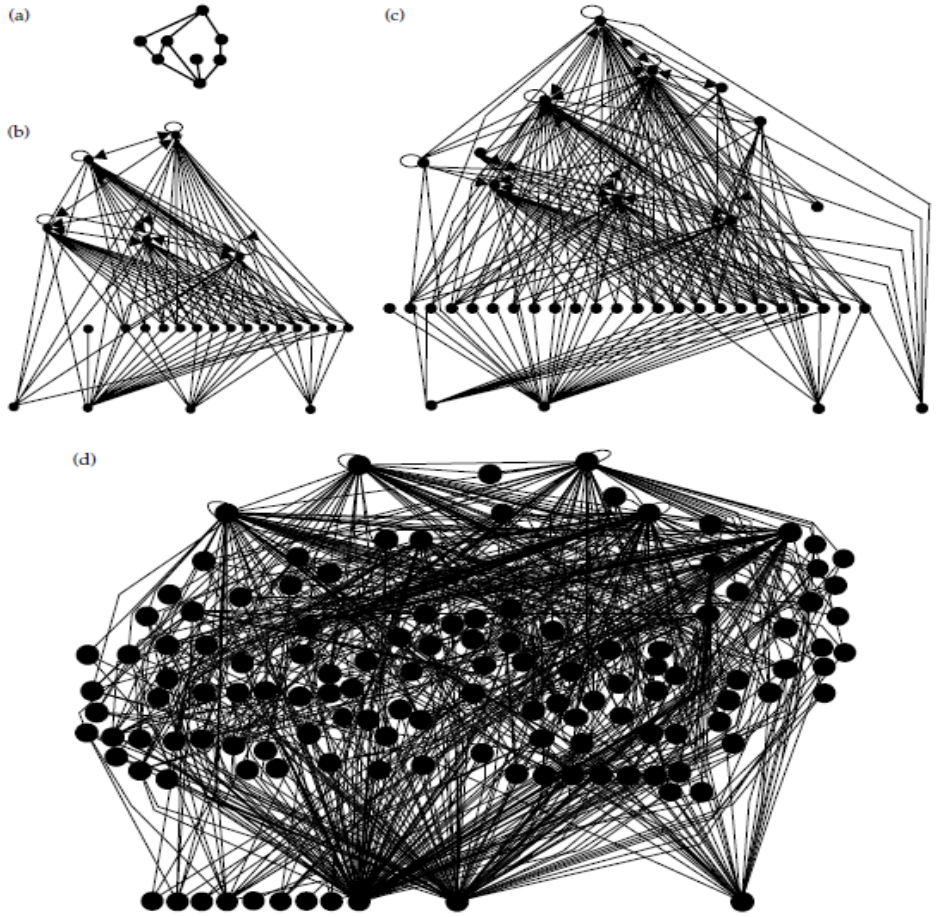
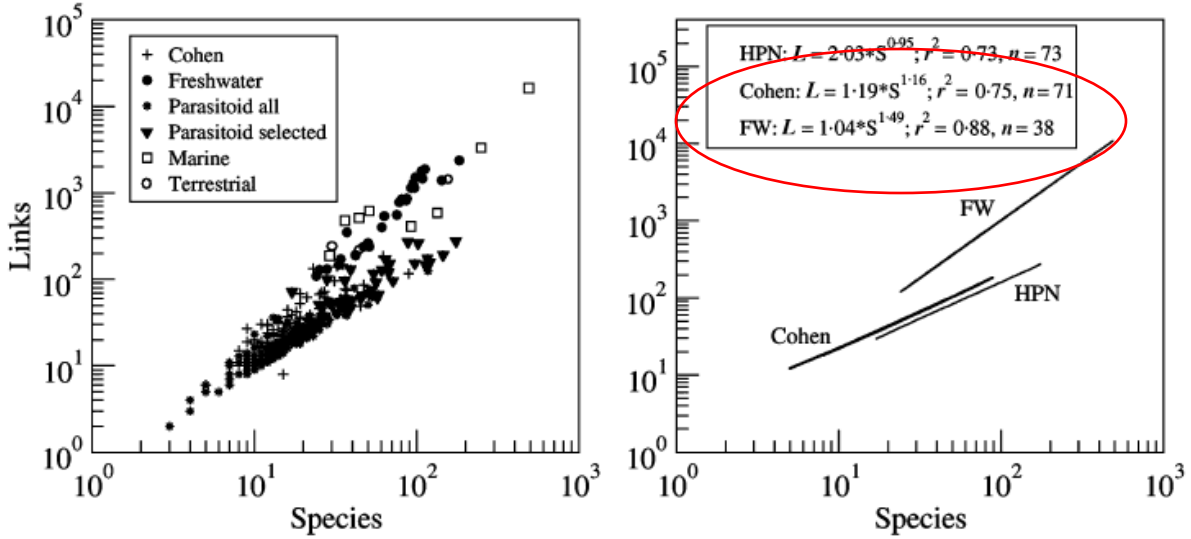


Figure 5.1 Connectance food webs from the early and more recent stream literature: (a) Early stream food-web (redrawn from Cohen 1978) (b) Initial connectance web from Broadstone Stream (after Hildrew et al. 1985) (c) Intermediate resolution web from Broadstone Stream (after Woodward and Hildrew 2001) (d) Highly resolved Broadstone Stream food-web (after Schmid-Araya et al. 2002a).



Ings et al. 2009

The diversity – connectance relationship

A matter of data resolution?

Test with simulated food webs:

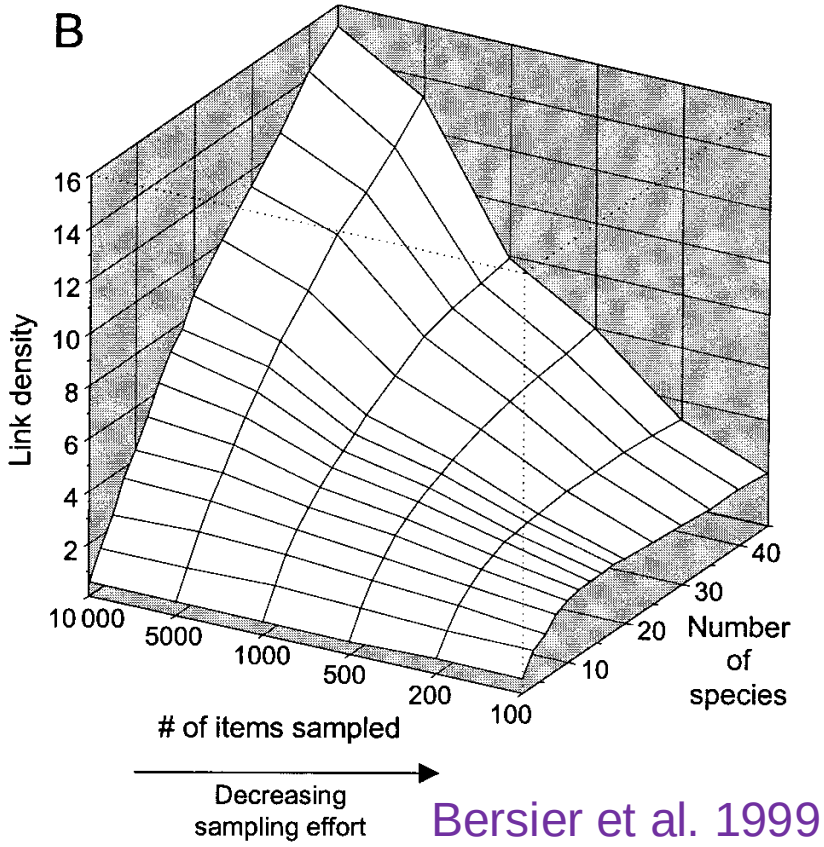
Generate food web from cascade model, with species diversity S and connectance C

↓

Trophic links with varying probabilities of observation

↓

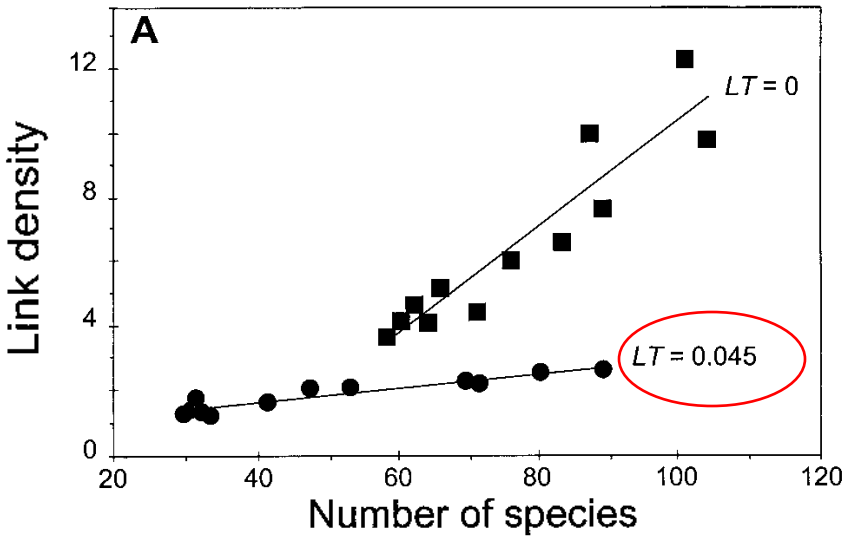
« Observed » networks as a function of sampling intensity



Bersier et al. 1999

The diversity – connectance relationship

A matter of data resolution?

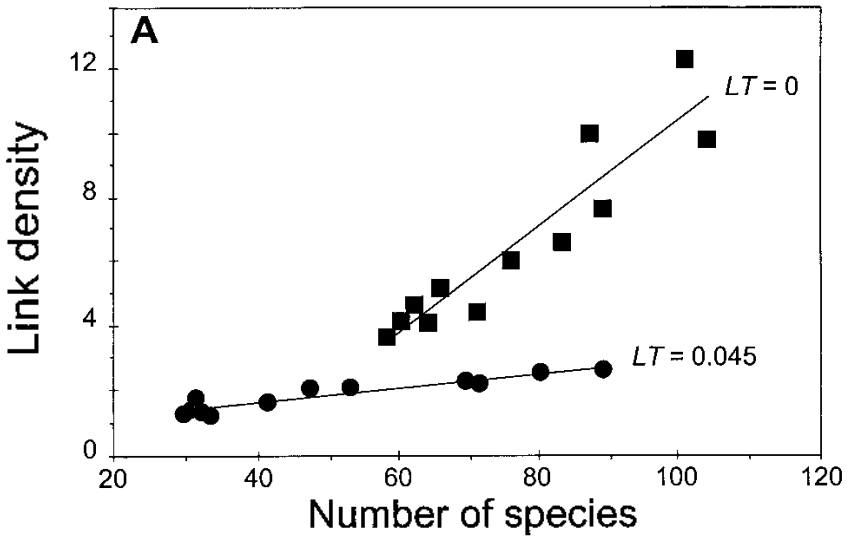


Remove prey in each fish species diet corresponding to less than 4.5% of total prey

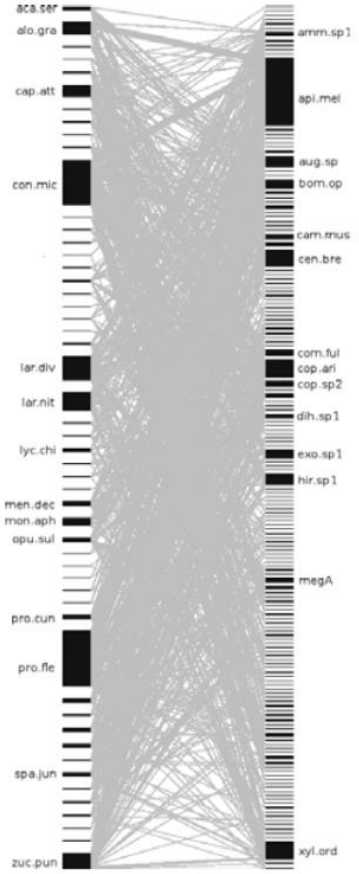
Bersier et al. 1999

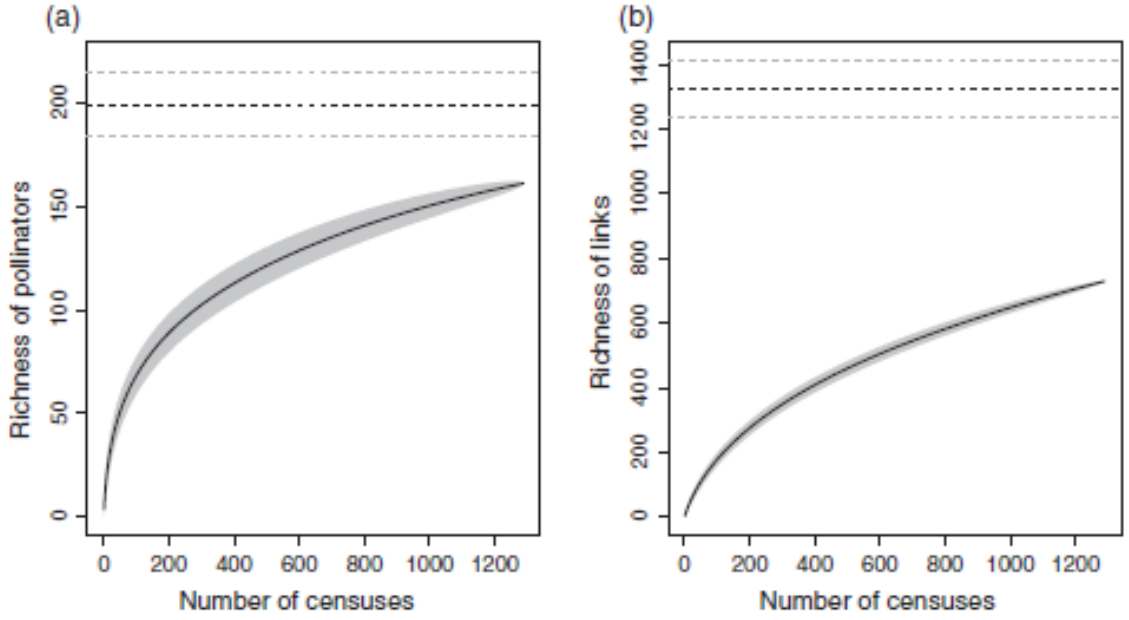
The diversity – connectance relationship

A matter of data resolution?



Bersier et al. 1999

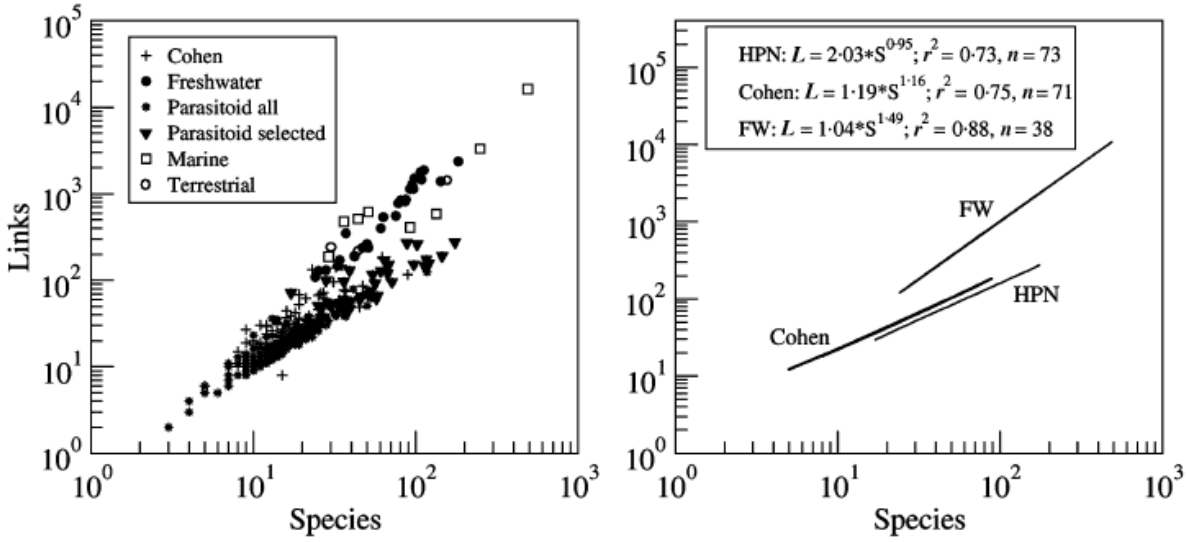




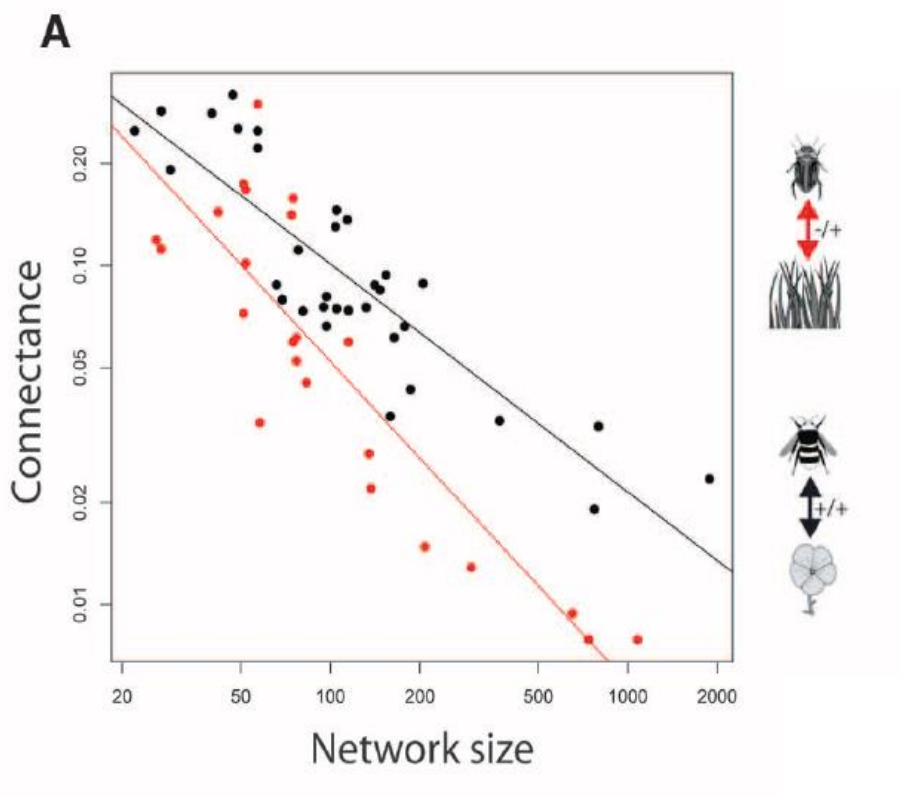
Chacoff et al. 2011

The diversity – connectance relationship

Depends on interaction type, ecosystem type, etc.



Ings et al. 2009



Thébault & Fontaine 2010

Analysing the structure of ecological networks: looking for general patterns?

