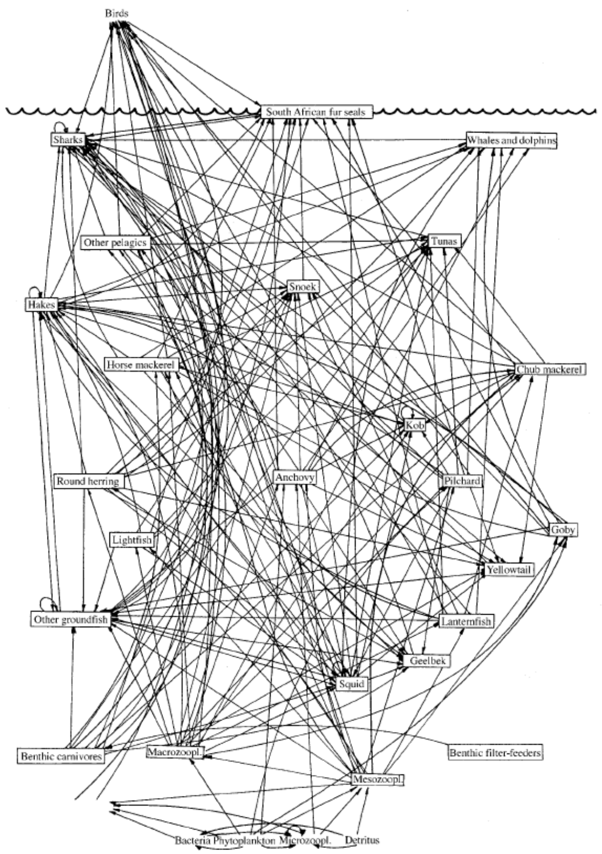
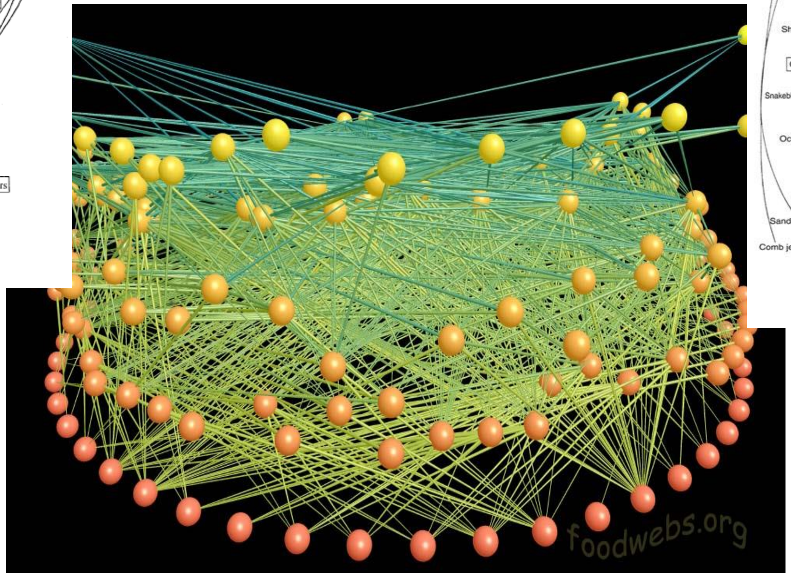
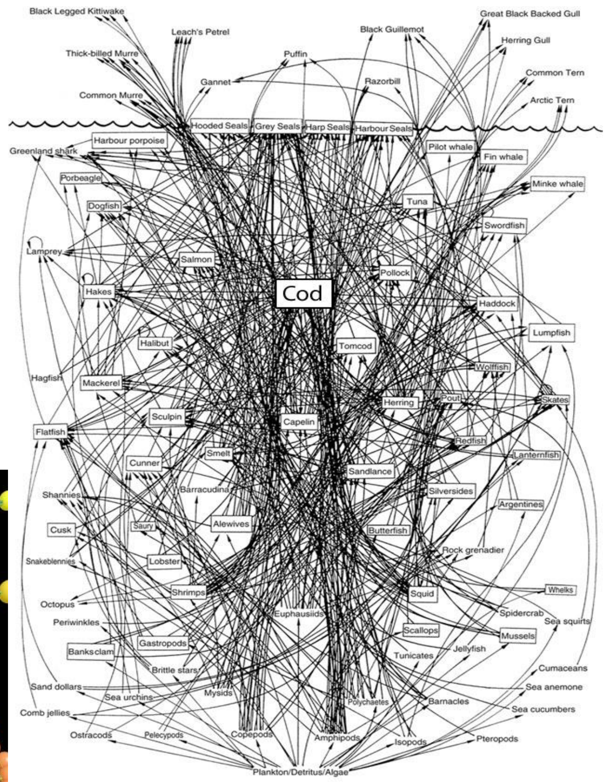
Structure of ecological networks: what do we know?

Elisa Thébault

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

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- **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

?

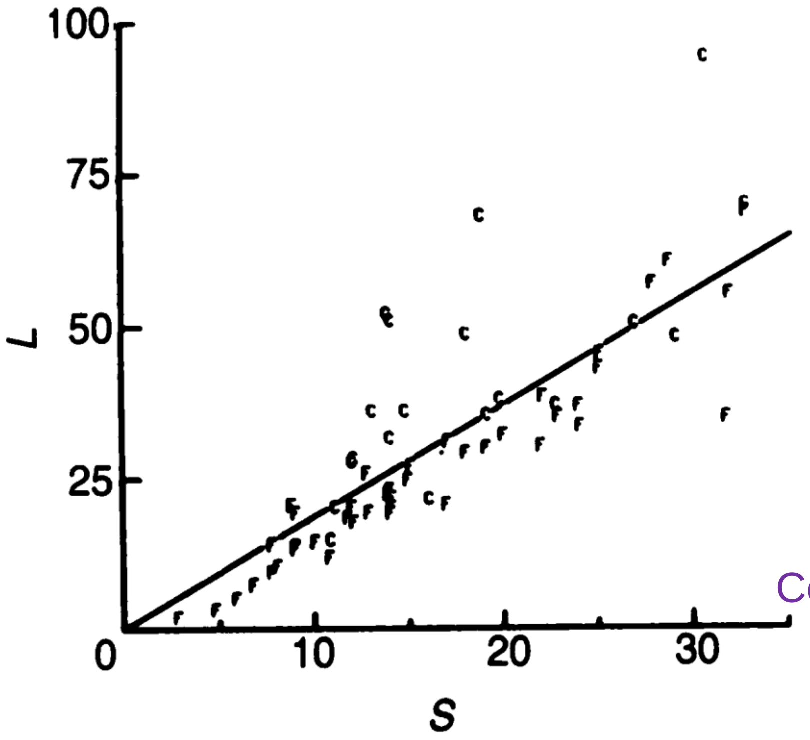
Cohen and Briand 1984

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)

Cohen and Briand 1984

vs.