Part 1: examples of two historical patterns studied in food webs:

- The relationship between species diversity and the number of links/connectance

- **The maximum food chain length**

Specific food web metrics

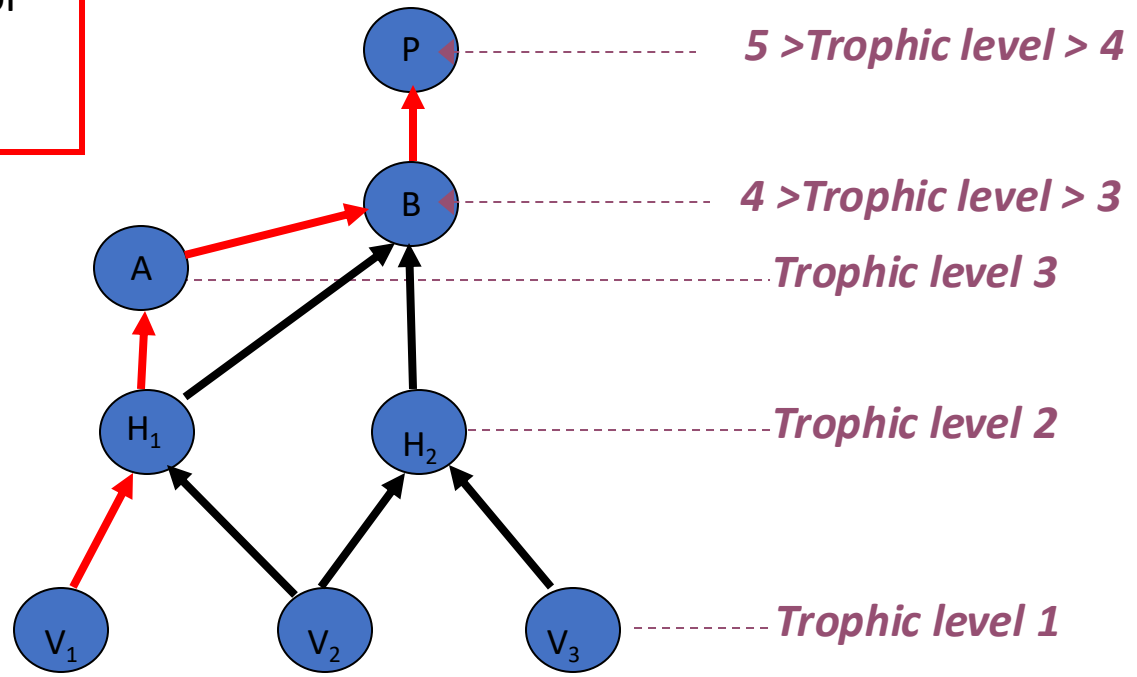
- Number of trophic levels (or minimal chain length between top predators and basal species)
- Relative species number at the different trophic levels
- Proportion of omnivores

$$TL_i = 1 + \sum_{j=1}^{N_{fw}} g_{ij} TL_j$$

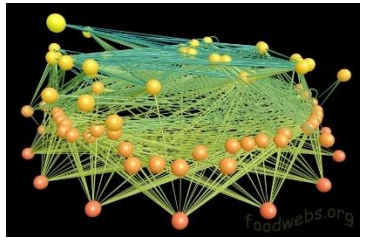
$$TL = [(I-G)^{-1}]\,1$$

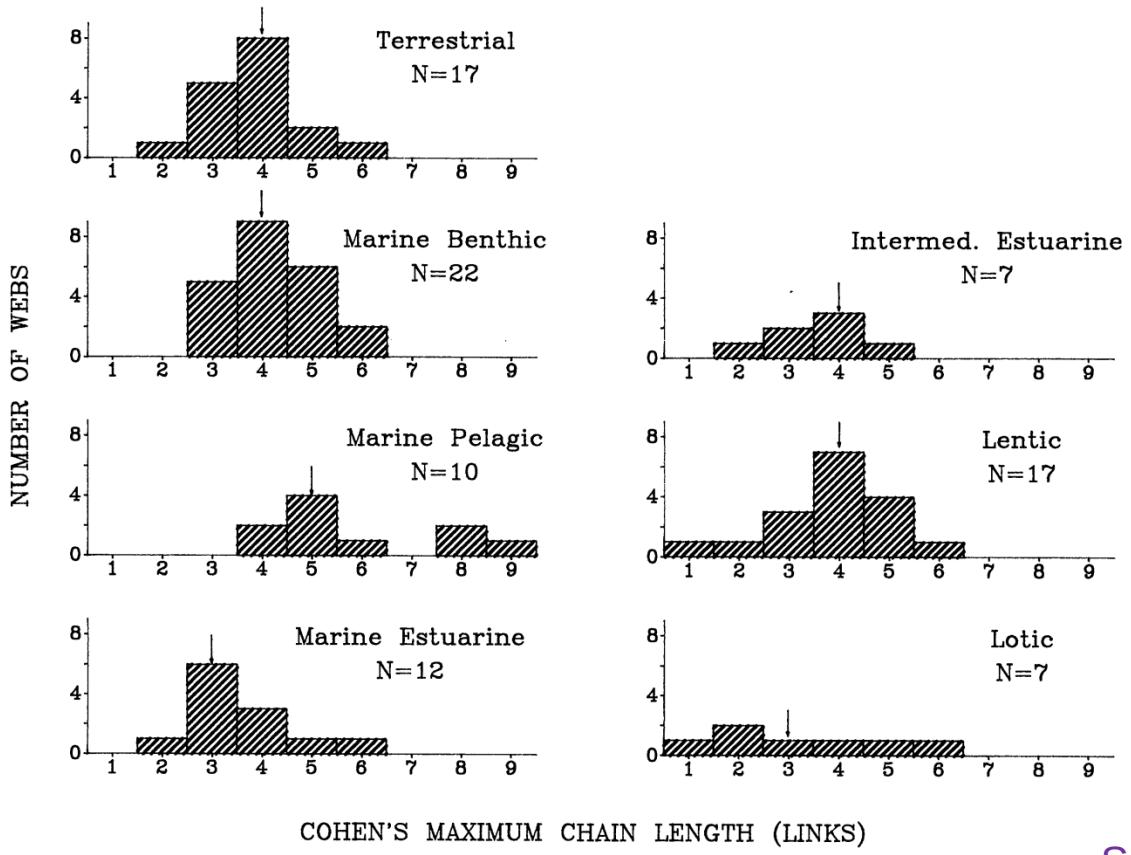
Trophic chain: representation of matter or energy flow from a basal species to a top predator.

Trophic level: position in the trophic chain, determined by the number of energy transfers up to this level.



Maximum food chain length is generally low (<6)





Schoener 1989

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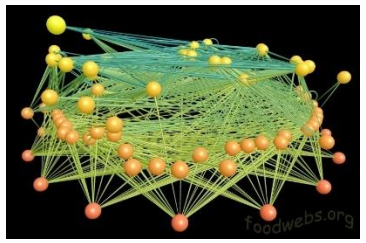

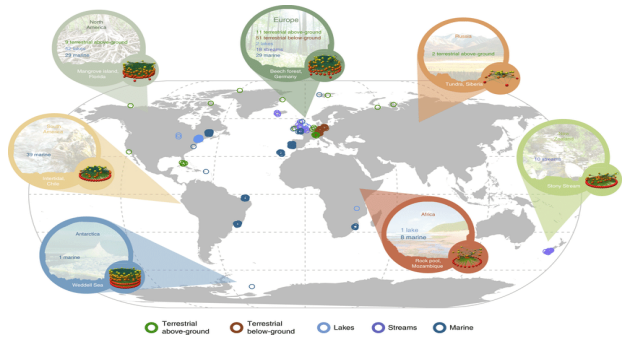

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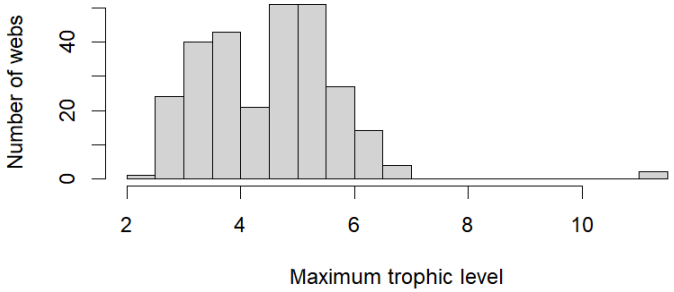
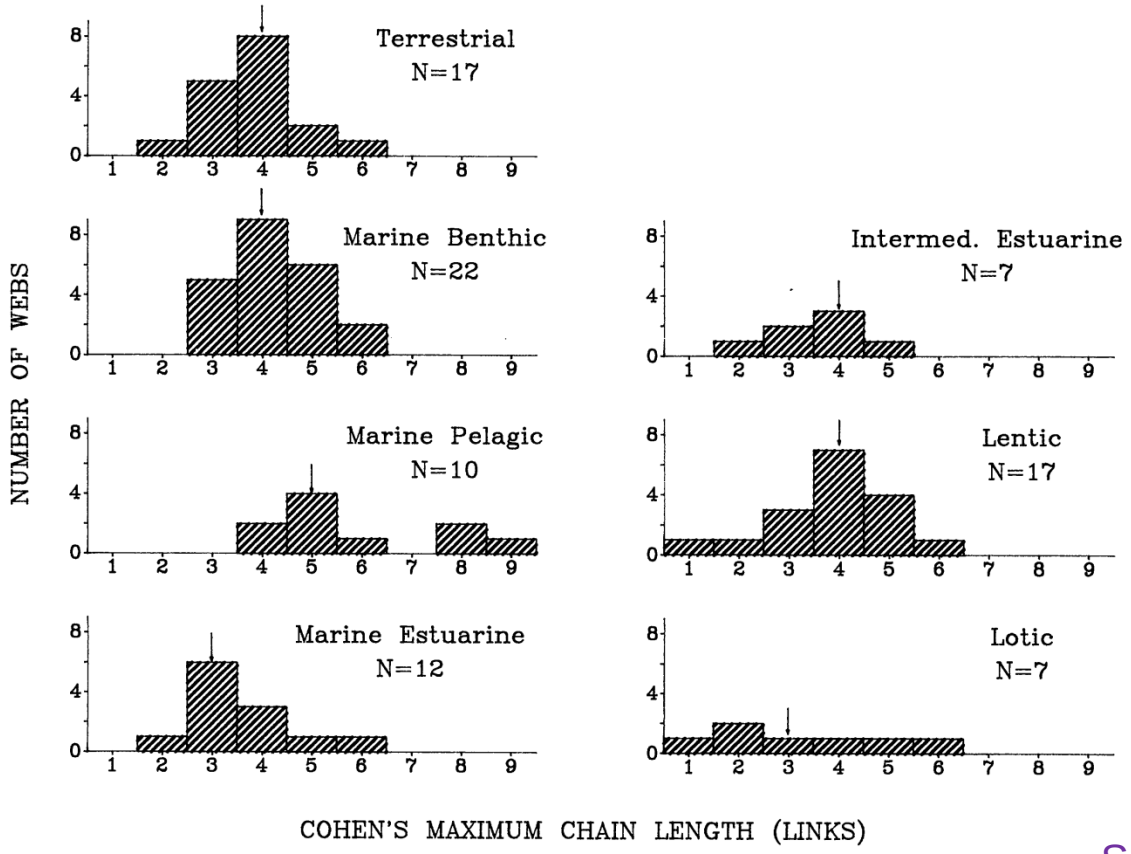




Schoener 1989

What limits food chain length?
Several theories

- Limitation by available resources

Hutchinson 1959, Oksanen 1981, …

Inefficiency of energy transfer: Typically only about 10-15% of consumed prey biomass is converted into predator biomass. (Slobodkin 1960)

What limits food chain length?
Several theories

- Limitation by available resources

Hutchinson 1959, Oksanen 1981, …

tad poles

↑

mosquito larvae

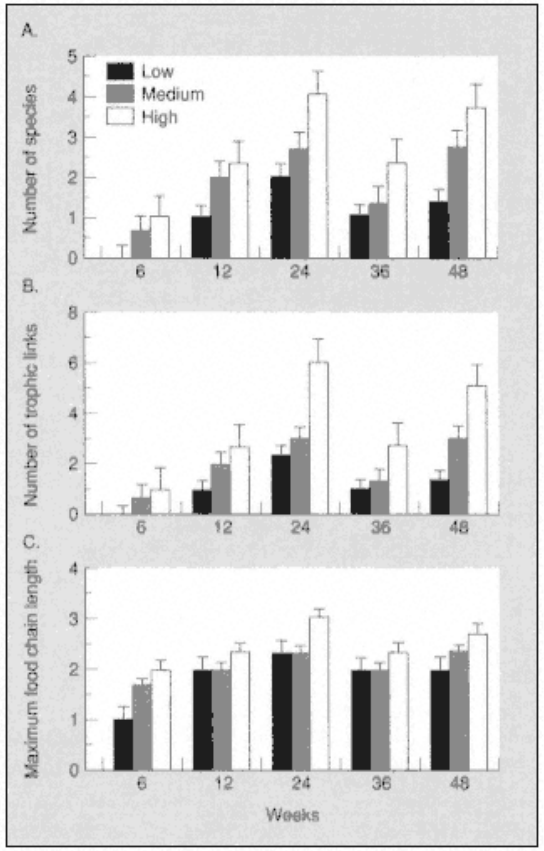
↑

micro invertebrates

↑

detritus

Srivastava & Lawton Am Nat 1998



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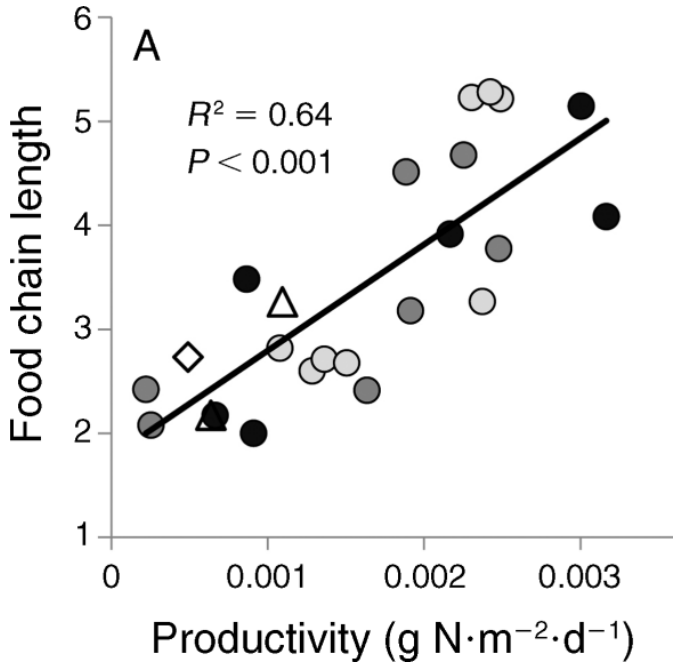
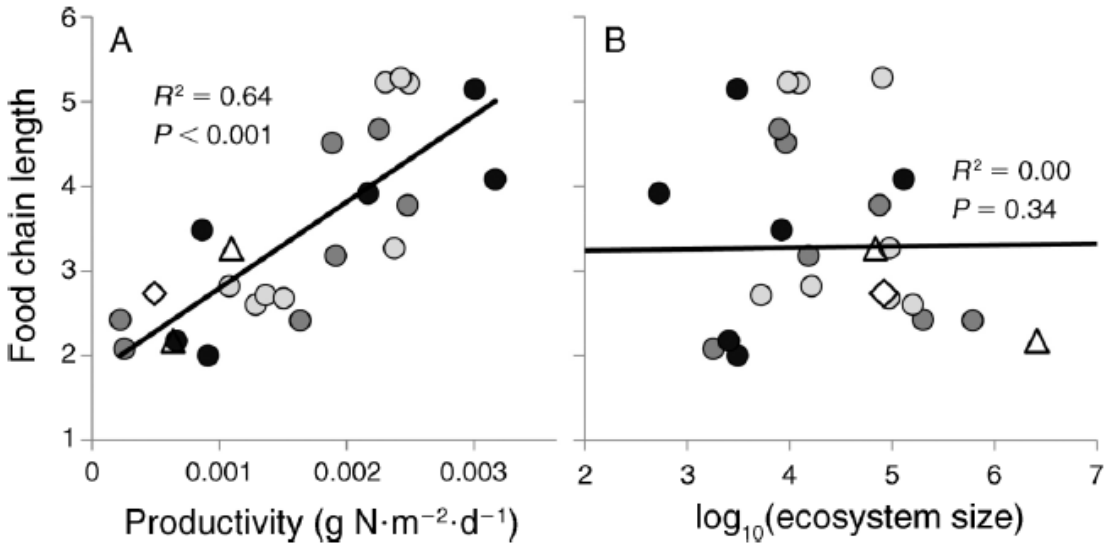


Young et al. 2013

What limits food chain length?
Several theories

- Limitation by ecosystem size

Schoener 1989, Cohen & Newman 1991, …



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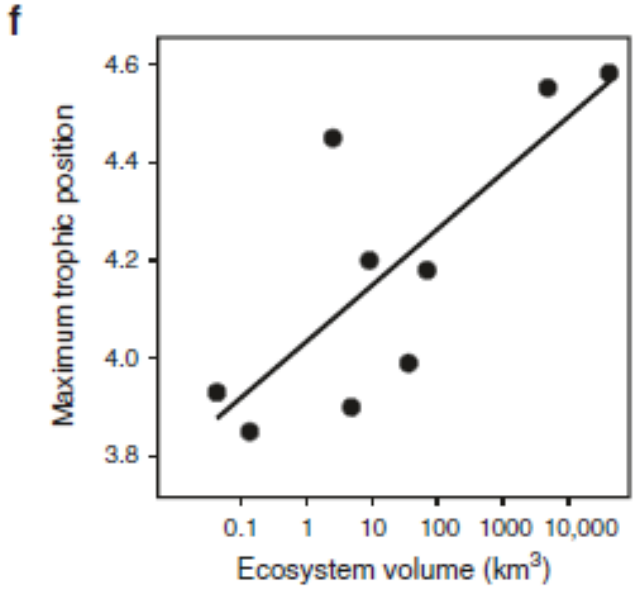


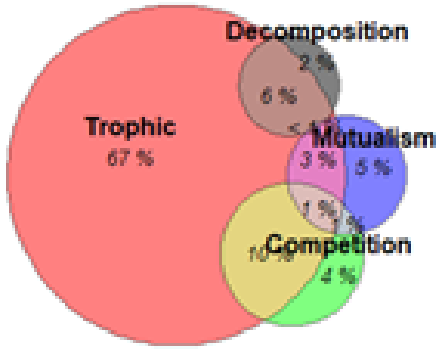
Ward & McCann 2017

Analysing the structure of ecological networks: looking for general patterns?

Part 1: examples of two historical patterns studied in food webs:

- The relationship between species diversity and the number of links/connectance
- The maximum food chain length

- **Historically focused on a few sets of network and species level properties**
- **A strong focus on food webs**



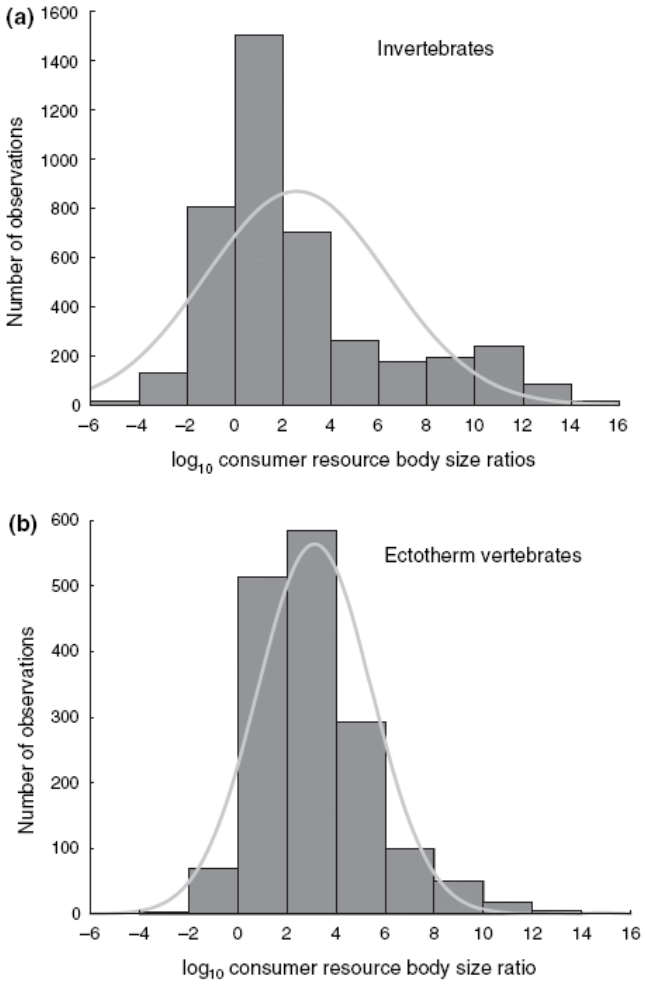
Analysing the structure of ecological networks: looking for general patterns?

Part 2: examples of more recent patterns studied in ecological networks:

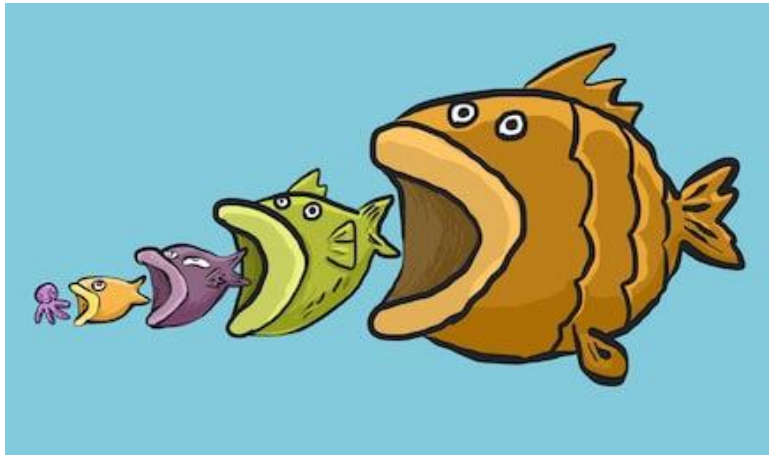
- **How species traits shape interactions in network**
- Distribution of degrees and interaction strengths
- Looking for groups
- How networks vary in space and time
- Comparing networks of different interaction types

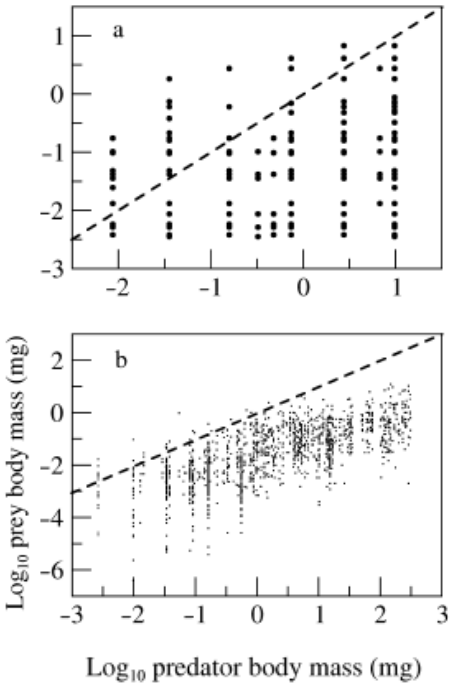
The example of body size in food webs

Trophic interactions and the ratio of body size between prey and predators



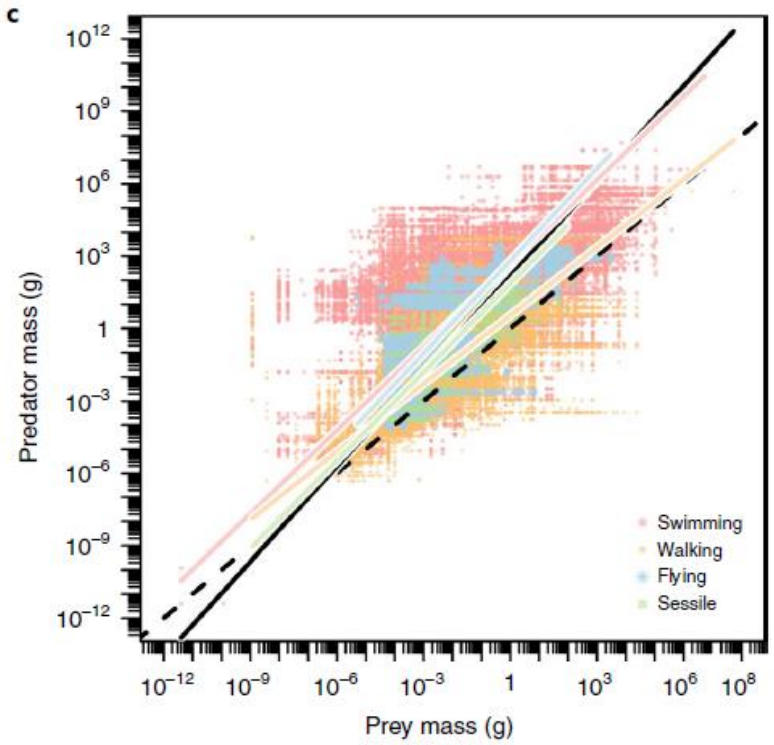
Brose et al. (2006)





Ings et al. (2009)

Relations that depend on consumer traits and ecosystem types



Brose et al. 2019

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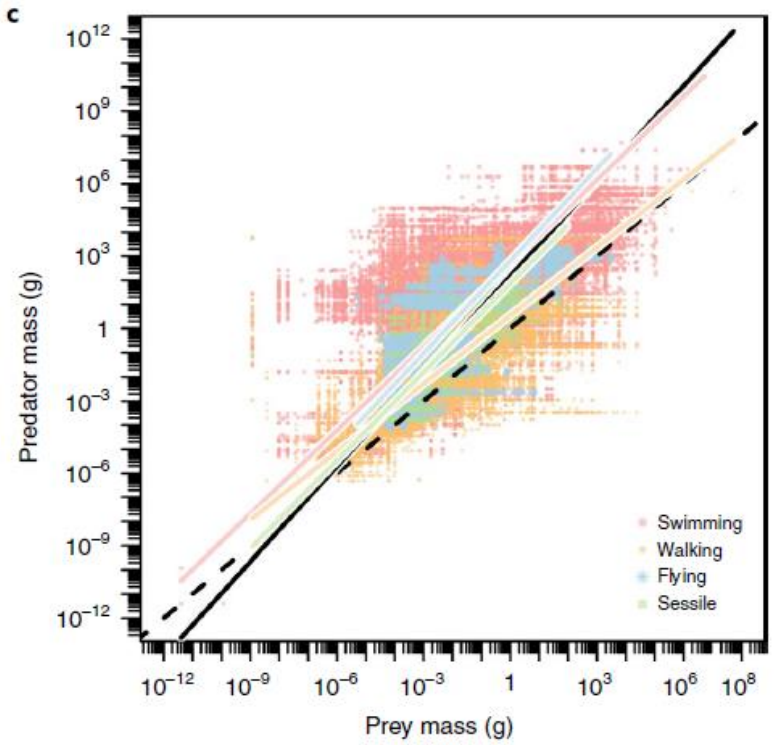

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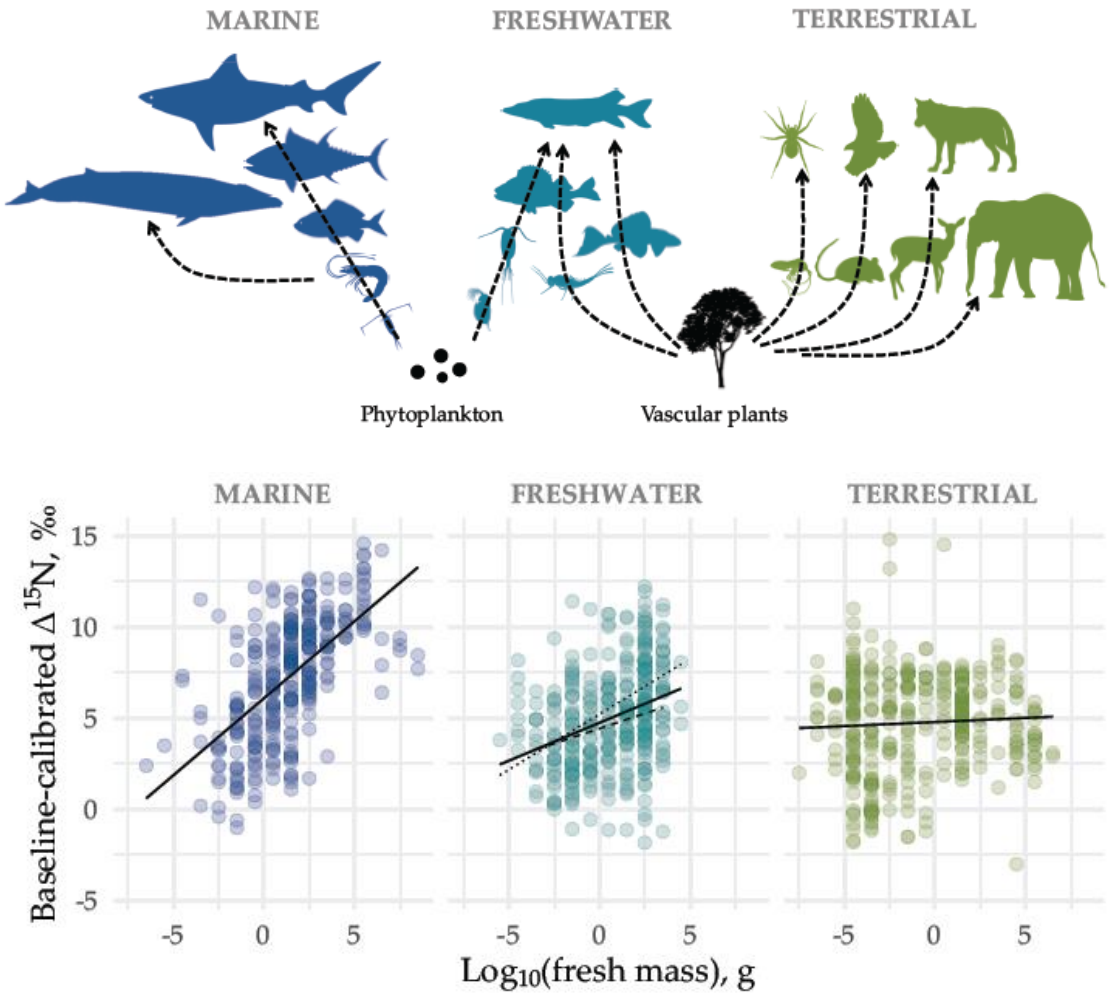
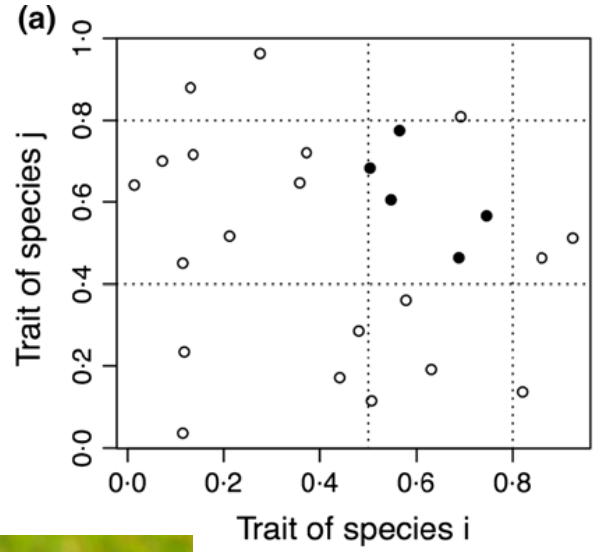
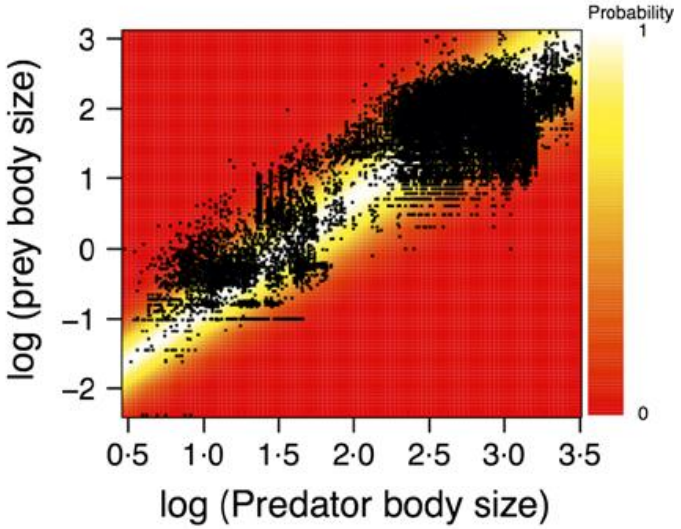


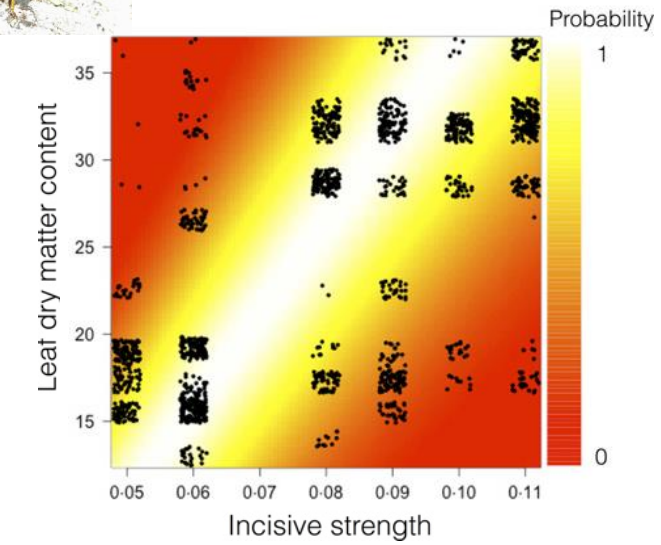
Potapov et al. 2019

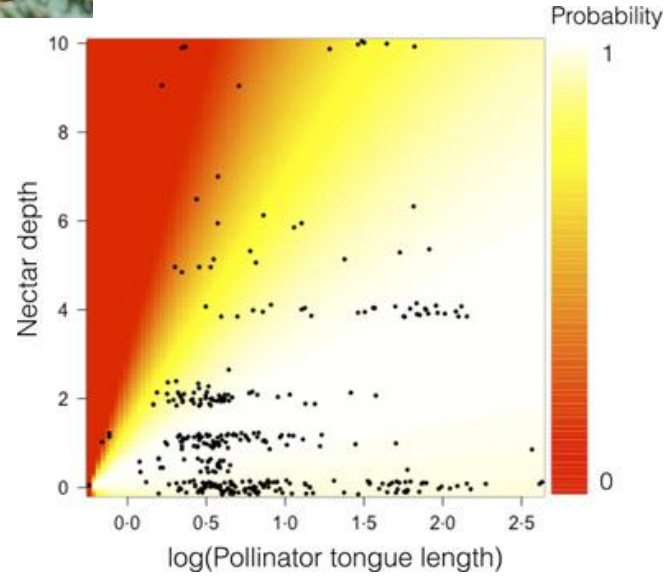
Different traits for different interaction types?



Bartomeus et al. 2016



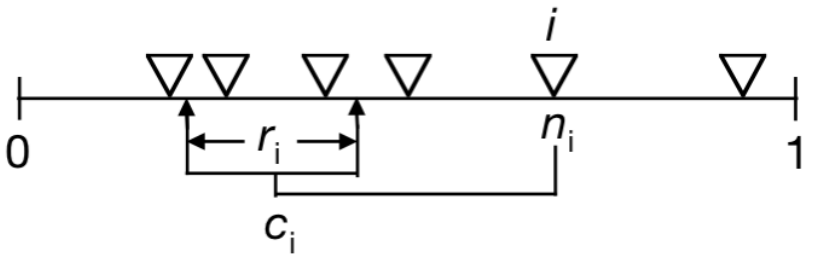




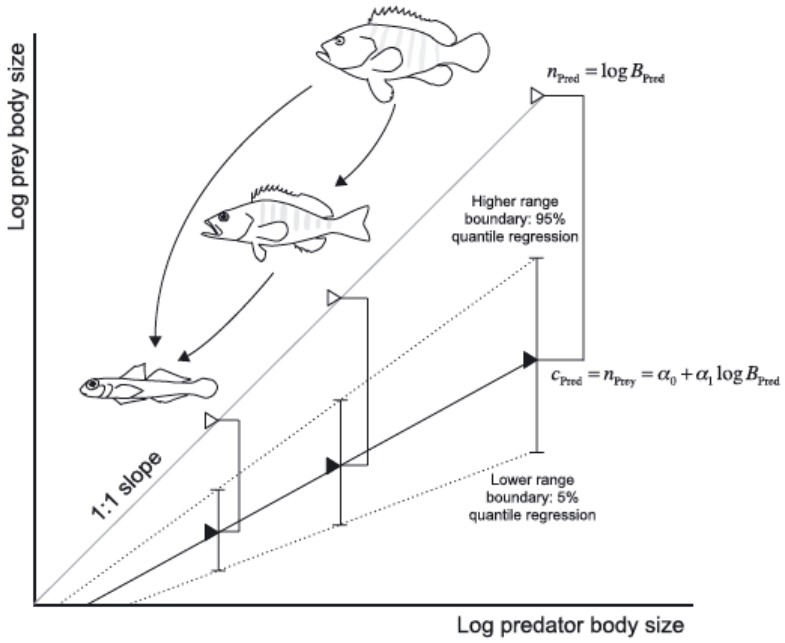
Infering trophic interaction and food web structure from body size

Starting from the niche model

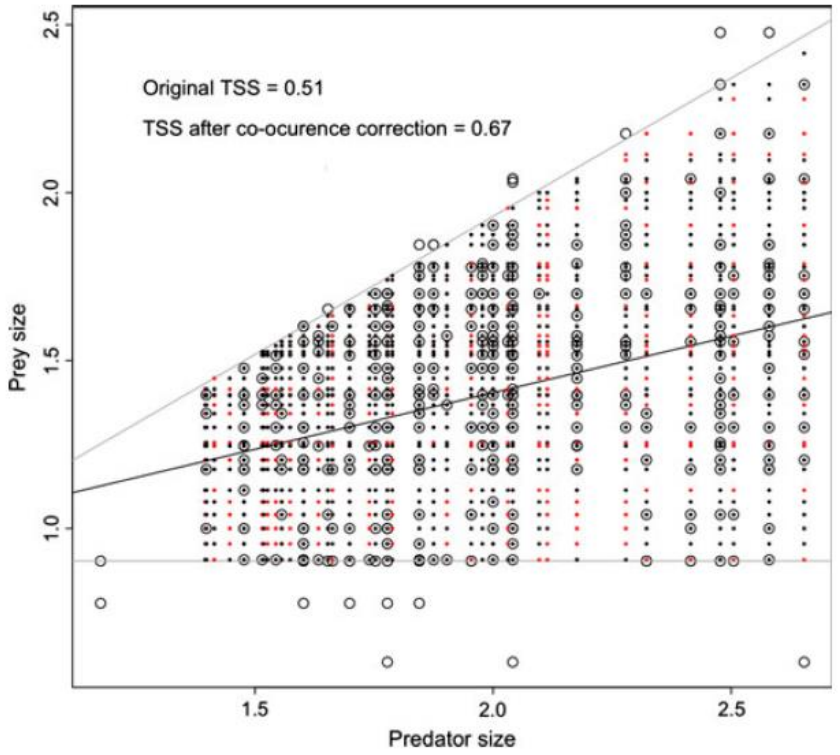
Williams & Martinez (2000)



Infer interactions from the niche model and species body size



Gravel et al. (2013)



The role of traits
Some conclusions and perspectives

- Importance of traits for understanding the structure of interaction networks: can we infer interactions between species?

- Relative importance of given traits depending on interaction types, ecosystems, environmental conditions?

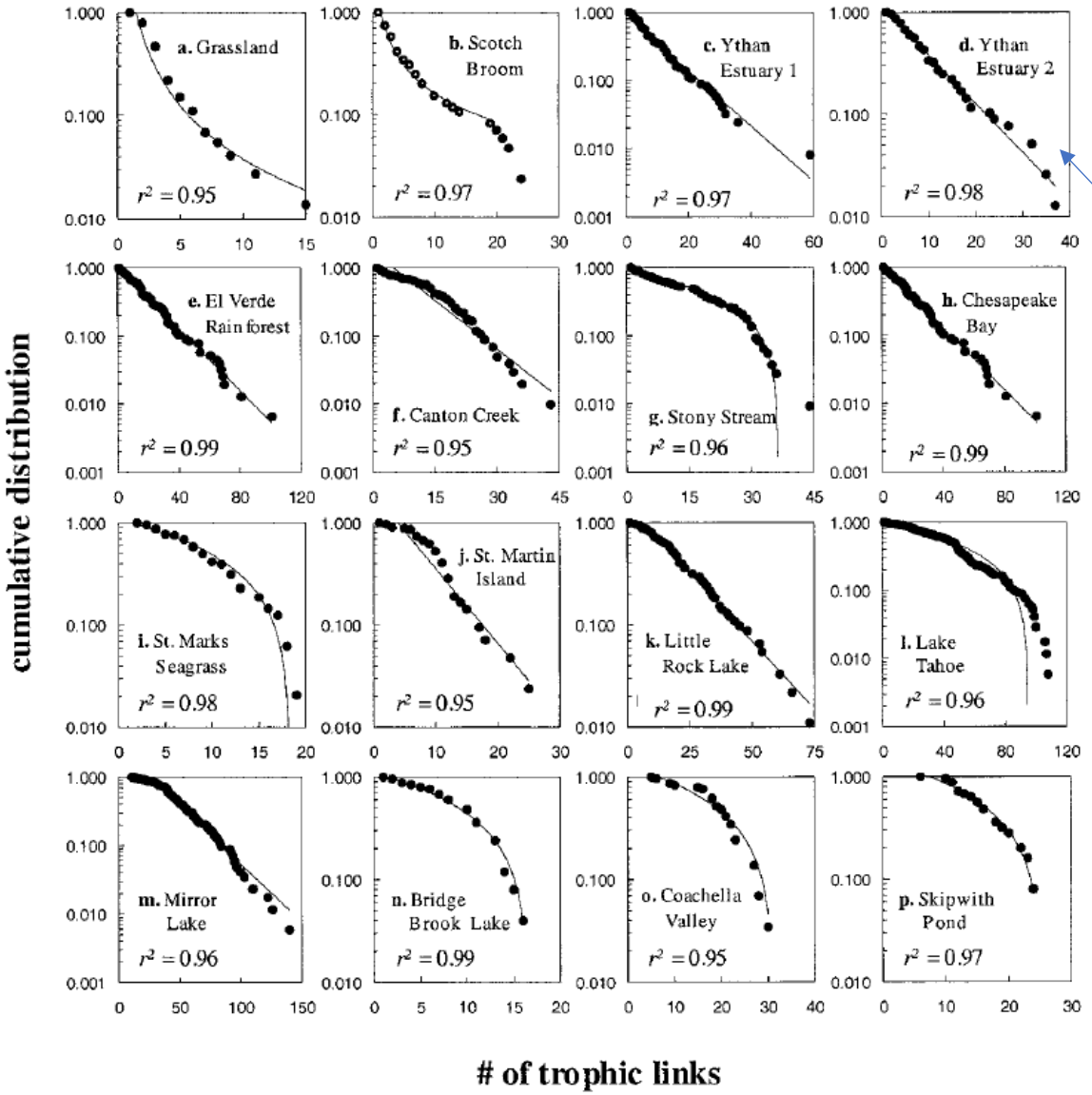
- Relative importance of traits vs. abundance? Importance of evolutionary history?