Constant connectance hypothesis

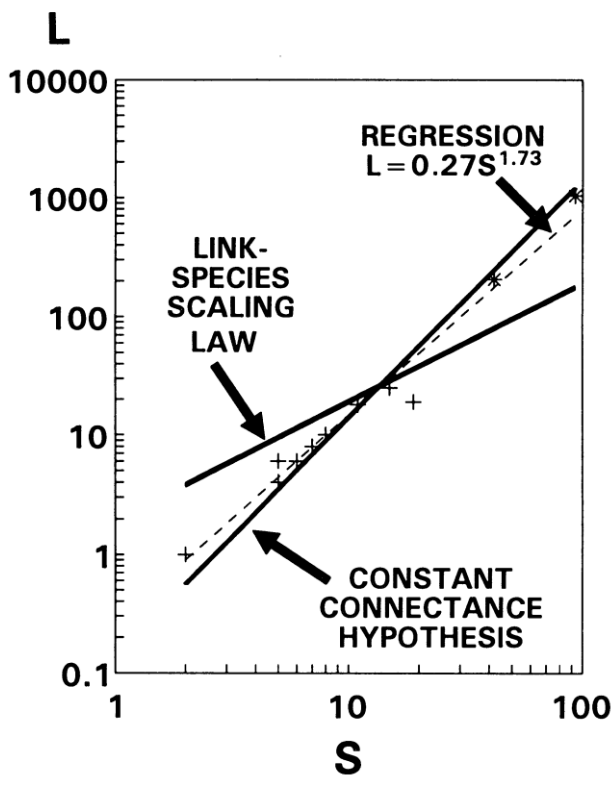
Martinez 1992

?

$$L = aS^b$$

C = *constant*

b = 2



Martinez 1992

The diversity – connectance relationship

A matter of data resolution?

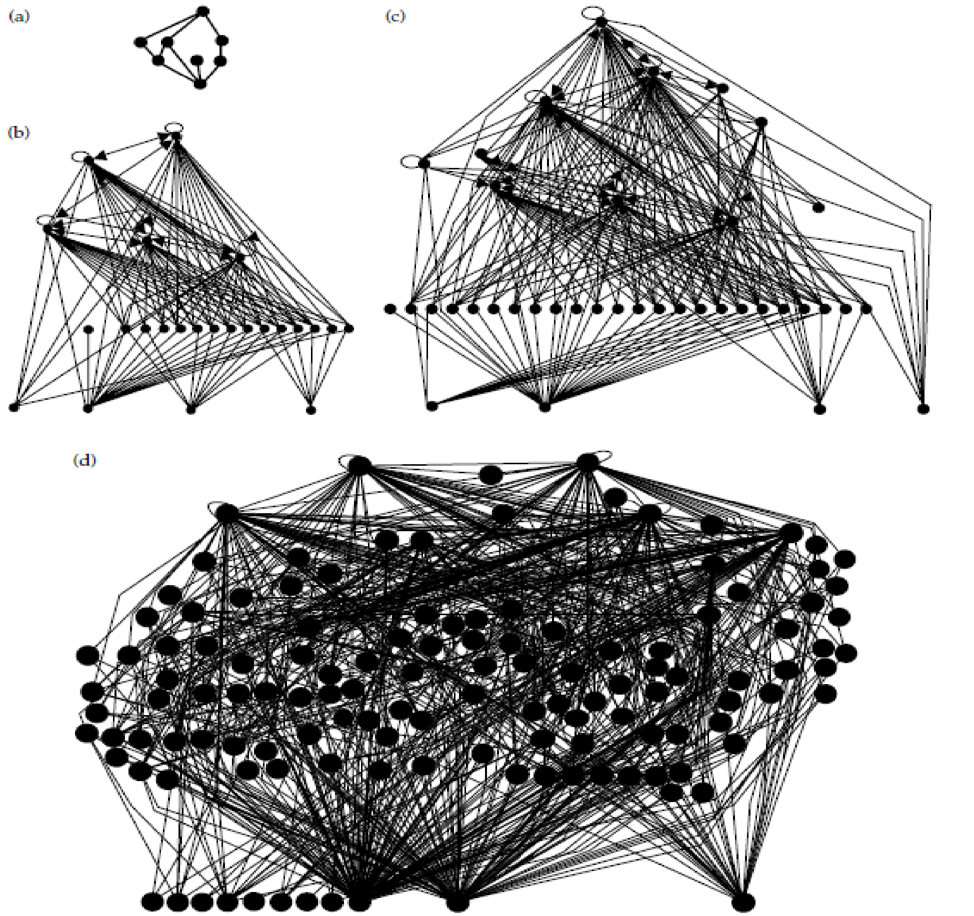
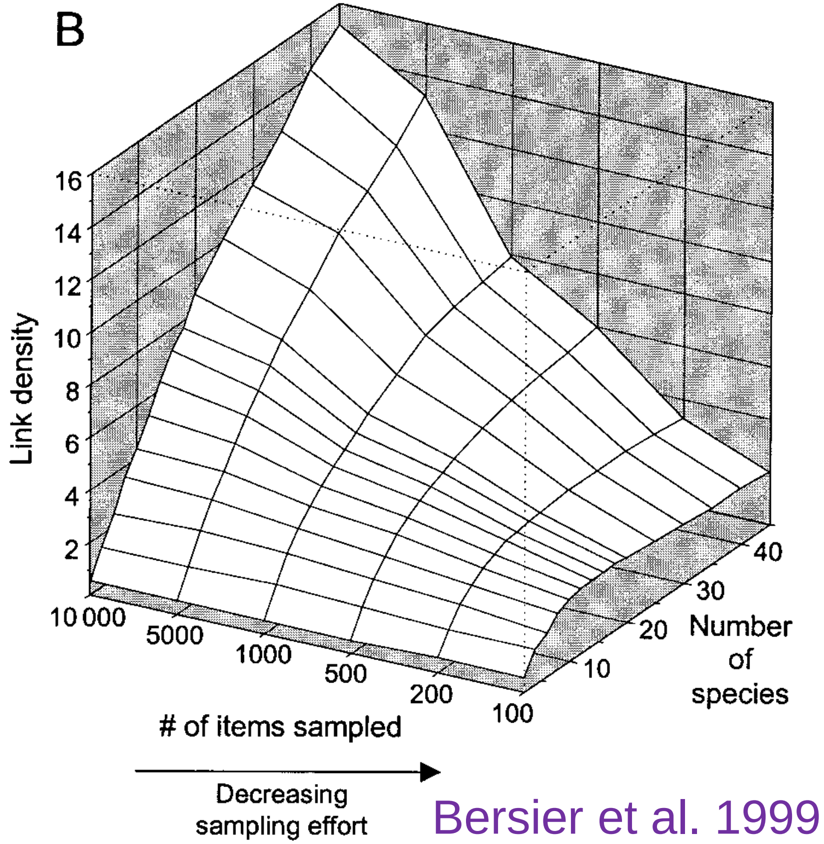