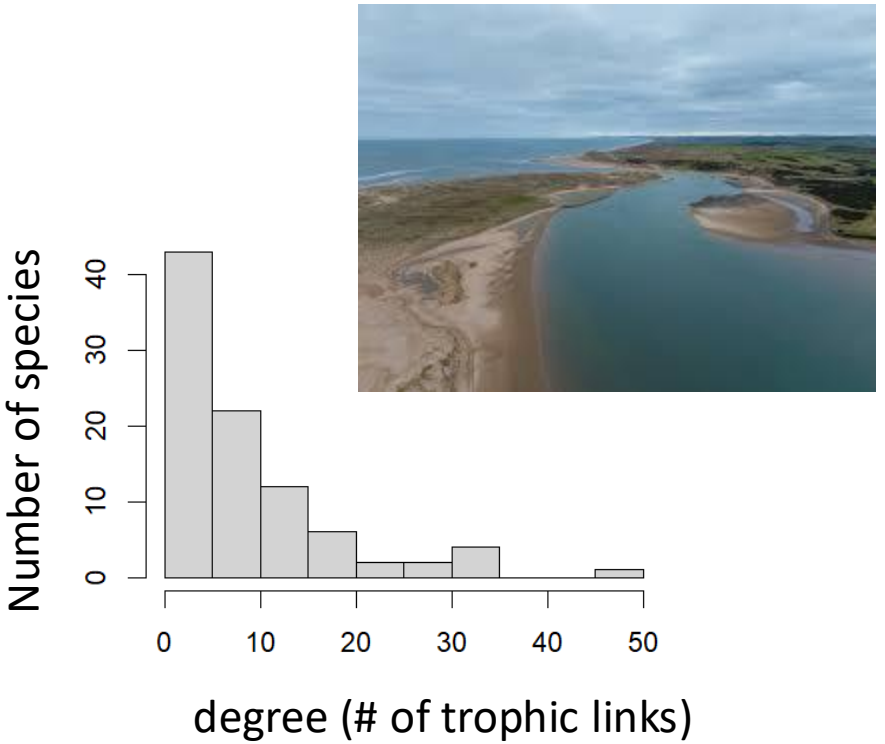
Analysing the structure of ecological networks: looking for general patterns?

Part 2: examples of more recent patterns studied in ecological networks:

- How species traits shape interactions in network
- **Distribution of degrees and interaction strengths**
- Looking for groups
- How networks vary in space and time
- Comparing networks of different interaction types

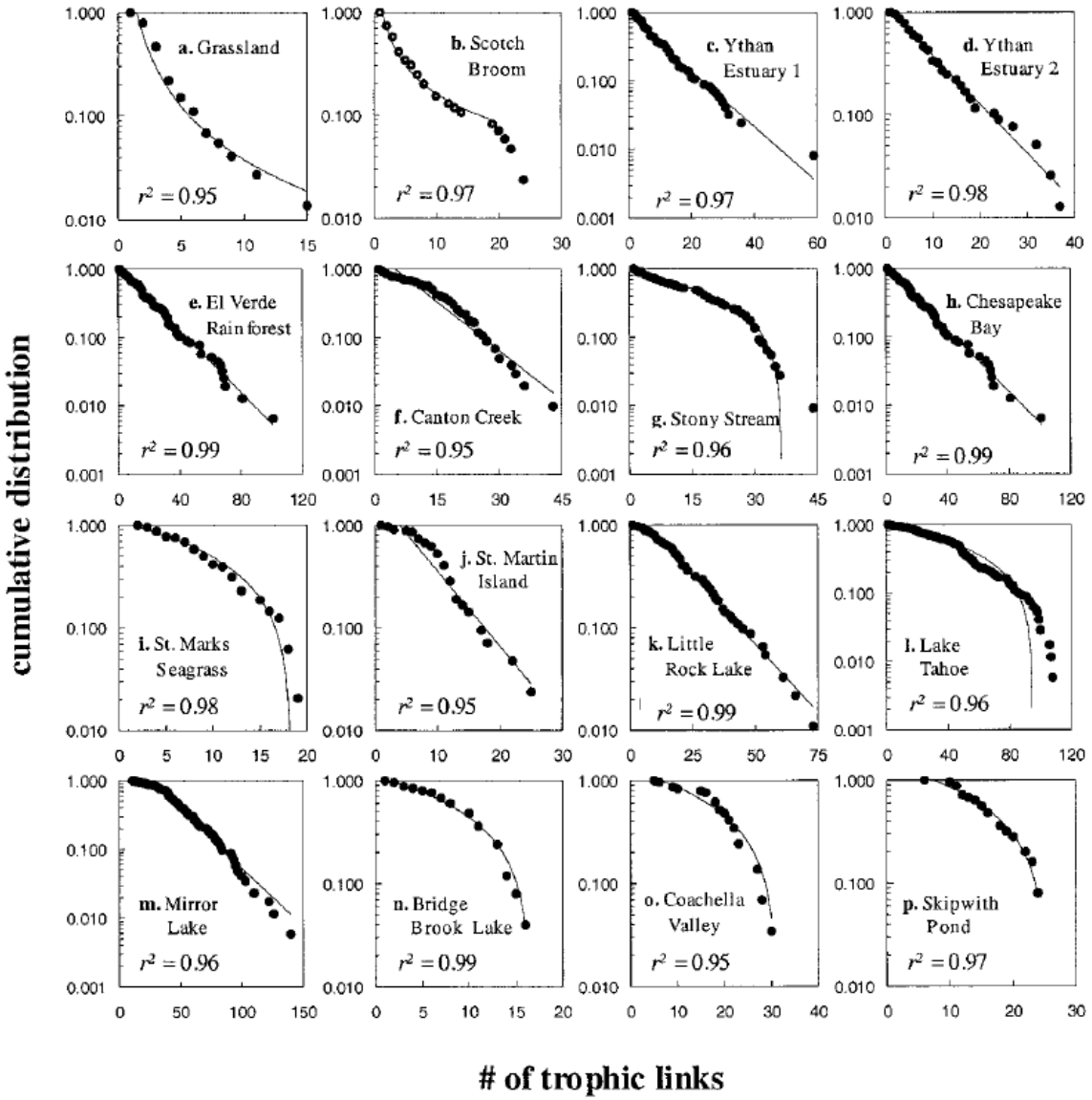
Degree distributions



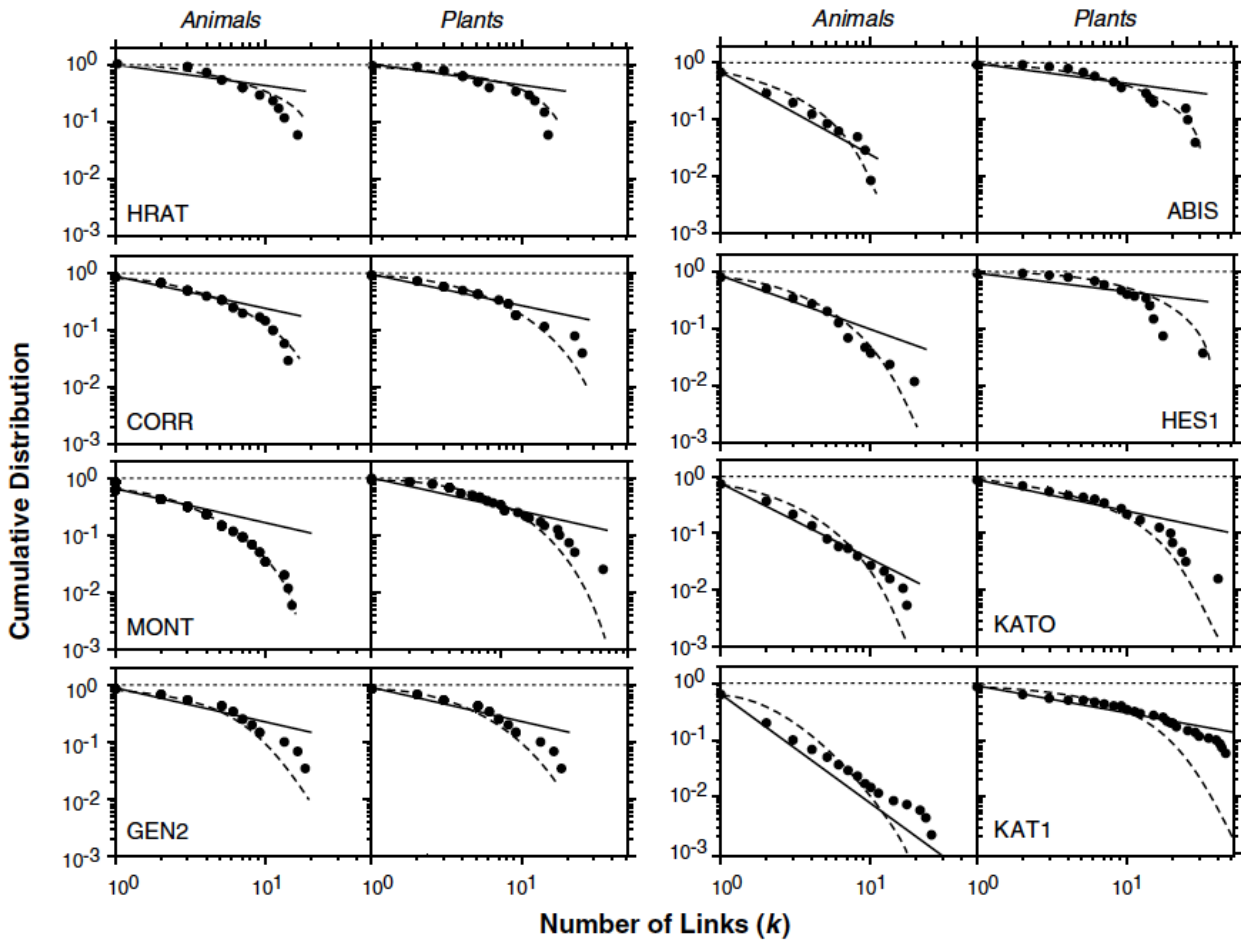


Dunne et al. 2002

Degree distributions

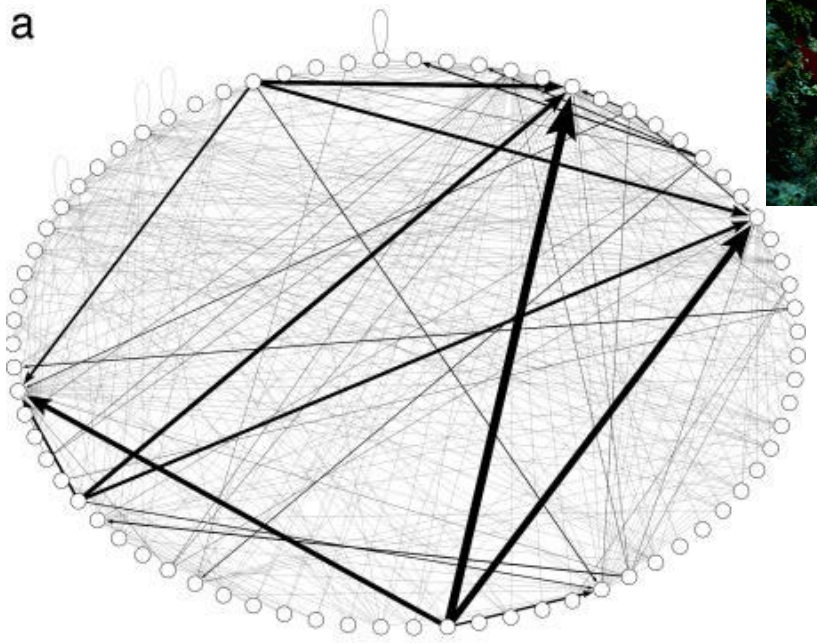


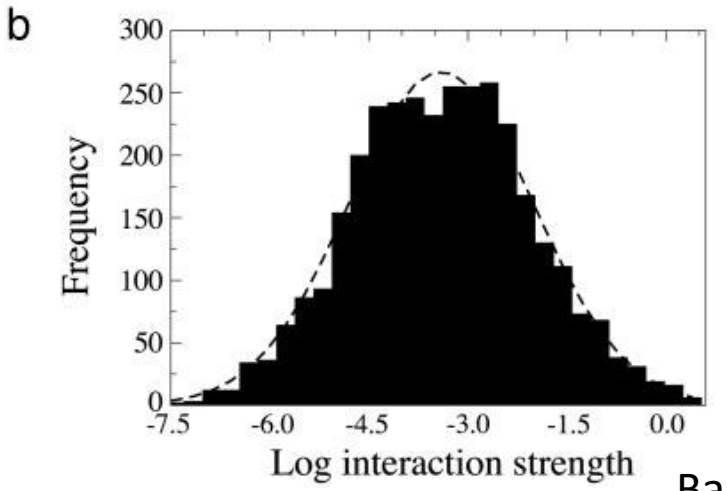
Dunne et al. 2002



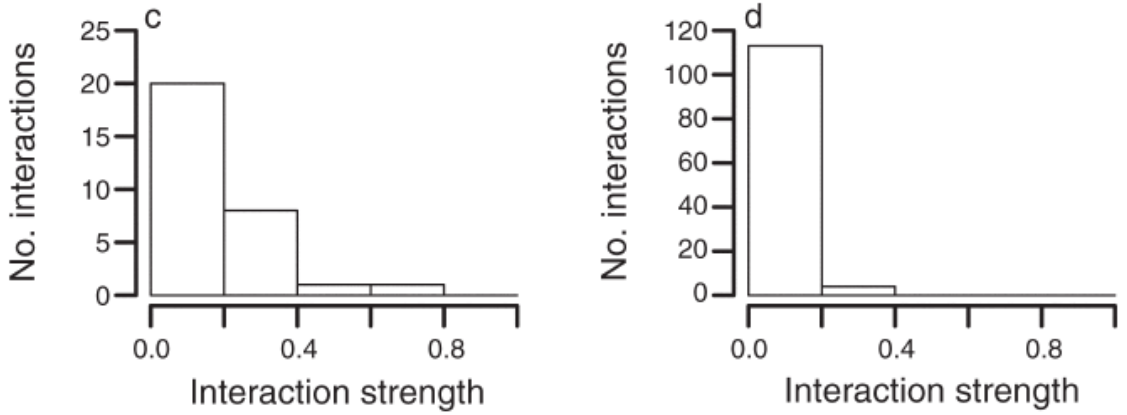
Jordano et al. 2003

Interaction strength distributions



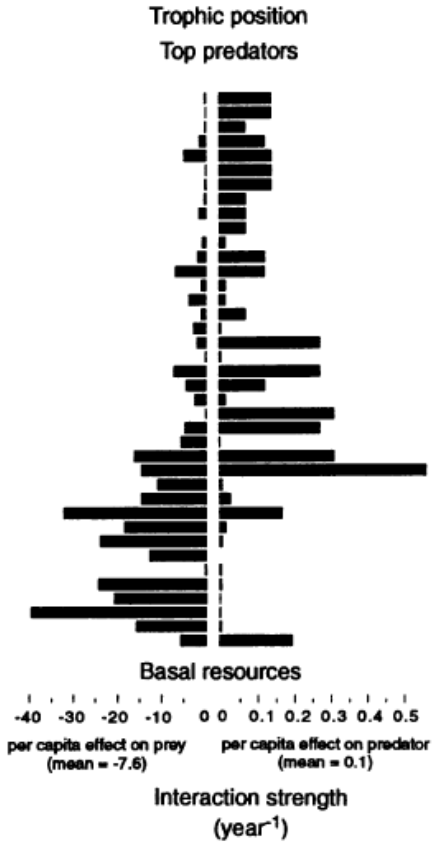


Bascompte et al. 2005



Vazquez et al. 2012

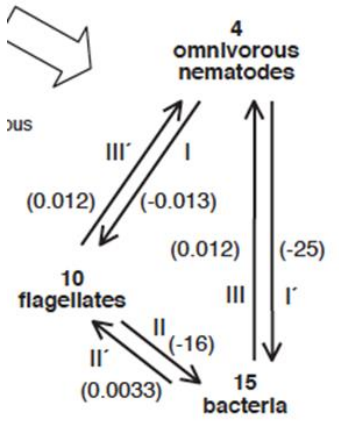
Interaction strength distributions: consequences on stability



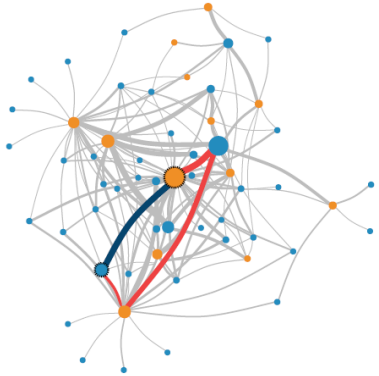
De Ruiter et al. 1995 Science

Stability in Real Food Webs: Weak Links in Long Loops

Anje-Margriet Neutel,[1]* Johan A. P. Heesterbeek,[2] Peter C. de Ruiter[1]



Neutel et al. 2002 Science



TOMORROW!

How does it relate with abundance distributions?

Ecology, 89(12), 2008, pp. 3387–3399

WHAT DO INTERACTION NETWORK METRICS TELL US ABOUT SPECIALIZATION AND BIOLOGICAL TRAITS?

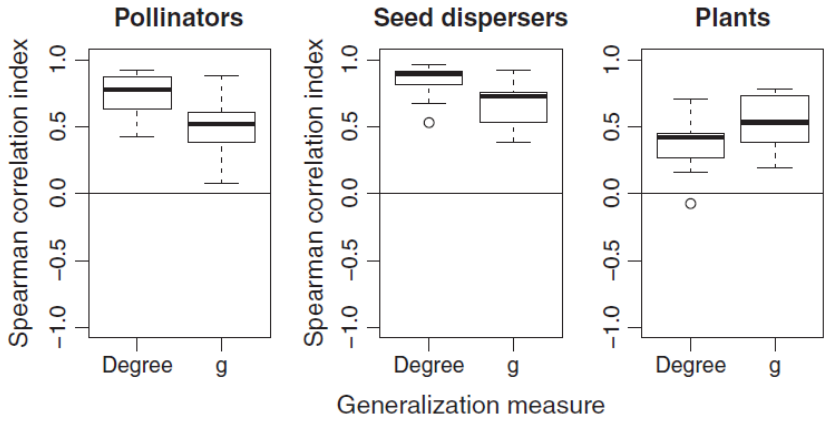
NICO BLÜTHGEN,[1,3] JOCHEN FRÜND,[1,4] DIEGO P. VÁZQUEZ,[2] AND FLORIAN MENZEL[1]

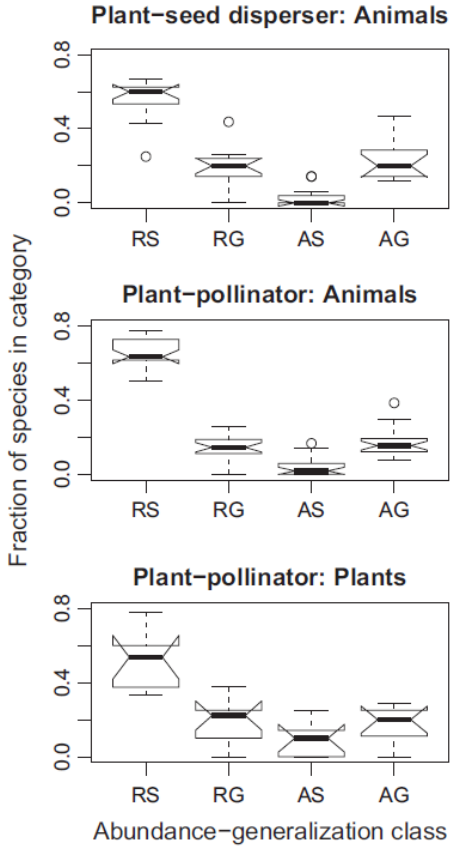
Ecology Letters, (2016) **19**: 4–11 doi: 10.1111/ele.12535

LETTER

Abundance and generalisation in mutualistic networks: solving the chicken-and-egg dilemma

Fort et al. 2016





Niche-based vs. impact-based network analysis?

ELSEVIER

GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 11 (2010) 185–195

Basic and Applied Ecology

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INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide

Nico Blüthgen*

Interpretations can be:

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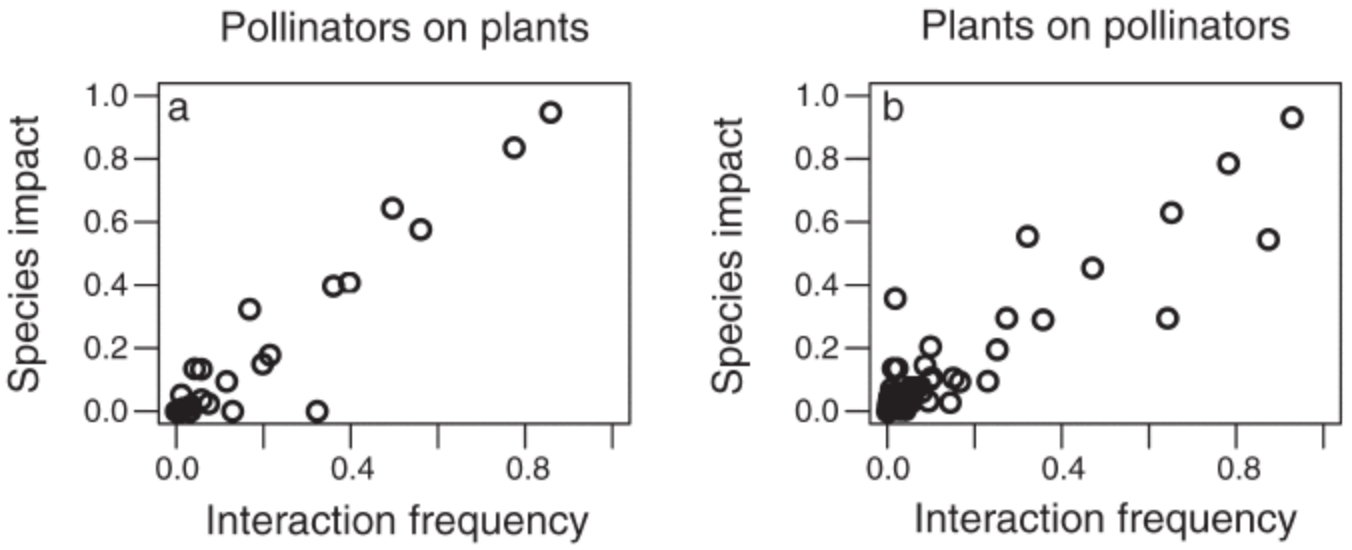

Vazquez et al. 2012

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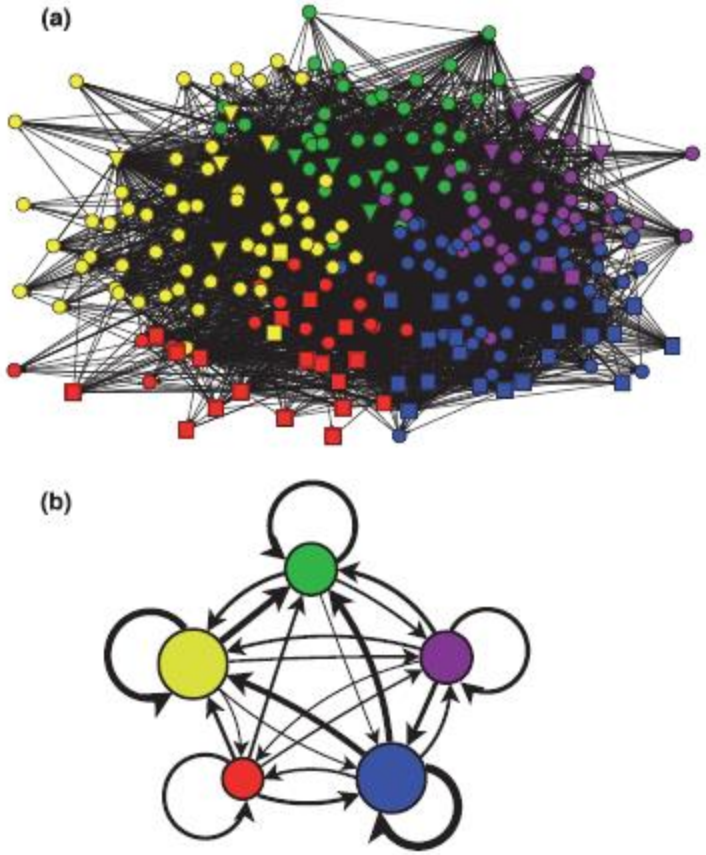
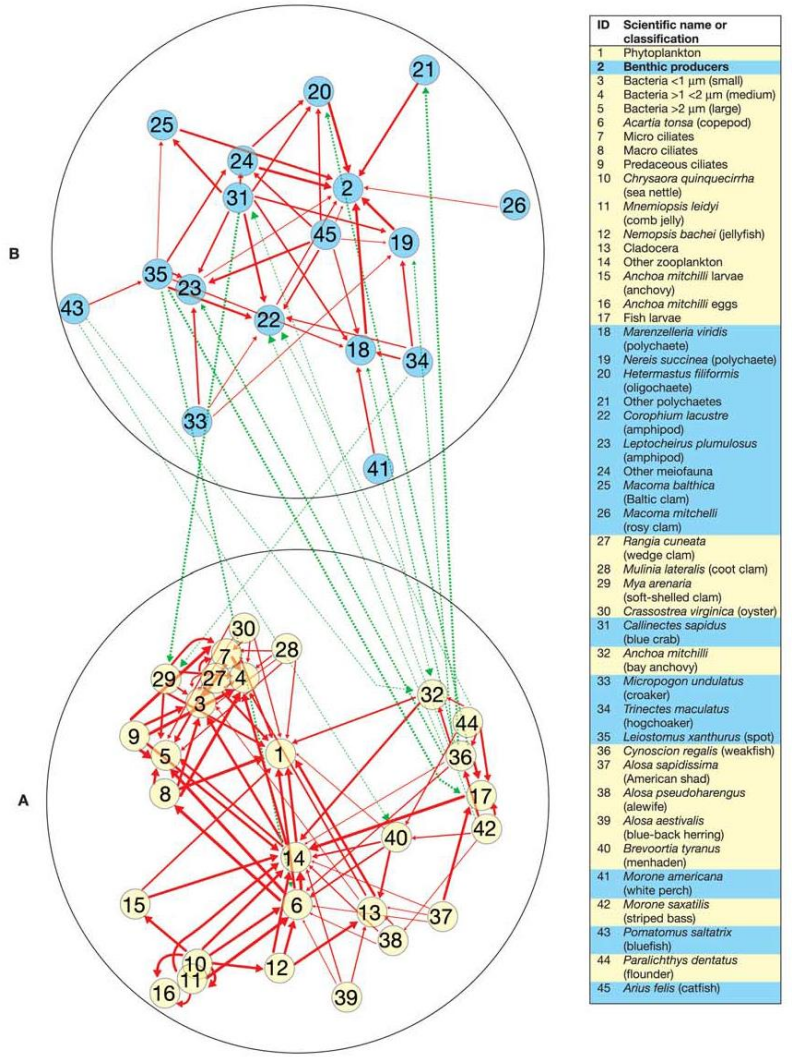
Modularity



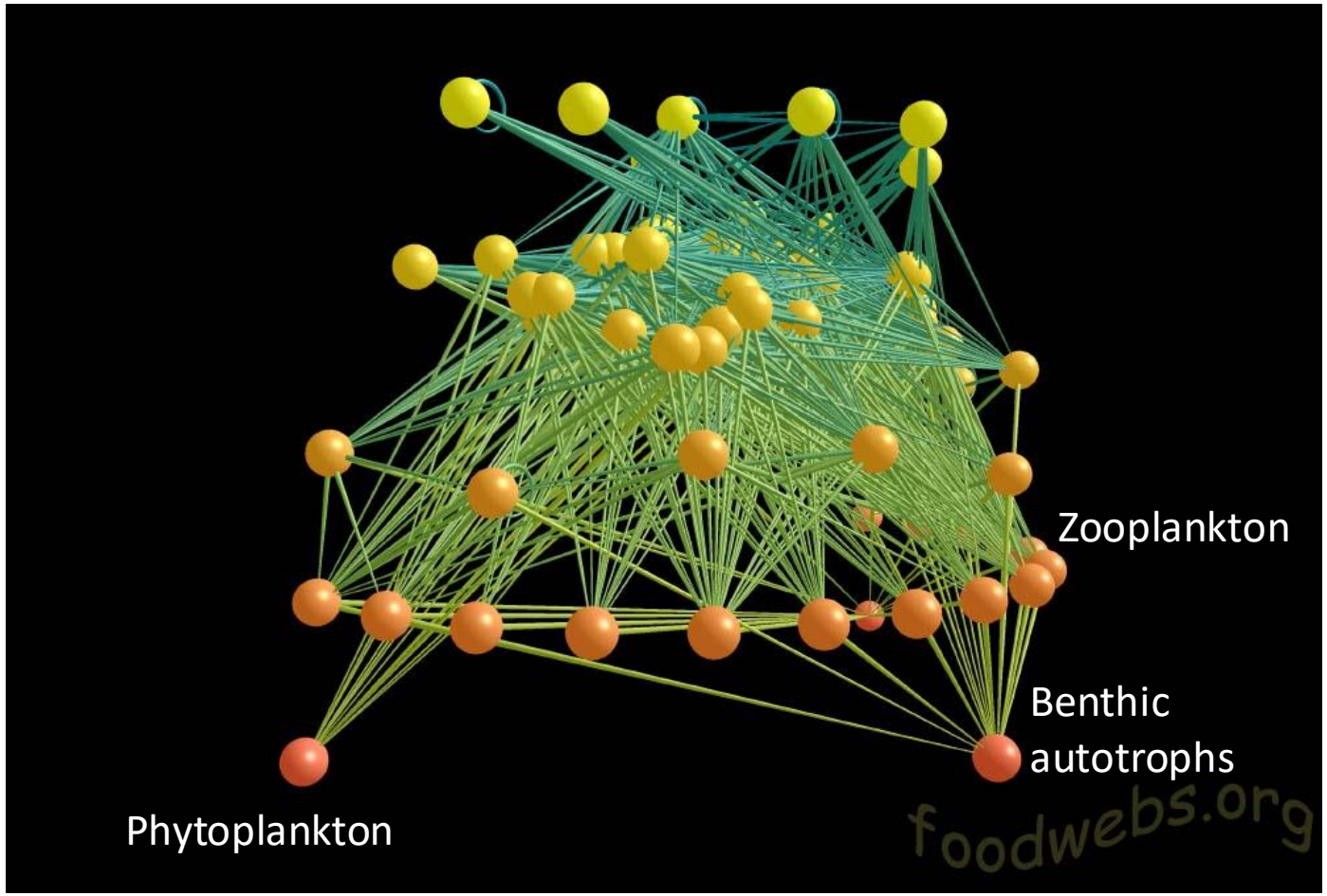
Caribbean food web
Rezende et al. (2009)



ID	Scientific name or classification
1	Phytoplankton
2	**Benthic producers**
3	Bacteria <1 µm (small)
4	Bacteria >1 <2 µm (medium)
5	Bacteria >2 µm (large)
6	*Acartia tonsa* (copepod)
7	Micro ciliates
8	Macro ciliates
9	Predaceous ciliates
10	*Chrysaora quinquecirrha* (sea nettle)
11	*Mnemiopsis leidyi* (comb jelly)
12	*Nemopsis bachei* (jellyfish)
13	Cladocera
14	Other zooplankton
15	*Anchoa mitchilli* larvae (anchovy)
16	*Anchoa mitchilli* eggs
17	Fish larvae
18	*Marenzelleria viridis* (polychaete)
19	*Nereis succinea* (polychaete)
20	*Hetermastus filiformis* (oligochaete)
21	Other polychaetes
22	*Corophium lacustre* (amphipod)
23	*Leptocheirus plumulosus* (amphipod)
24	Other meiofauna
25	*Macoma balthica* (Baltic clam)
26	*Macoma mitchelli* (rosy clam)
27	*Rangia cuneata* (wedge clam)
28	*Mulinia lateralis* (coot clam)
29	*Mya arenaria* (soft-shelled clam)
30	*Crassostrea virginica* (oyster)
31	*Callinectes sapidus* (blue crab)
32	*Anchoa mitchilli* (bay anchovy)
33	*Micropogon undulatus* (croaker)
34	*Trinectes maculatus* (hogchoaker)
35	*Leiostomus xanthurus* (spot)
36	*Cynoscion regalis* (weakfish)
37	*Alosa sapidissima* (American shad)
38	*Alosa pseudoharengus* (alewife)
39	*Alosa aestivalis* (blue-back herring)
40	*Brevoortia tyranus* (menhaden)
41	*Morone americana* (white perch)
42	*Morone saxatilis* (striped bass)
43	*Pomatomus saltatrix* (bluefish)
44	*Paralichthys dentatus* (flounder)
45	*Arius felis* (catfish)

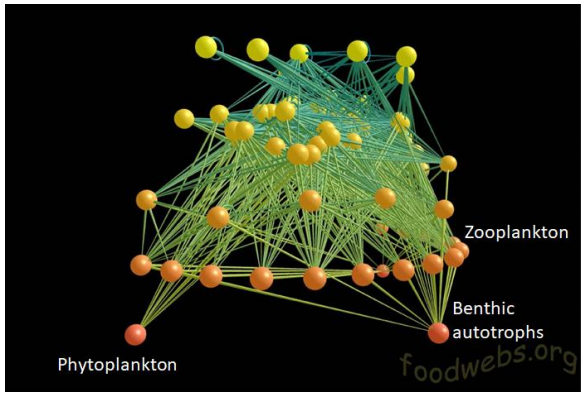
Chesapeake Bay food web
Krause et al. (2003)

The trophic group: a classical notion in food web ecology

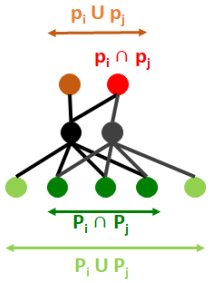


Which is the notion of group that best describes food web structure?

Trophic groups

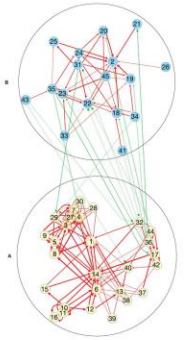


$$G(E) = \sum_{g=1}^{|E|} \frac{1}{|g|} \sum_{i,j \in G} (T(i,j) - E(T(i,j)))$$



$$T(i,j) = \frac{|P_i \cap P_j| + |p_i \cap p_j|}{|P_i \cup P_j| + |p_i \cup p_j|}$$

Modularity

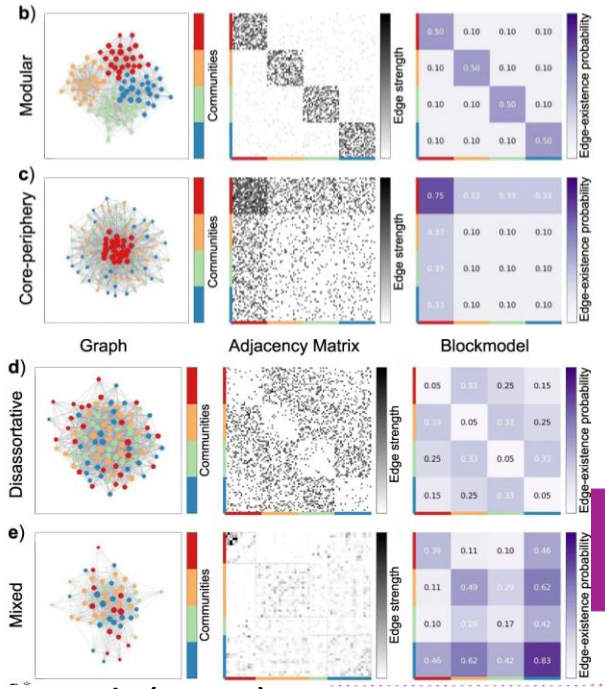


$$M(E) = \sum_{s=1}^{|E|} \left(\frac{l_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right)$$

	species (links)	TG	AP	M	TG-AP overlap	module-AP overlap
Benguala [35]	29 (203)					
Bridge Brooke Lake [36]	75 (553)					
Carribean Reef [37]	249 (3313)					
Chesapeake Bay [38]	33 (72)					
Créteil Lake SI3	67 (718)					
Tuesday Lake [45]	73 (410)					
Carpinteria [40]	128 (2290)					
DempsterSu [41]	107 (966)					
Ythan estuary [42]	92 (409)					

Gauzens et al. (2015)

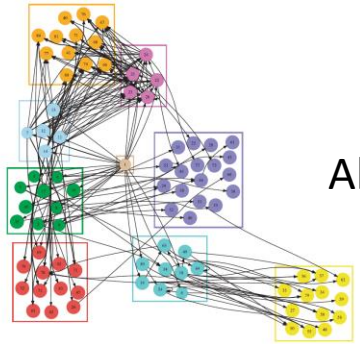
Which is the notion of group that best describes food web structure?



Faskowitz et al. (2018)

Stochastic block model

$$P(a_{ij} > 0|\mathbf{O}) = \omega_{G_i G_j}$$



Allesina & Pascual (2009)

species (links)	TG	AP	M	TG-AP overlap	module-AP overlap

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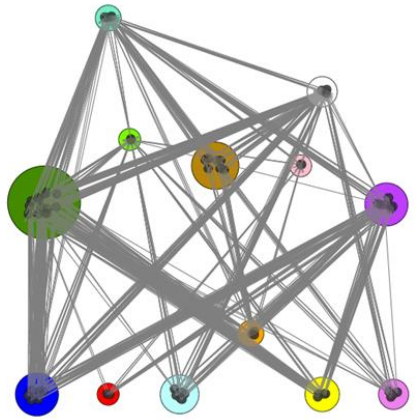
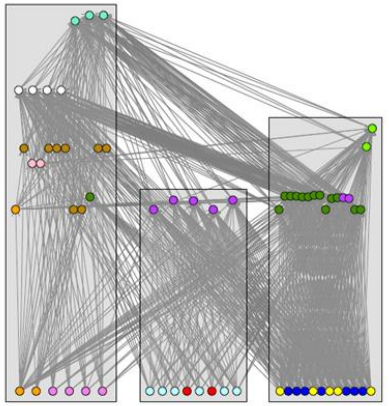


Trophic groups

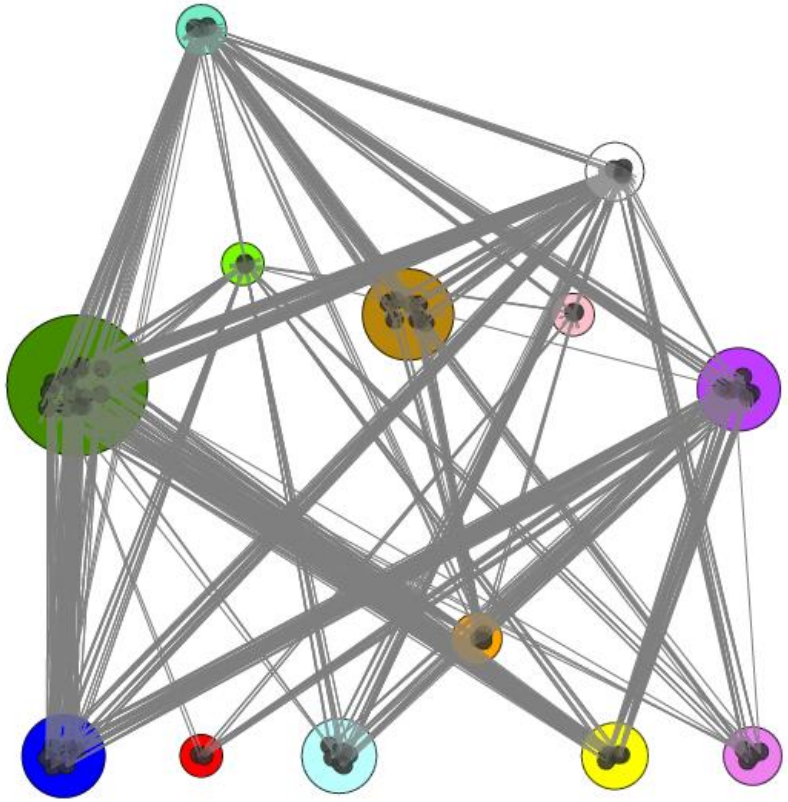


Modules

	species (links)	TG	AP	M	TG-AP overlap	module-AP overlap
Benguala [35]	29 (203)	7	7	3	0.841	0.397
Bridge Brooke Lake [36]	75 (553)	12	9	3	0.92	0.631
Carribean Reef [37]	249 (3313)	46	28	3	0.775	0.365
Chesapeake Bay [38]	33 (72)	13	7	3	0.745	0.428
Créteil Lake SI3	67 (718)	13	12	3	0.922	0.4738
Tuesday Lake [45]	73 (410)	17	11	2	0.834	0.449
Carpinteria [40]	128 (2290)	37	28	3	0.872	0.379
DempsterSu [41]	107 (966)	25	12	3	0.7129	0.410
Ythan estuary [42]	92 (409)	26	13	3	0.755	0.317

Gauzens et al. (2015)

Groupes trophiques vs. modules?