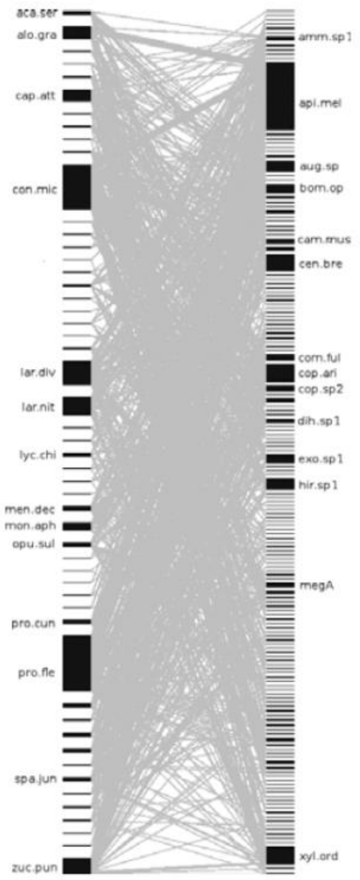
Figure 5.1 Connectance food webs from the early and more recent stream literature: (a) Early stream food-web (redrawn from Cohen 1978) (b) Initial connectance web from Broadstone Stream (after Hildrew et al. 1985) (c) Intermediate resolution web from Broadstone Stream (after Woodward and Hildrew 2001)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

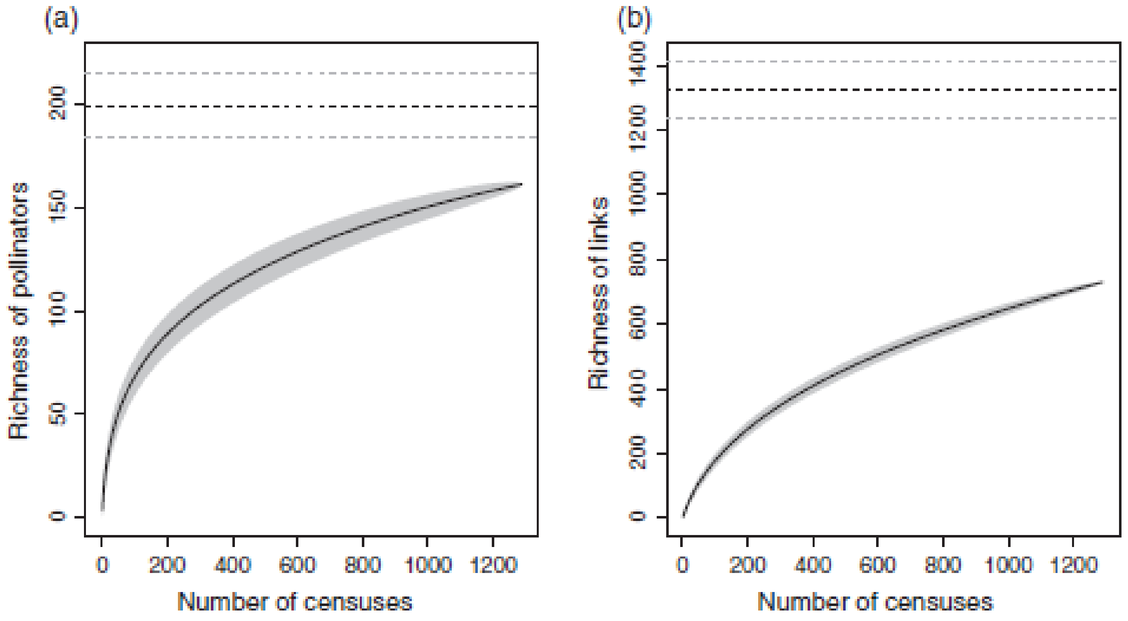


Bersier et al. 1999

The diversity – connectance relationship

A matter of data resolution?