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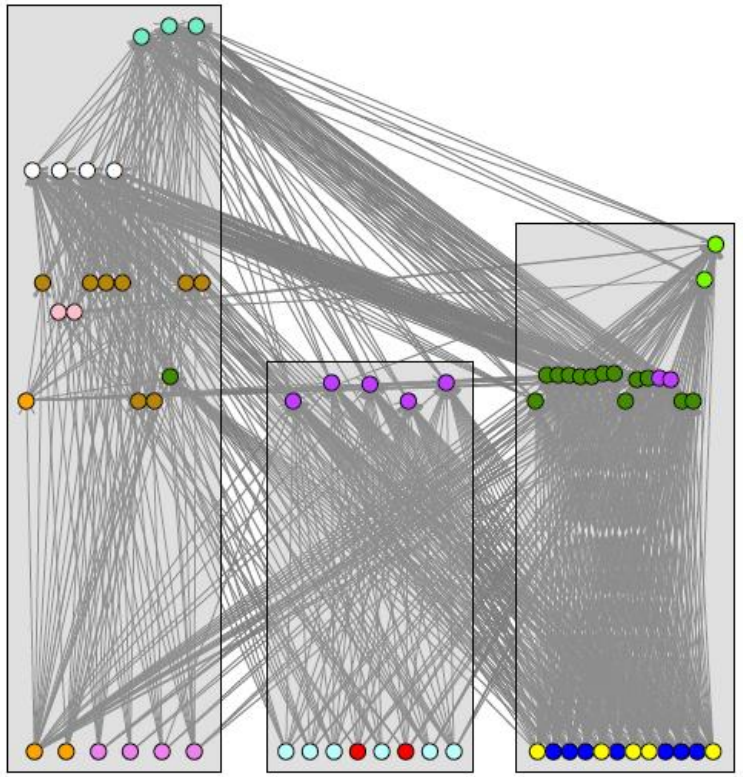

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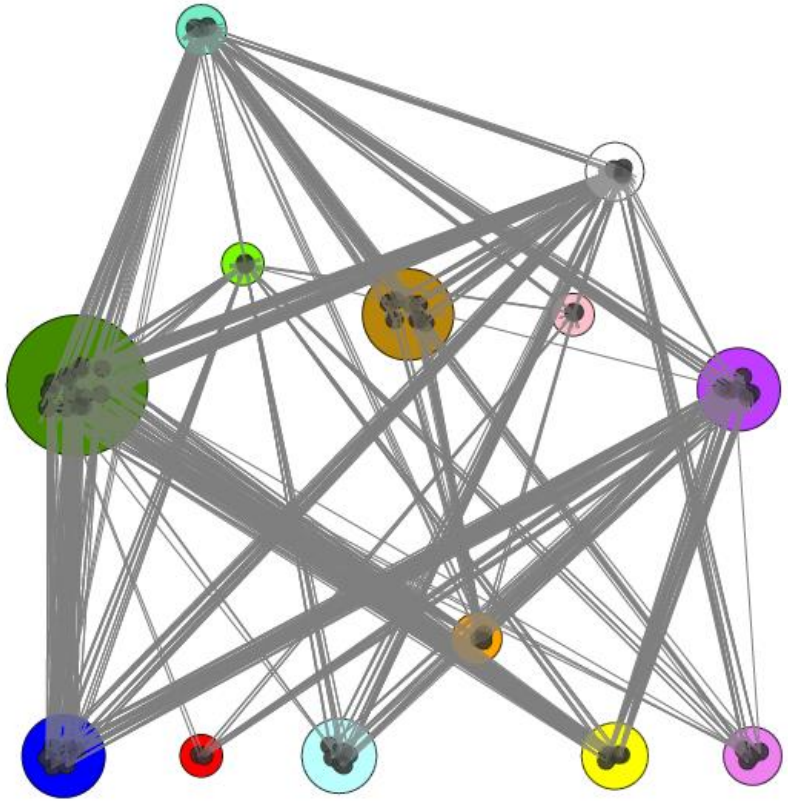

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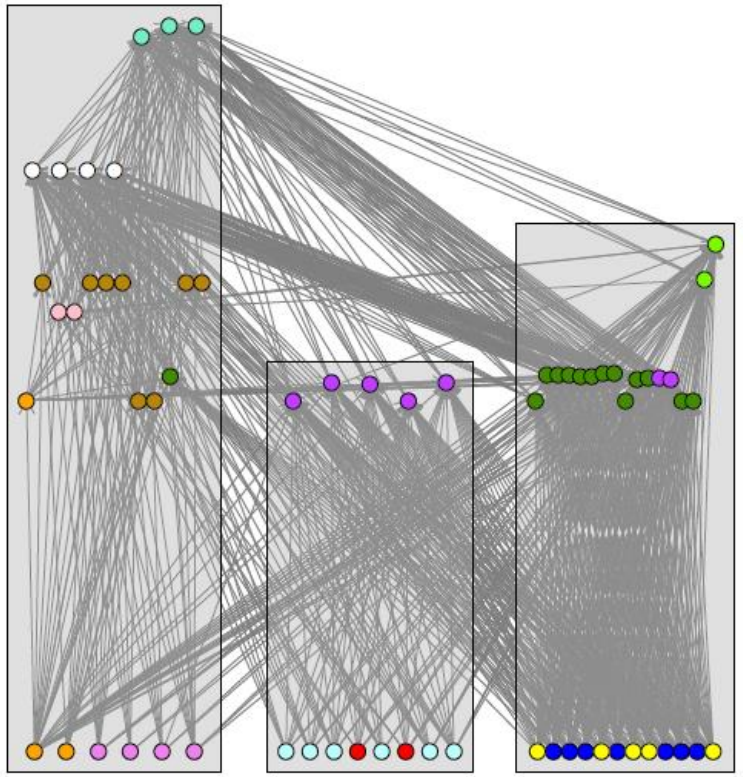
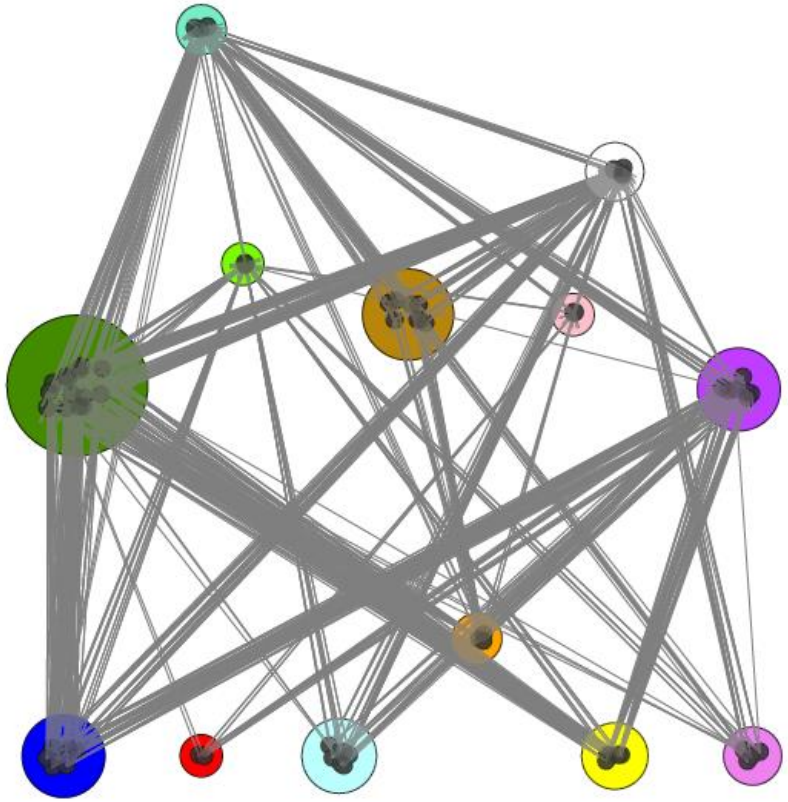


Modules

Diversity of module affiliation in trophic groups is significantly lower than random expectations ($p<0.0001$ for all 9 food webs)

Each trophic group belongs generally to a single module.

Groupes trophiques vs. modules?



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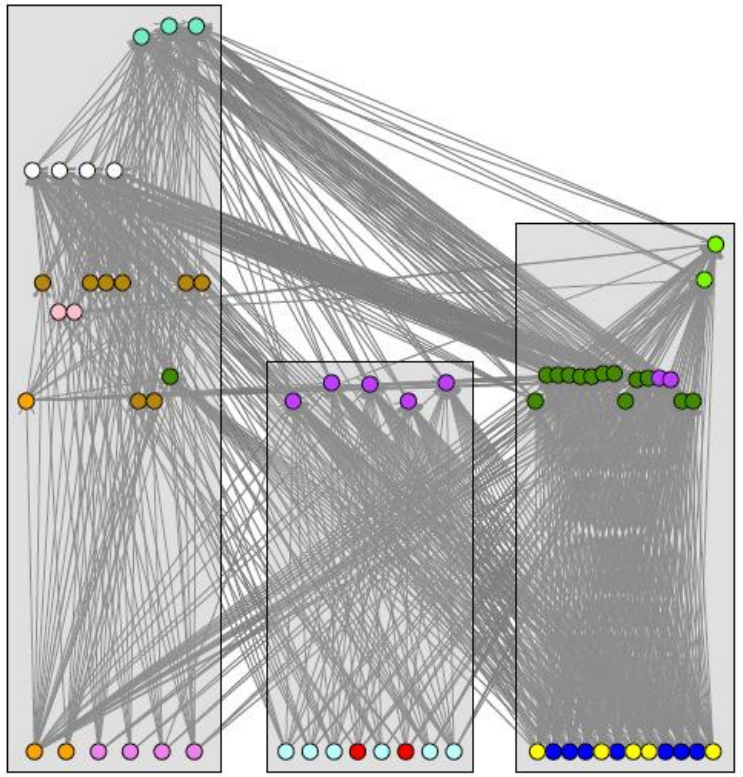


Modules

Variance of species trophic levels within trophic groups is always lower than random expectations ($p<0.0001$ for all 9 food webs)

Variance of species trophic levels within modules is always higher than random expectations ($p<0.0001$ for all 9 food webs)

Looking for groups, a classical question with interesting insights on the structure of ecological networks

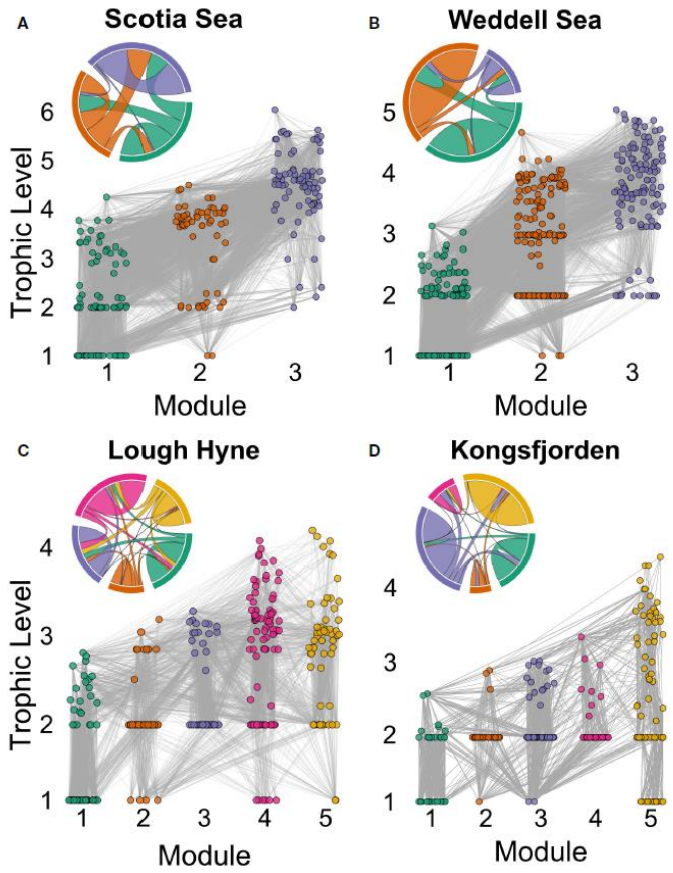
Food webs have a 2-level hierarchical structure:

(1) modules partition food webs into large bottom-top trophic pathways

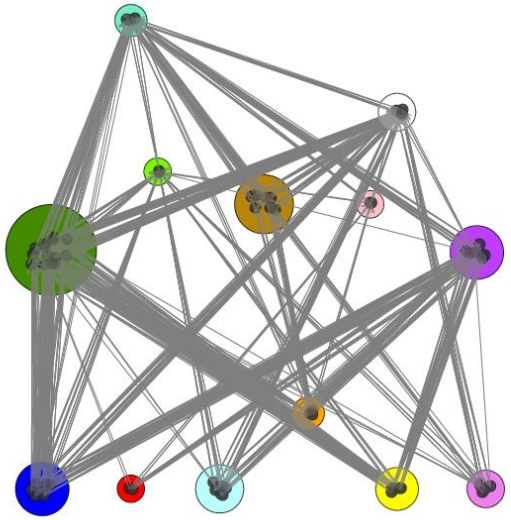
(2) trophic groups further partition these pathways into sets groups of species with similar trophic connections.

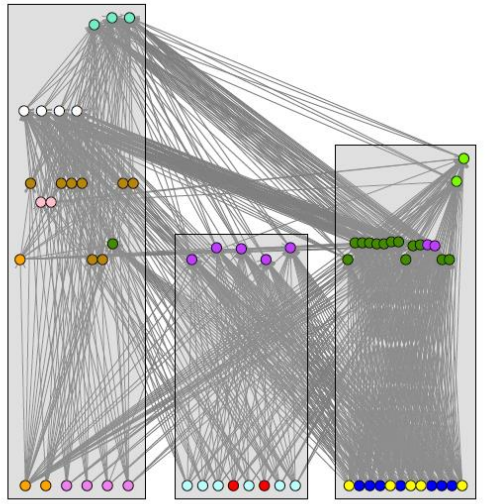
Modules and trophic groups thus provide complementary pictures of food-web structure

Consequences for ecosystem functioning and stability?



Eskuche-Keith et al. 2023





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Network beta-diversity in time

Ecology Letters, (2017) **20**: 385–394 doi: 10.1111/ele.12740

LETTER

Interaction rewiring and the rapid turnover of plant–pollinator networks

CaraDonna et al. 2017

"few species and interactions were consistently present in all four annual plant–pollinator networks (53% of the plant species, 21% of the pollinator species and 4.9% of the interactions). The high turnover in species-to-species interactions was mainly the effect of species turnover (c. 70% in pairwise comparisons among years), and less the effect of species flexibility to interact with new partners (c. 30%)."

Petanidou et al. 2008

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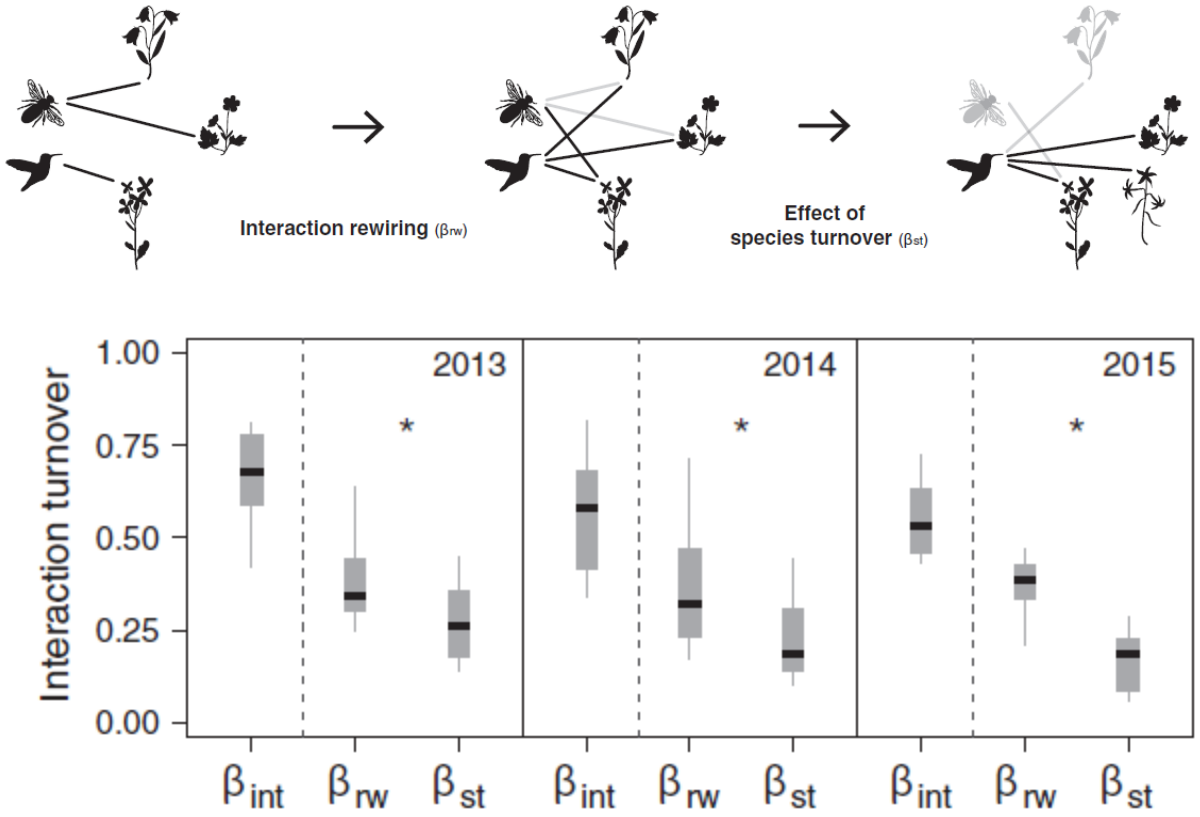
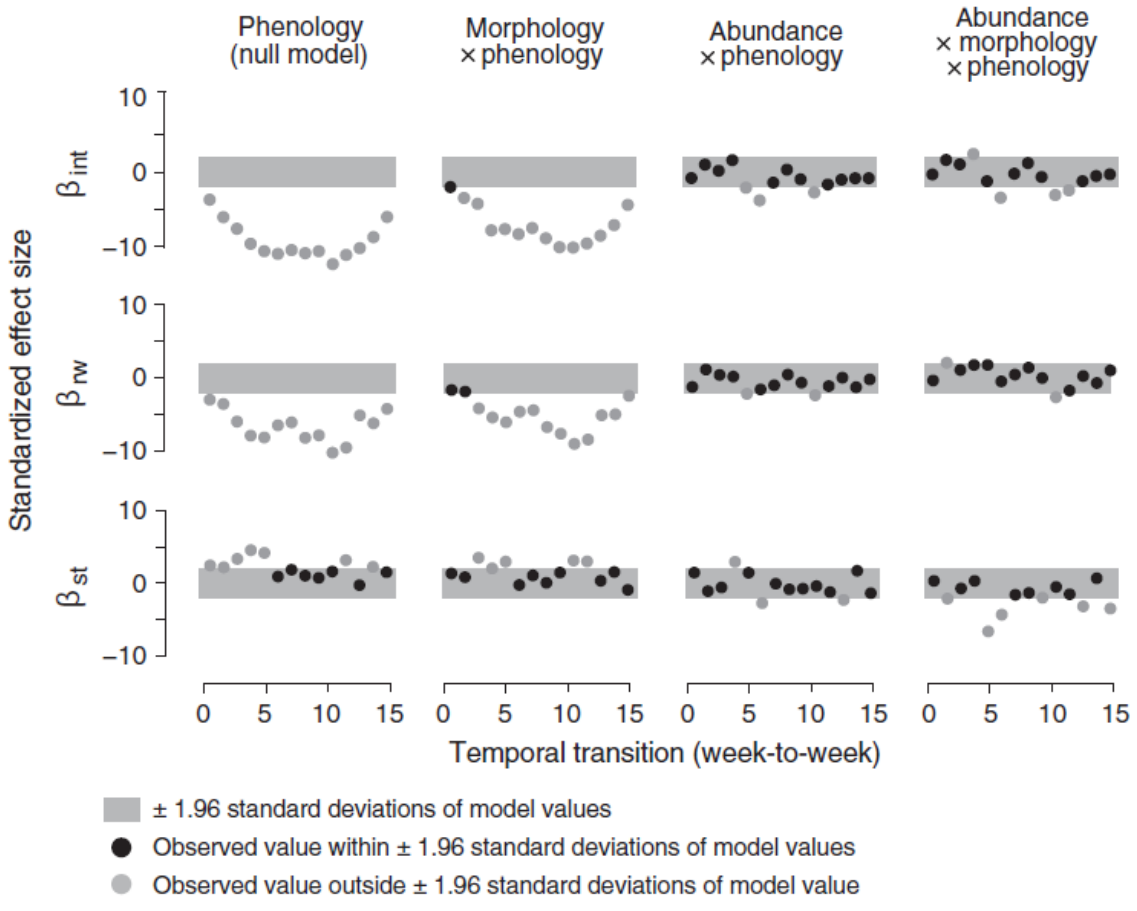
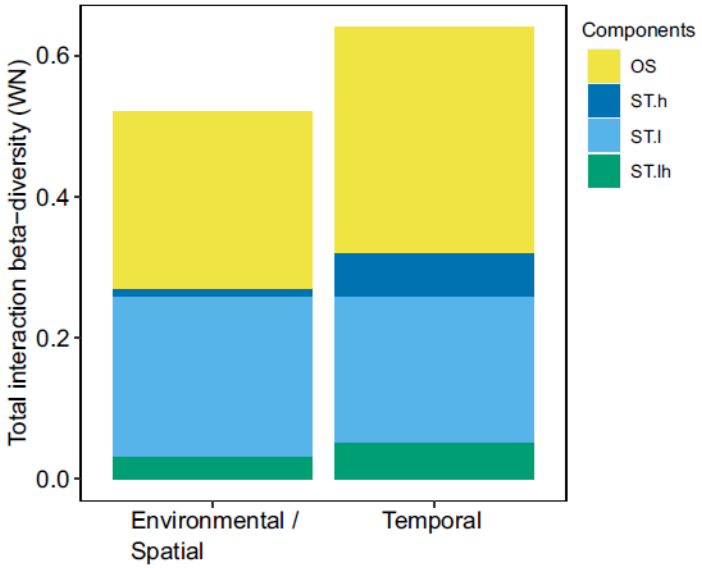
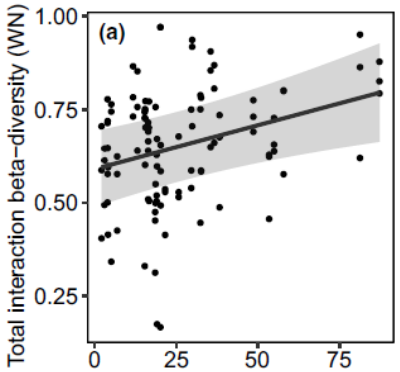


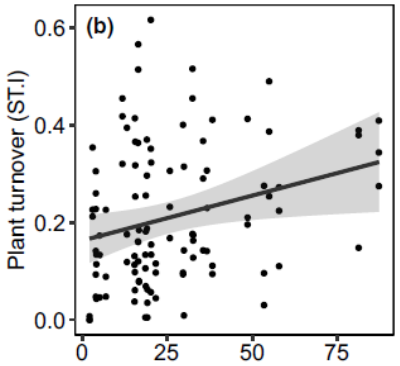


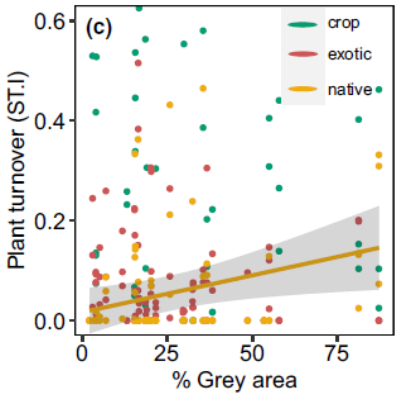
Beta-diversity of networks in space and time



Marcacci et al. 2023







Beta-diversity of networks in space and time

- Ecological interactions among species vary a lot in space and time, even at small spatial and temporal scales

- Structure of networks might vary less over space and time, how species change their network role in space and time?

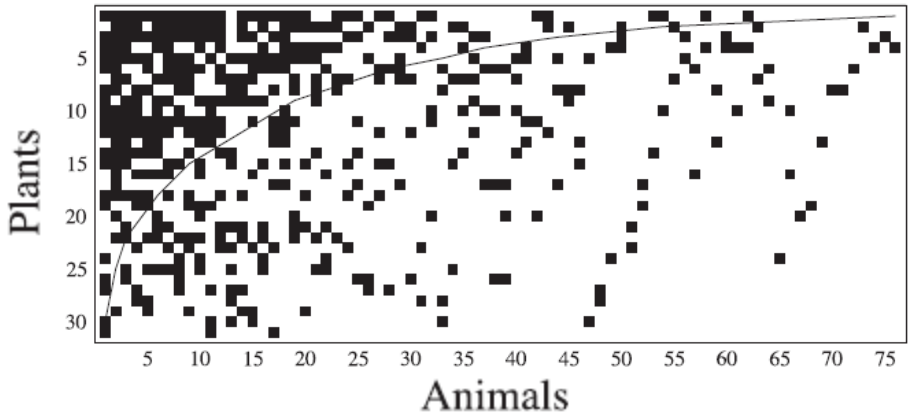
- Need to understand how species traits, abundances, environmental conditions affect such variations in space and time

Analysing the structure of ecological networks: looking for general patterns?

Part 2: examples of more recent patterns studied in ecological networks:

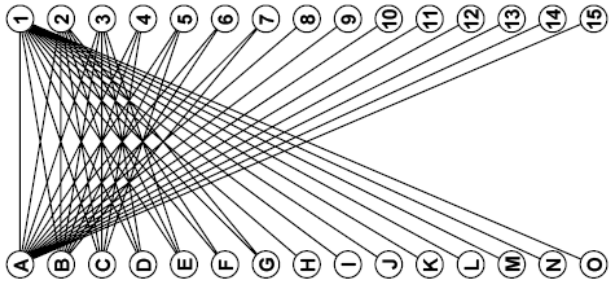
- How species traits shape interactions in network
- Distribution of degrees and interaction strengths
- Looking for groups
- How networks vary in space and time
- **Comparing networks of different interaction types**

Mutualistic webs : a focus on nestedness



Seed dispersal

pollination



Nested structure

- Continuum between specialist and generalist species
- Presence of a core of highly connected species
- Asymmetrical specialization

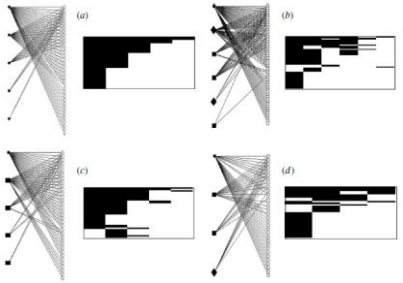
Bascompte et al. (2003)

Mutualistic webs : a focus on nestedness

biology letters
Biol. Lett.
doi:10.1098/rsbl.2006.0562
Published online

The nested structure of marine cleaning symbiosis: is it like flowers and bees?

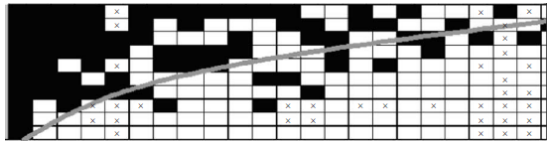
Paulo R. Guimarães Jr[1,2], Cristina Sazima[1], Sérgio Furtado dos Reis[1,*] and Ivan Sazima[1]



PROCEEDINGS OF THE ROYAL SOCIETY B
Proc. R. Soc. B (2007) 274, 591–598
doi:10.1098/rspb.2006.3758
Published online 29 November 2006

Finding NEMO: nestedness engendered by mutualistic organization in anemonefish and their hosts

Jeff Ollerton[1,*], Duncan McCollin[1], Daphne G. Fautin[2] and Gerald R. Allen[3]



VOL. 172, NO. 6 THE AMERICAN NATURALIST DECEMBER 2008

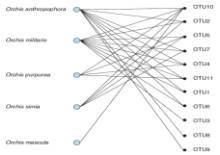
The Nested Assembly of Plant Facilitation Networks Prevents Species Extinctions

Miguel Verdú[1,*] and Alfonso Valiente-Banuet[2,†]

MOLECULAR ECOLOGY
Molecular Ecology (2010) 19, 4086–4095
doi: 10.1111/j.1365-294X.2010.04785.x

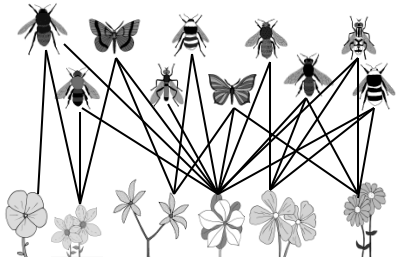
Low specificity and nested subset structure characterize mycorrhizal associations in five closely related species of the genus *Orchis*

HANS JACQUEMYN,* OLIVIER HONNAY,* BRUNO P. A. CAMMUE,† REIN BRYS‡ and BART



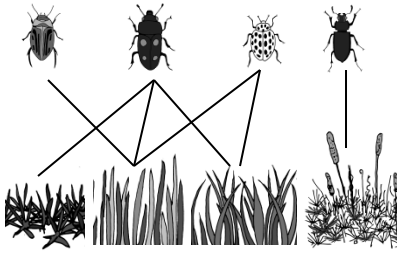
Comparing mutualistic and antagonistic webs: the example of plant-pollinator and plant-herbivore webs

Mutualistic



42 plant-pollinator webs

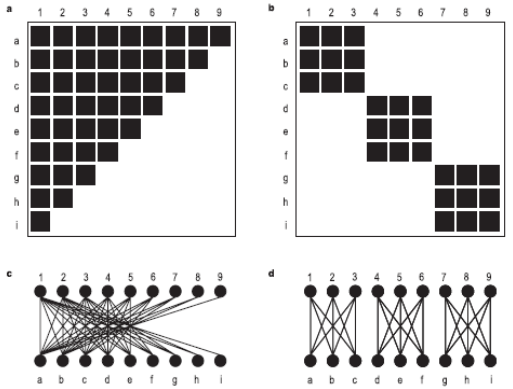
Antagonistic



27 plant-herbivore webs

Higher connectance
Nested

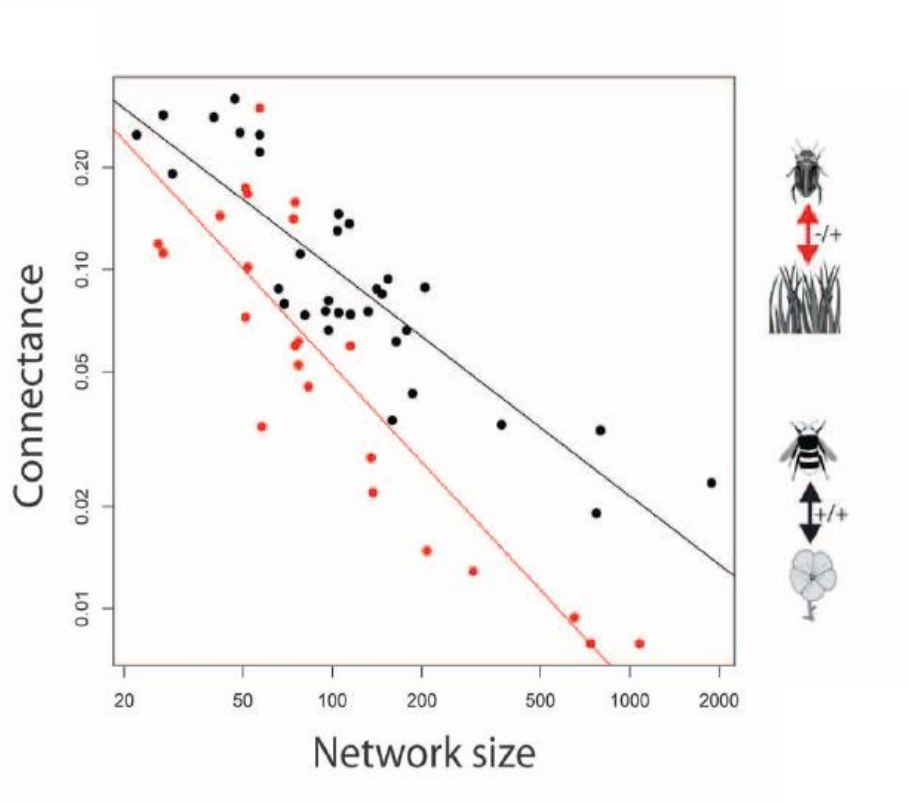
Bascompte et al. 2003



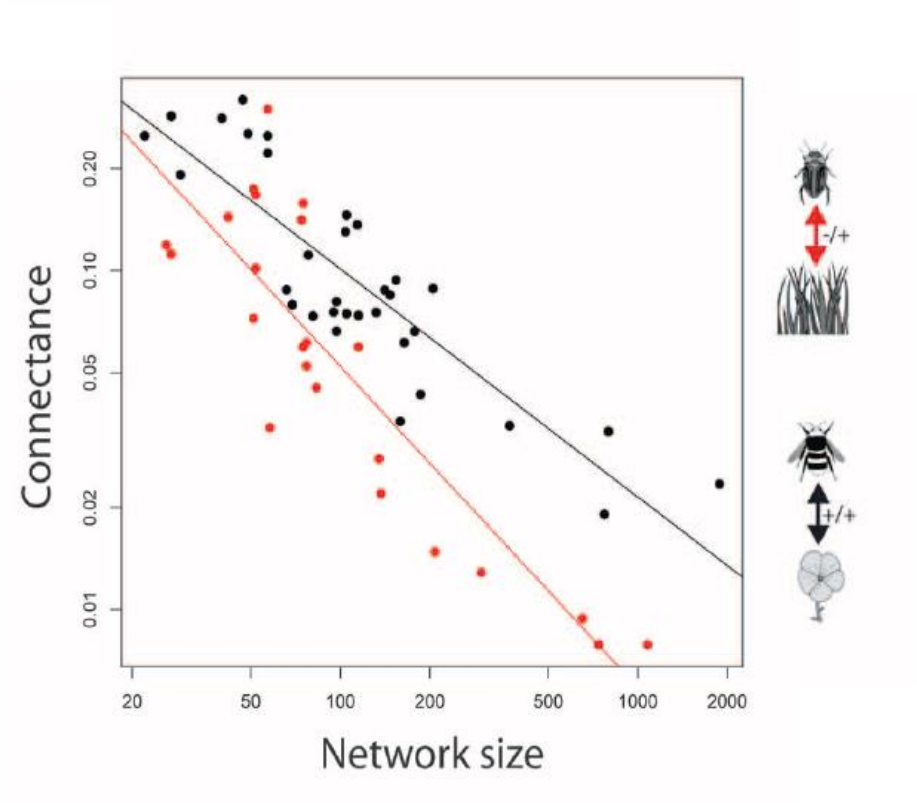
Lower connectance
Compartmented

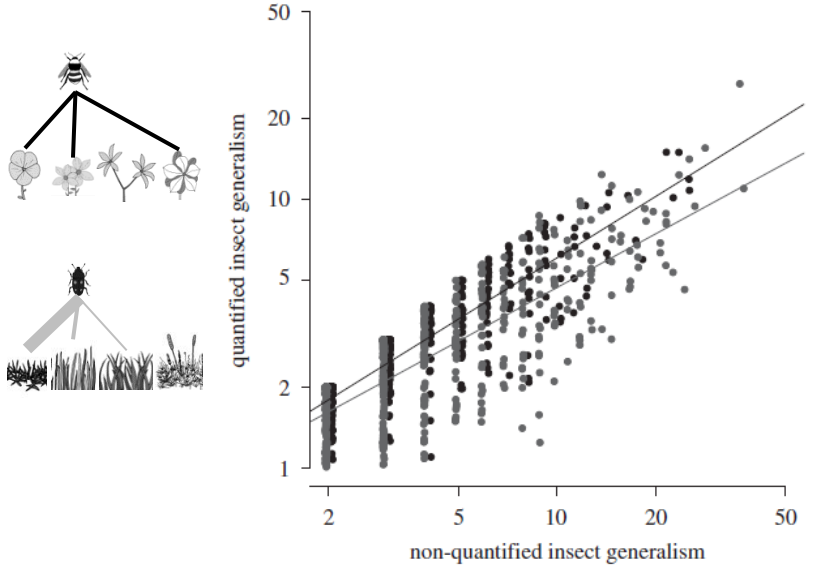
Lewinsohn et al. 2006

Connectance and interaction type



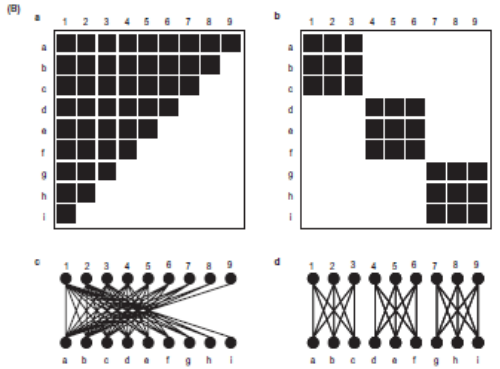
Connectance and interaction type

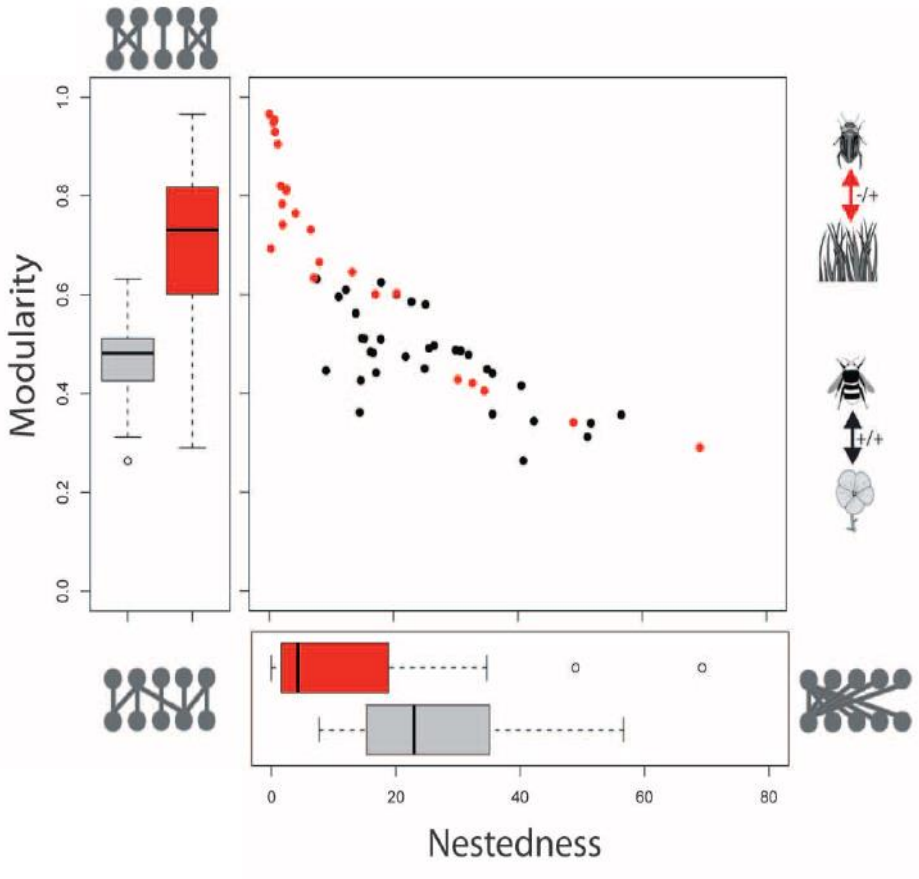




Fontaine et al. (2009) *Proc. R. Soc. B*

Nestedness and modularity



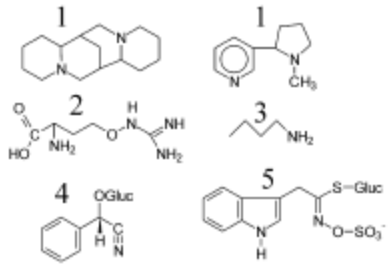


Thébault & Fontaine (2010) *Science*

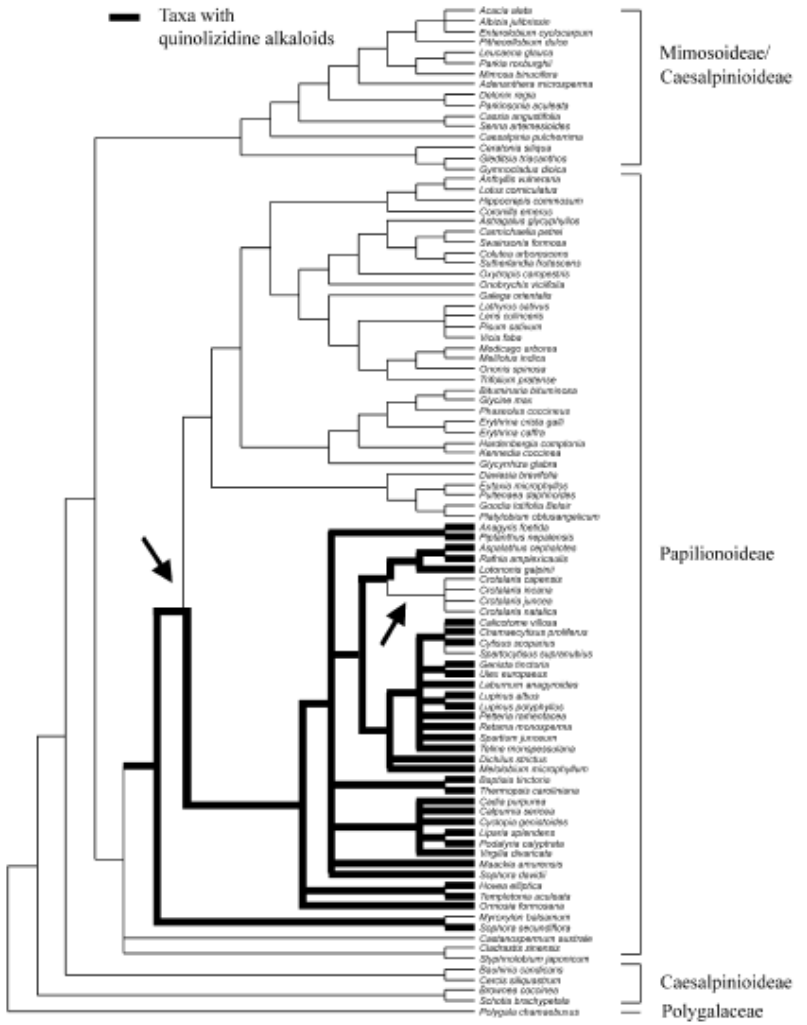
The structure of plant-insect networks partly depends on the type of interaction considered (mutualism or antagonism)

What could explain these different structures?