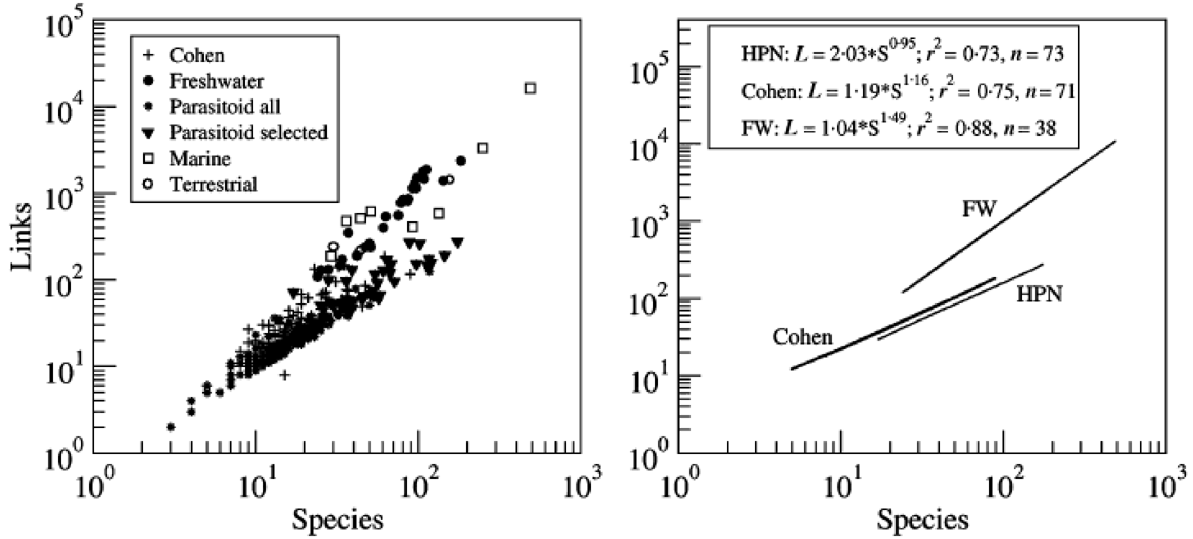




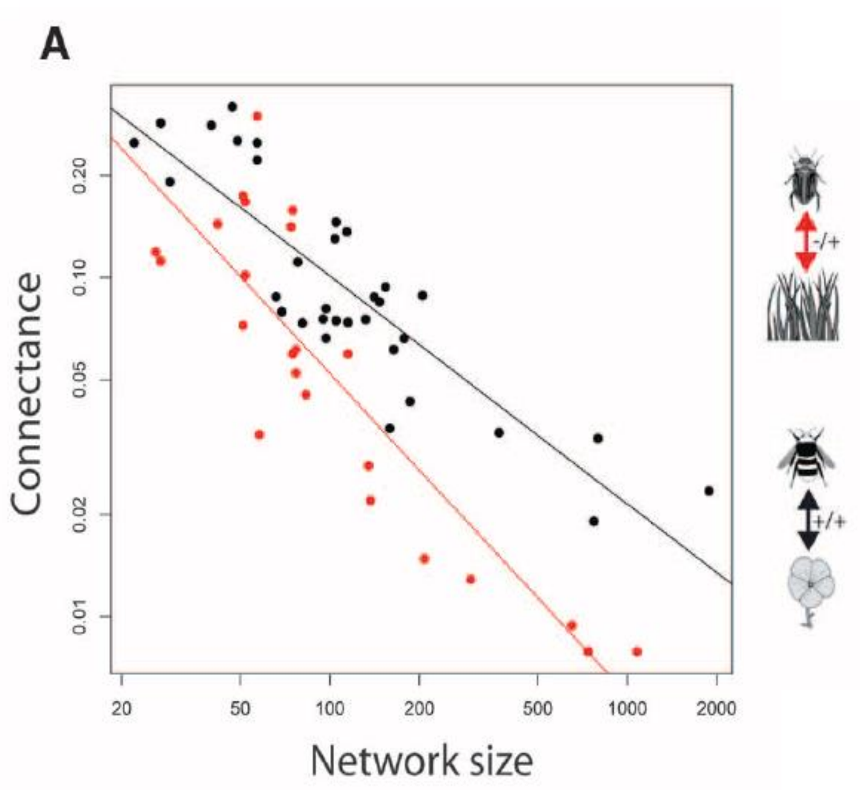
Chacoff et al. 2011

The diversity – connectance relationship

Depends on interaction type, ecosystem type, etc.



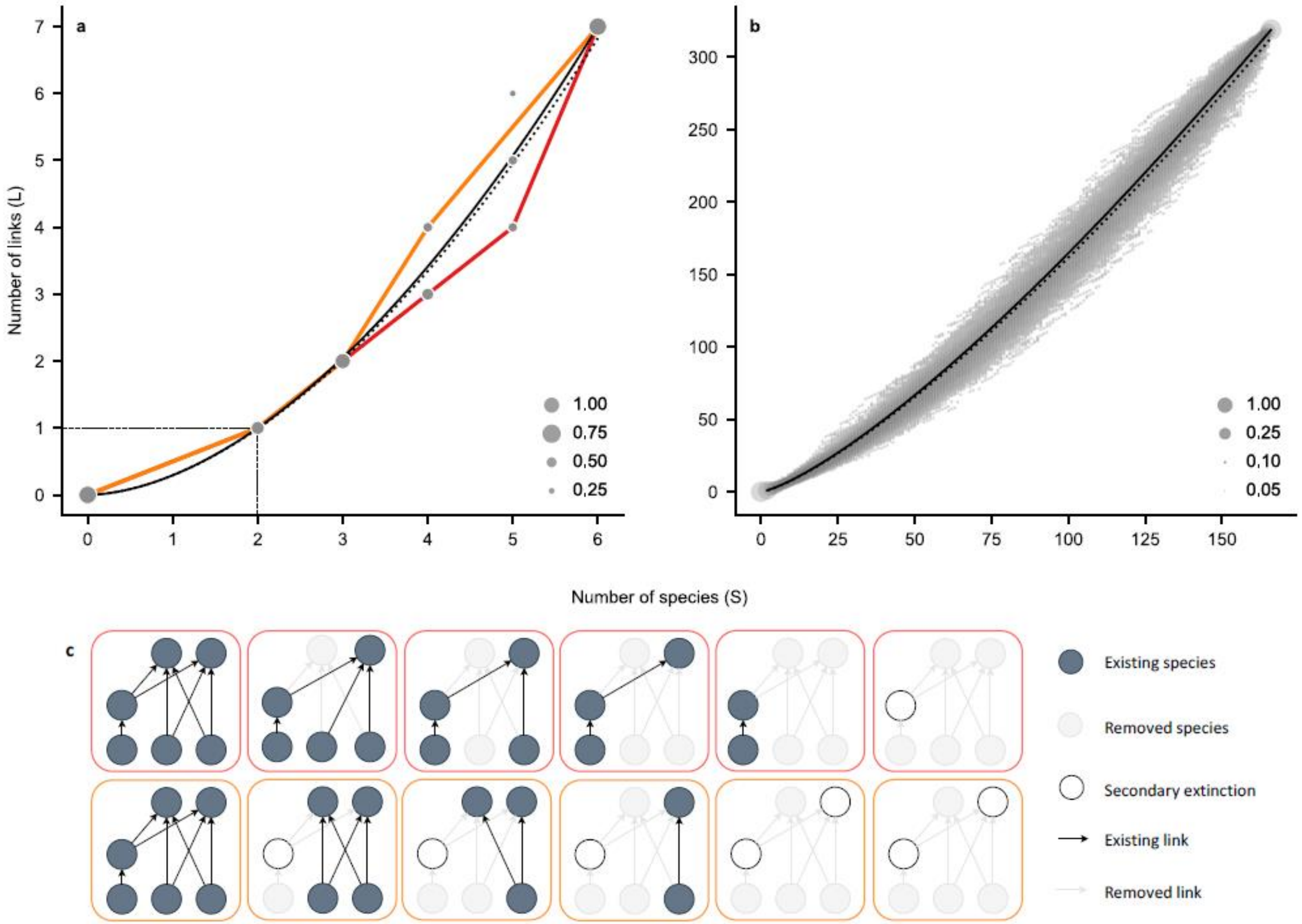
Ings et al. 2009

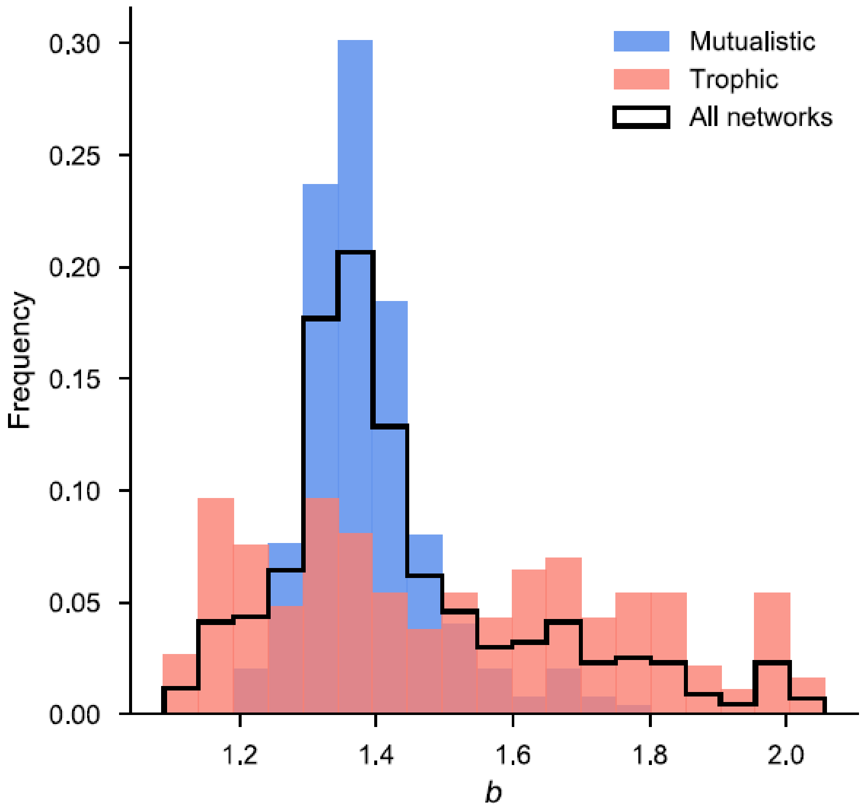


Thébault & Fontaine 2010

The diversity – connectance relationship

Relation at the network level?





Carpentier et al. 2021

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

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

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Specific food web metrics

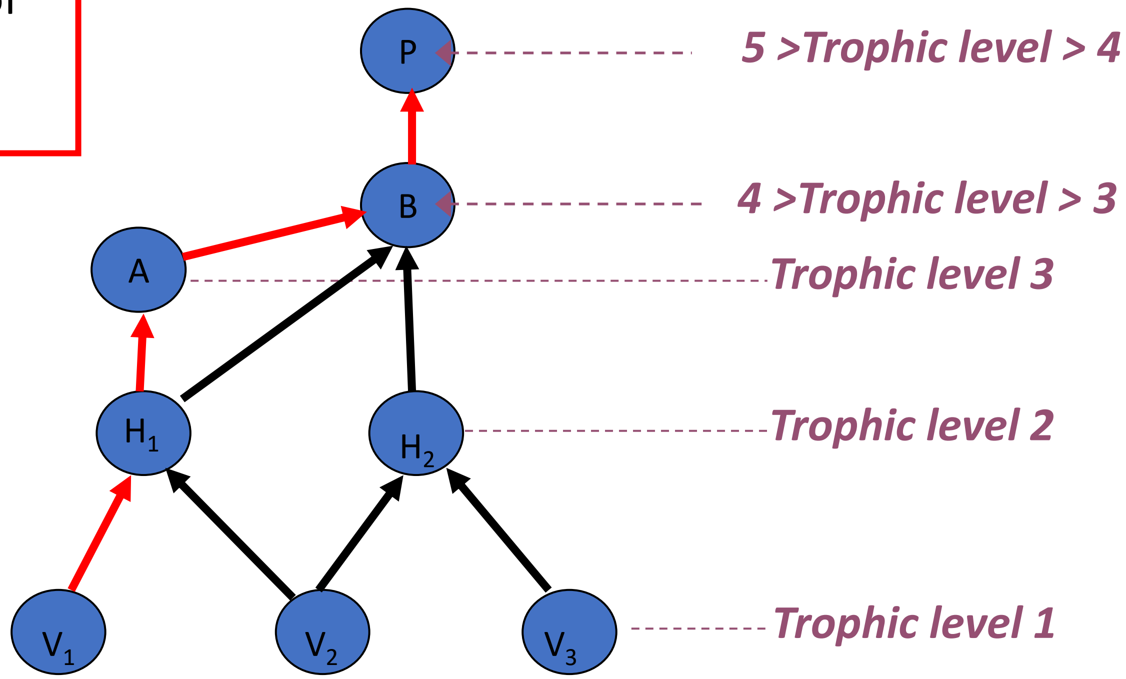
- Number of trophic levels (or minimal chain length between top predators and basal species)
- Relative species number at the different trophic levels
- Proportion of omnivores