- Different plant traits involved in these interactions



Wink (2003)



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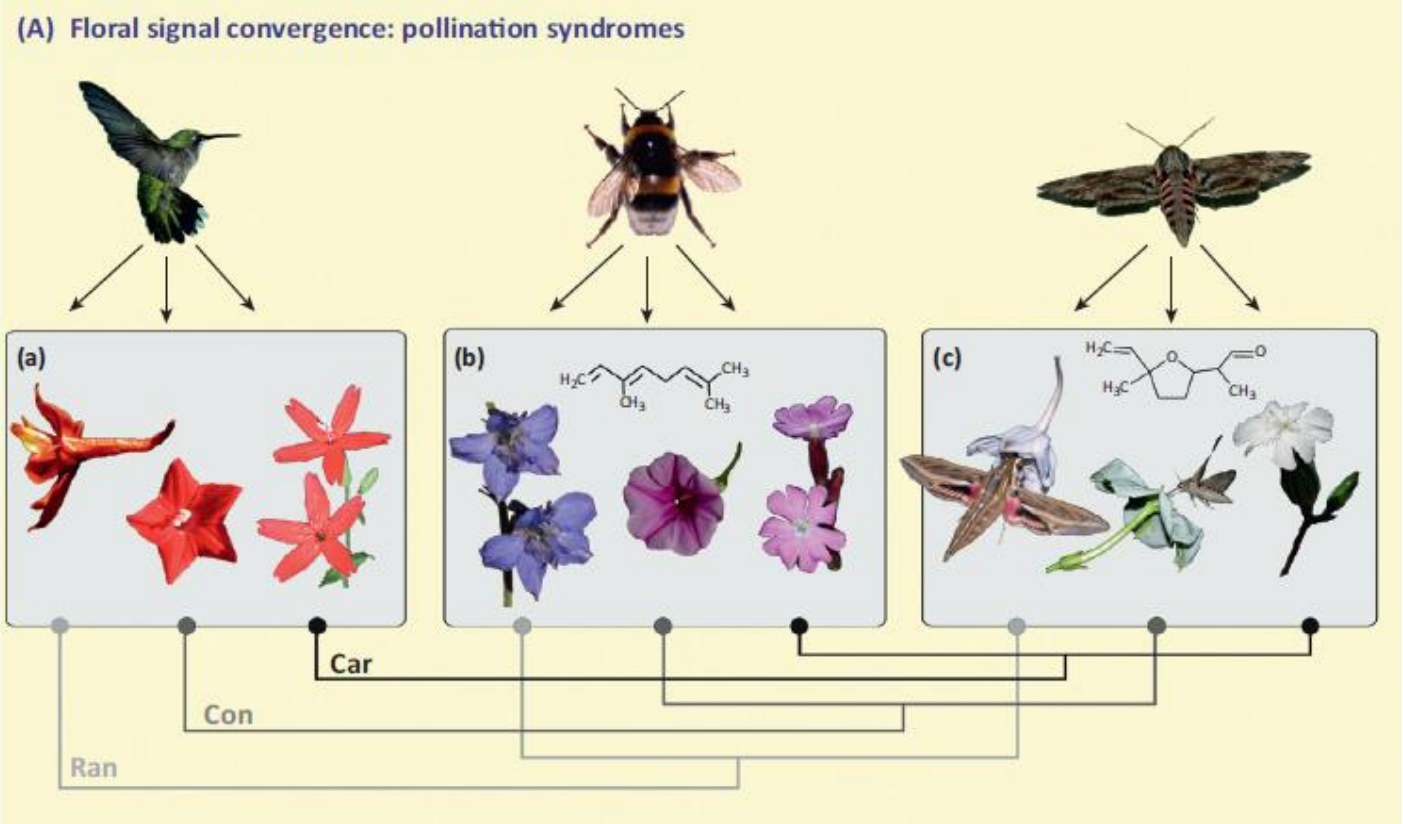
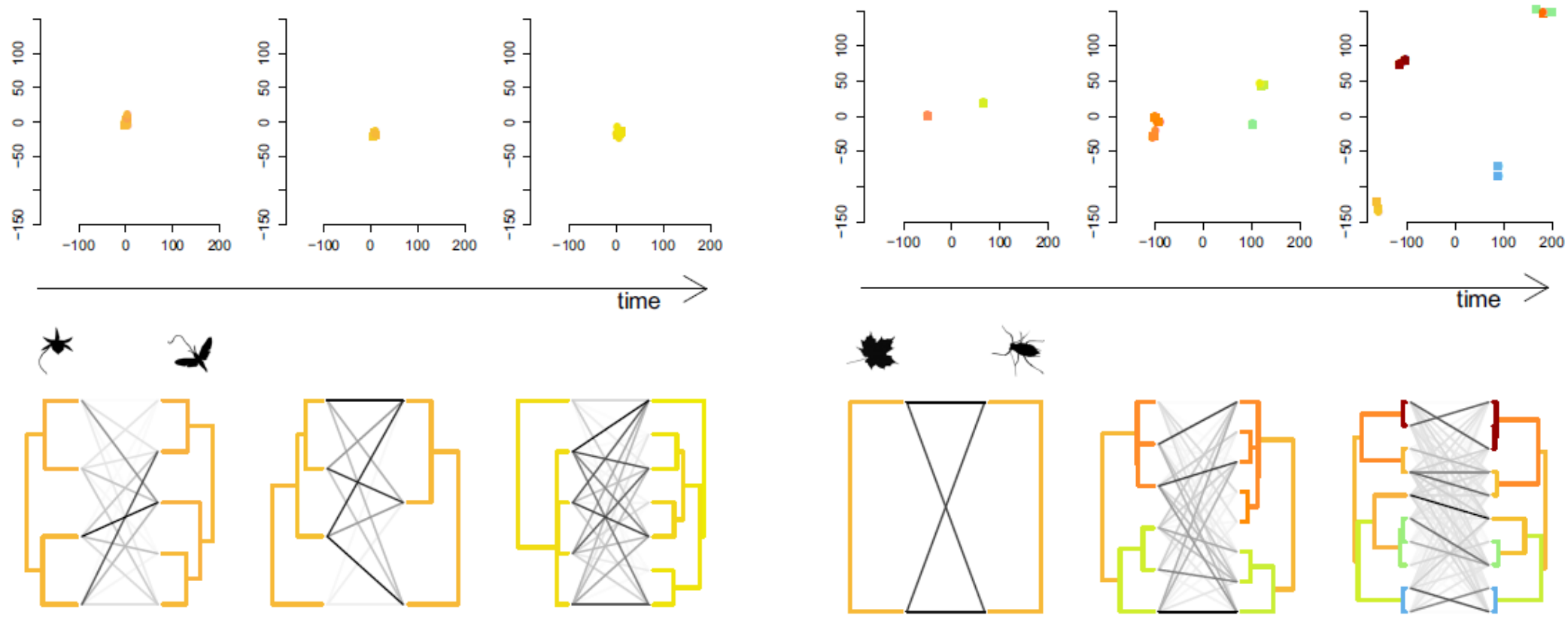


Schiestl and Johnson (2013)

What could explain these different structures?

- Evolutionary and neutral processes



Maliet et al. (2020)

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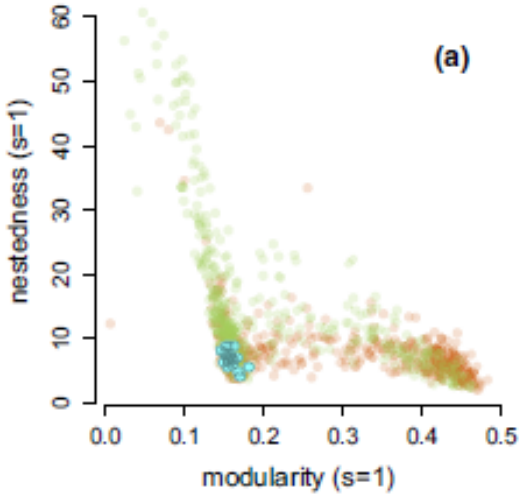
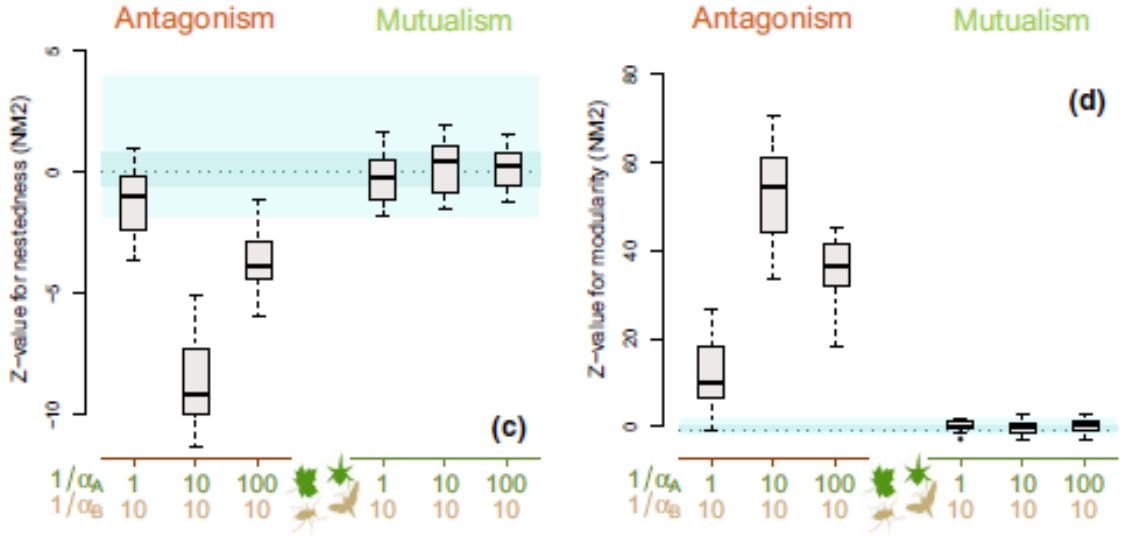
- Evolutionary and neutral processes





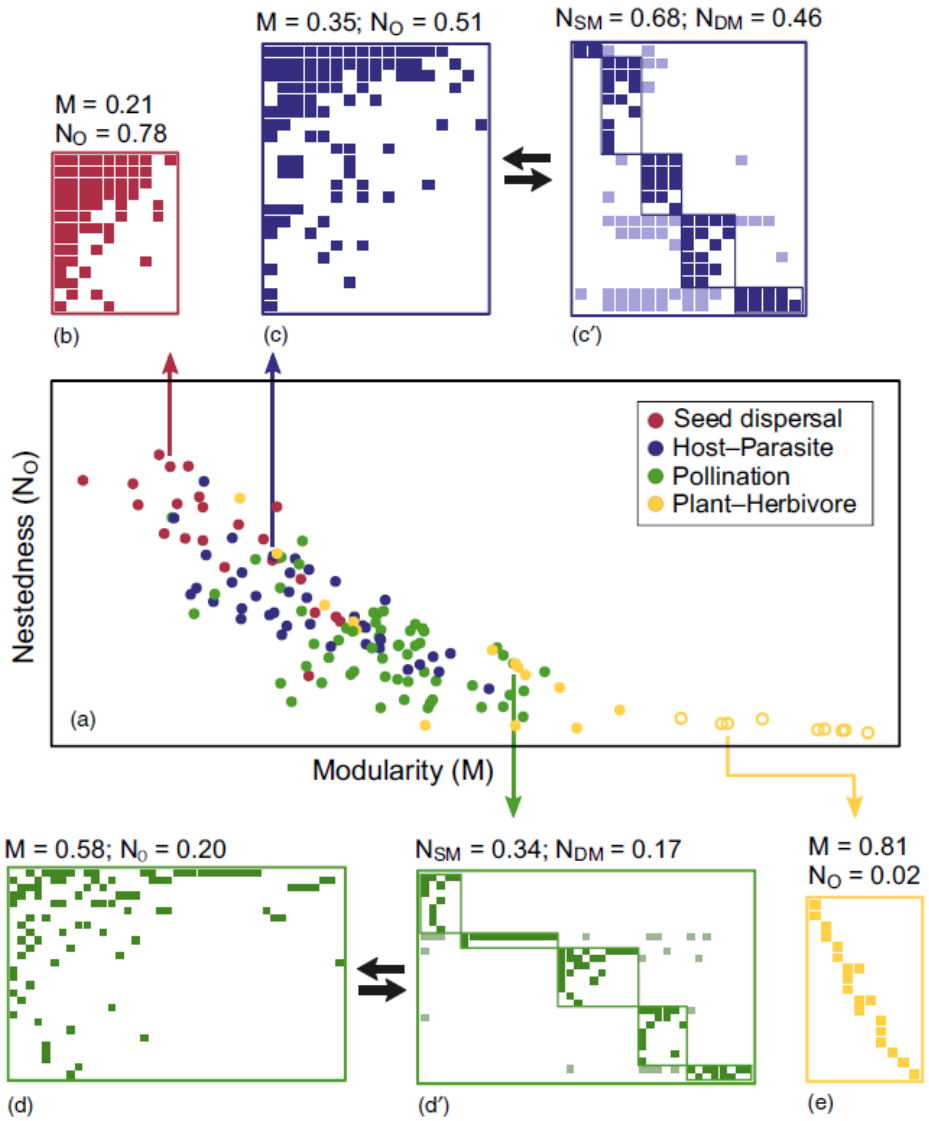
Maliet et al. (2020)

Does the structure of ecological networks differ between different types of interactions?
Conclusion and perspectives

- Structures of plant-herbivore and plant-pollinator networks seem to differ

- Need to compare other interaction webs: how general are the observed patterns? Does it relate to particular traits involved in different interactions?

Does the structure of ecological networks differ between different types of interactions?
Conclusion and perspectives

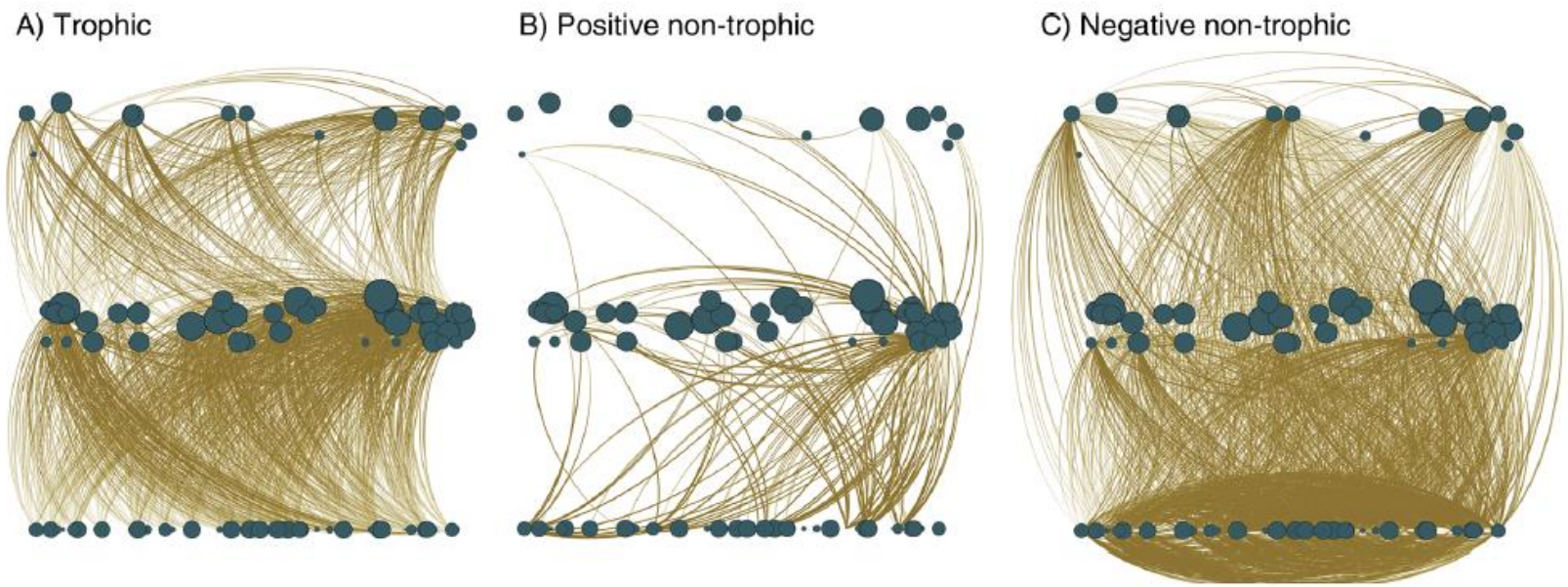


Pinheiro et al. (2022)

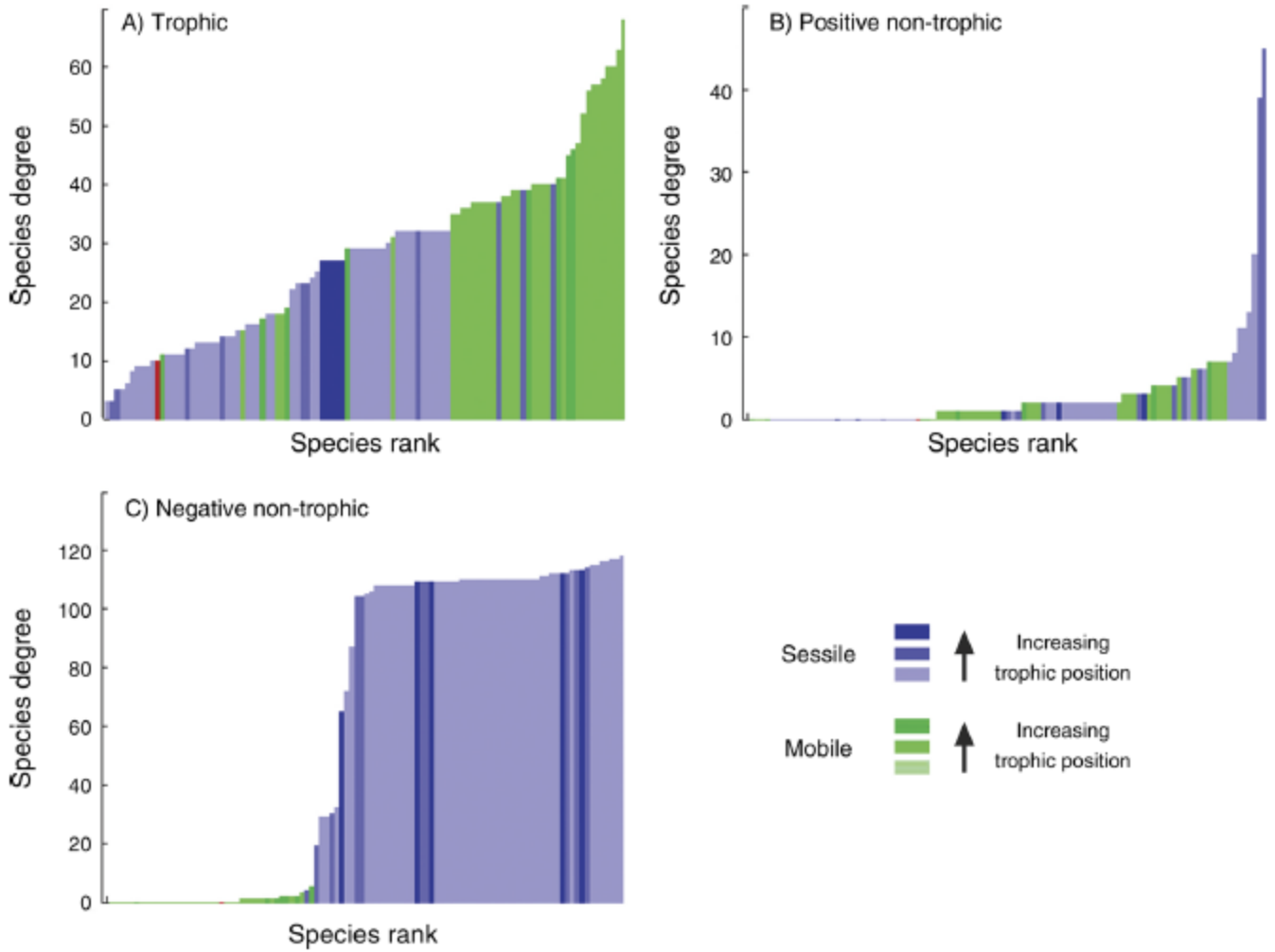
Does the structure of ecological networks differ between different types of interactions? Conclusion and perspectives

- Trophic and non-trophic interactions: the example of the network of a coastal ecosystem in Chile

Kéfi et al. (2015)



Does the structure of ecological networks differ between different types of interactions?
Conclusion and perspectives



Kéfi et al. (2015)

Does the structure of ecological networks differ between different types of interactions?
Conclusion and perspectives

- Structures of plant-herbivore and plant-pollinator networks seem to differ
- Need to compare other interaction webs: how general are the observed patterns? Does it relate to particular traits involved in different interactions?
- Need new theory to understand how ecological and evolutionary processes determine these different structures
- Move beyond studying networks of different interactions in isolation?

« Structure of ecological networks: what do we know? »
Some concluding thoughts

- Many metrics and ways to study ecological networks: easy to be lost
  - ➡ Keep in mind your questions of interest

- Some properties that seem consistent over different ecological networks

- Towards network analyses that integrate different interaction types and spatial and temporal dimensions

- Importance of traits and species phylogeny for understanding the structure of interaction networks: can we infer interaction between species?

- Still some limits to describe interactions between species in ecology: how to better integrate biases due to sampling in the study of network structure?