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

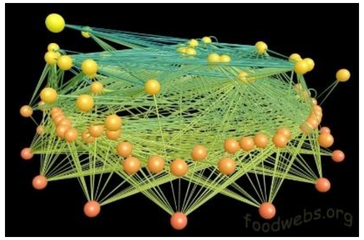
$$TL = [(I - G)^{-1}]\ 1$$

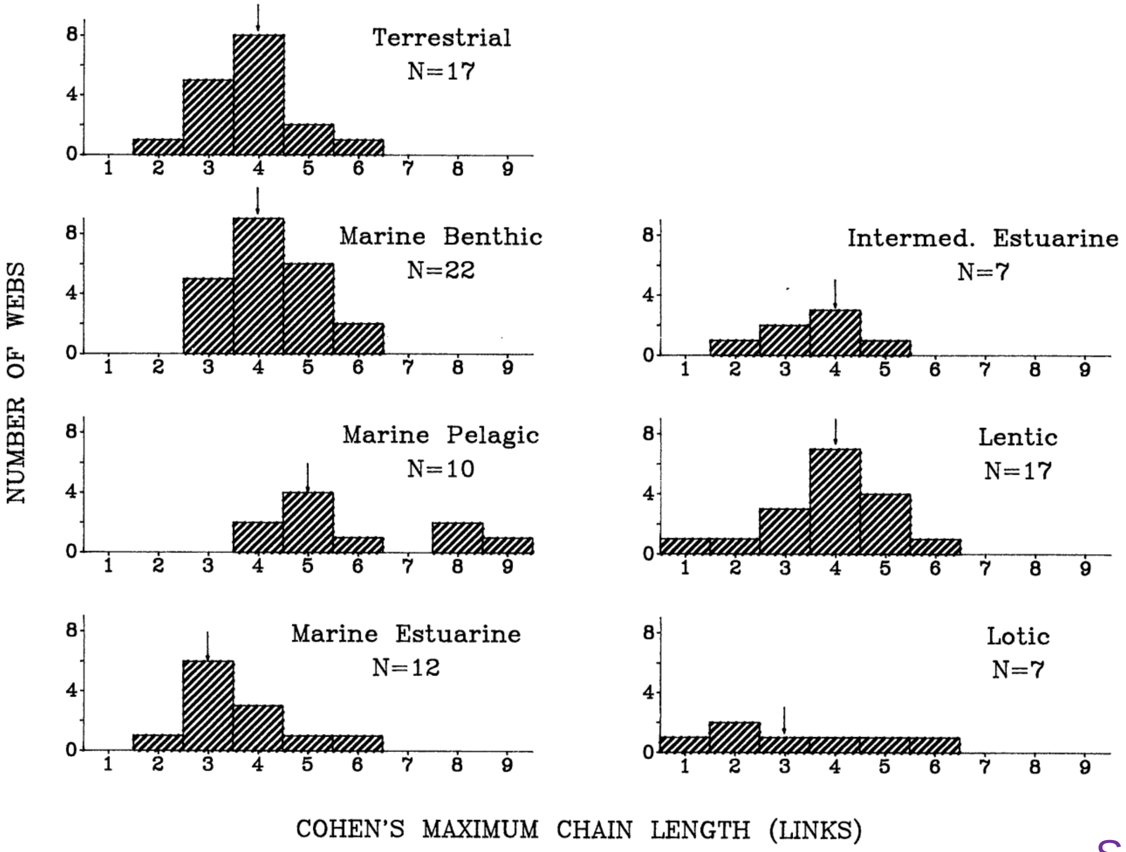
Trophic chain: representation of matter or energy flow from a basal species to a top predator.

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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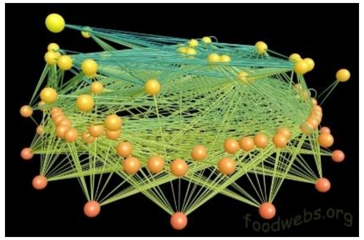
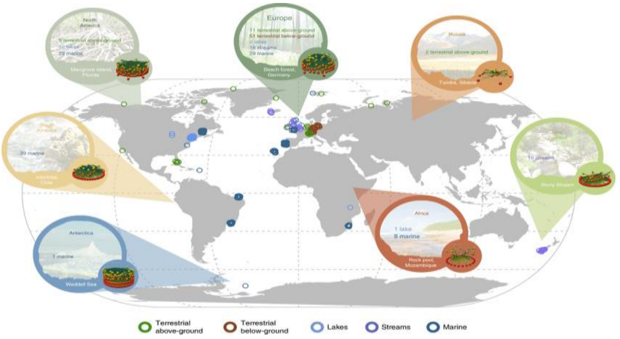
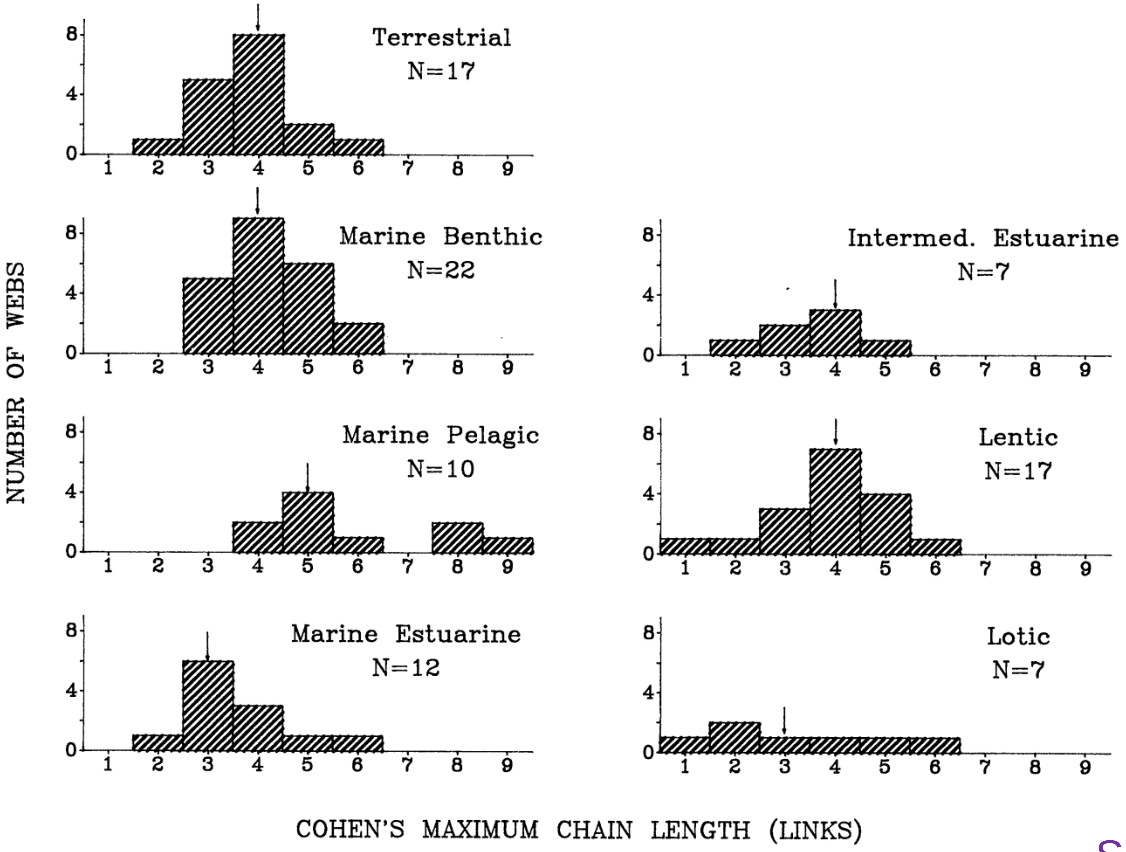
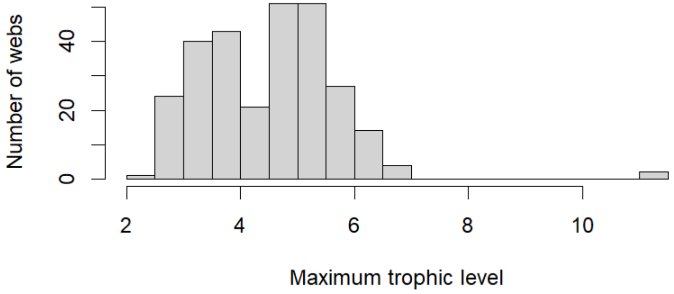




GATEWAy





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)

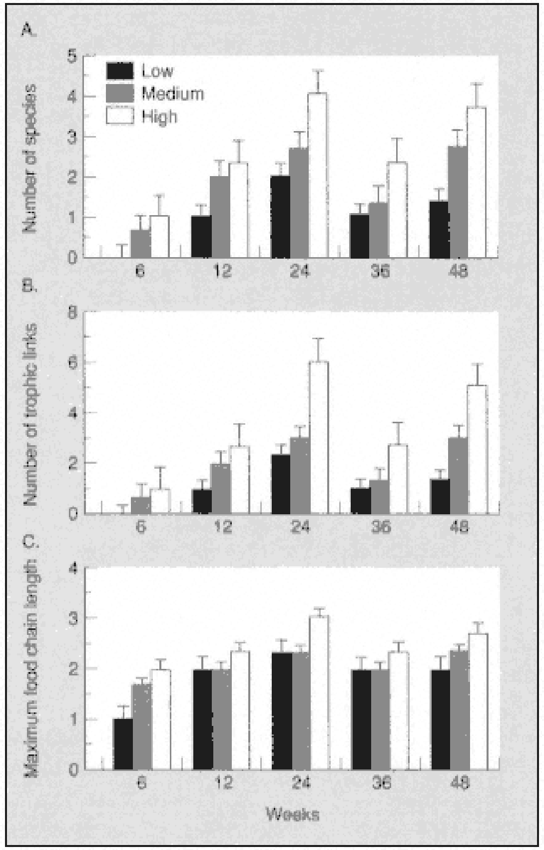
What limits food chain length?
Several theories

- ➢ Limitation by available resources

Hutchinson 1959, Oksanen 1981, …

tad poles
↑
mosquito larvae
↑
micro invertebrates
↑
detritus

Srivastava & Lawton Am Nat 1998



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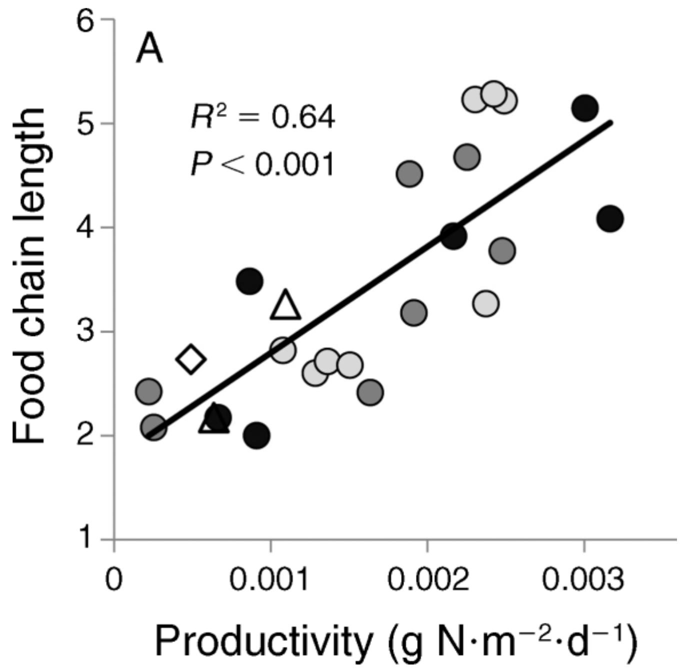

Young et al. 2013

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Several theories

- Limitation by ecosystem size

Schoener 1989, Cohen & Newman 1991, …

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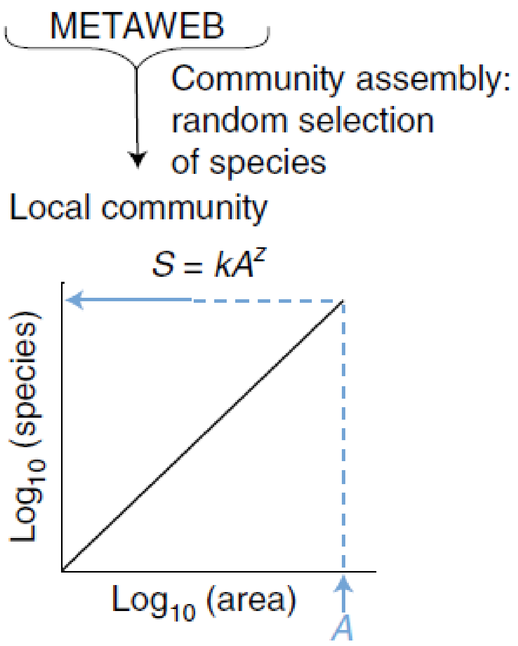
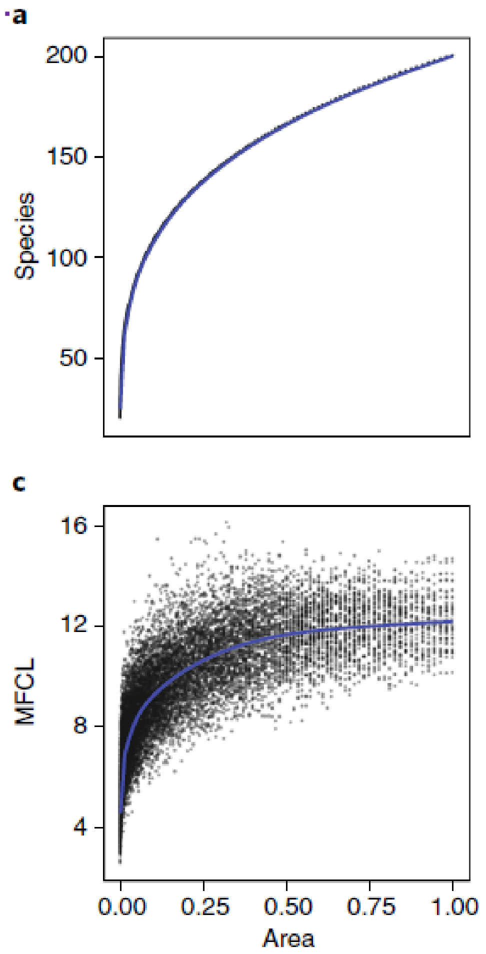


Number of species selected

Galiana et al. 2018



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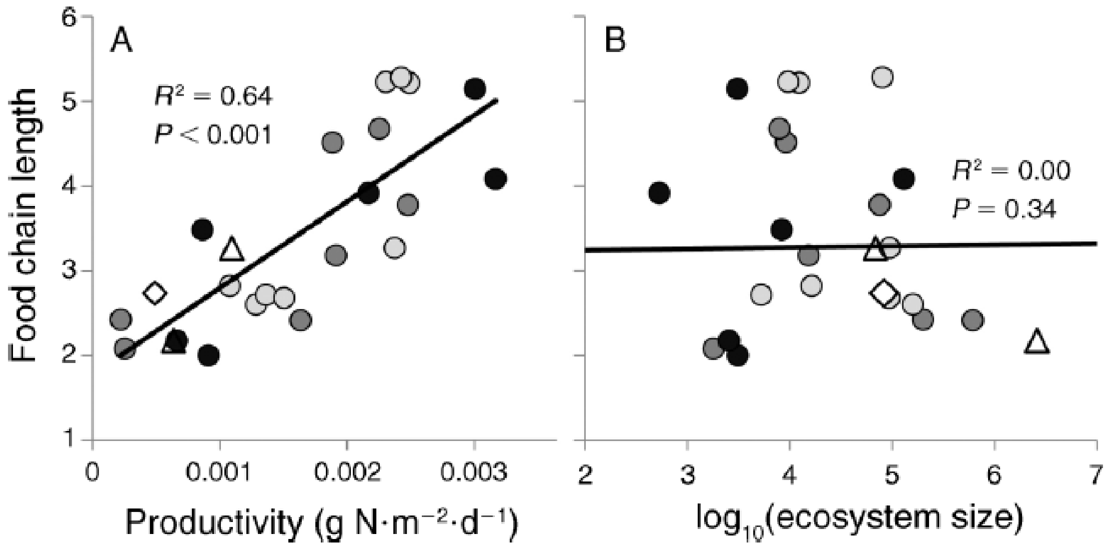
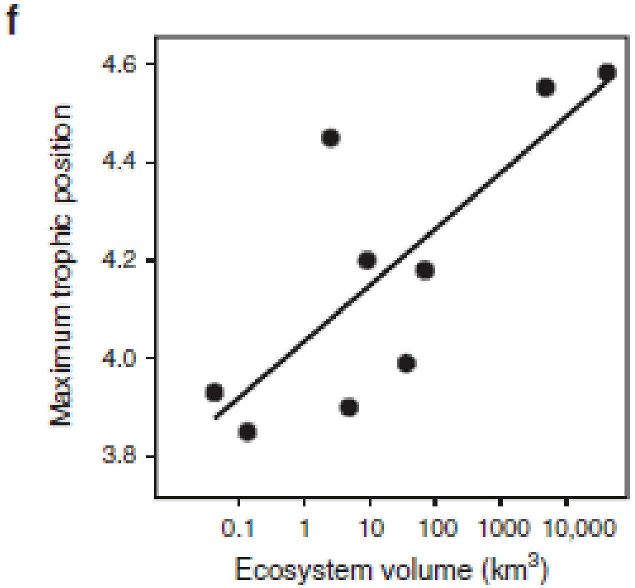
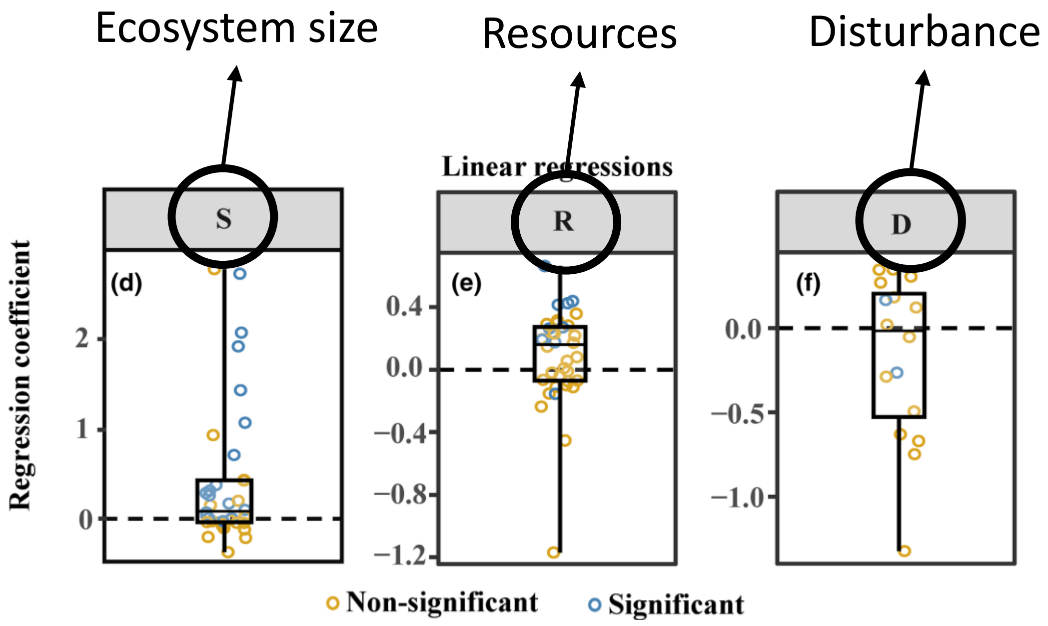




Ward & McCann 2017

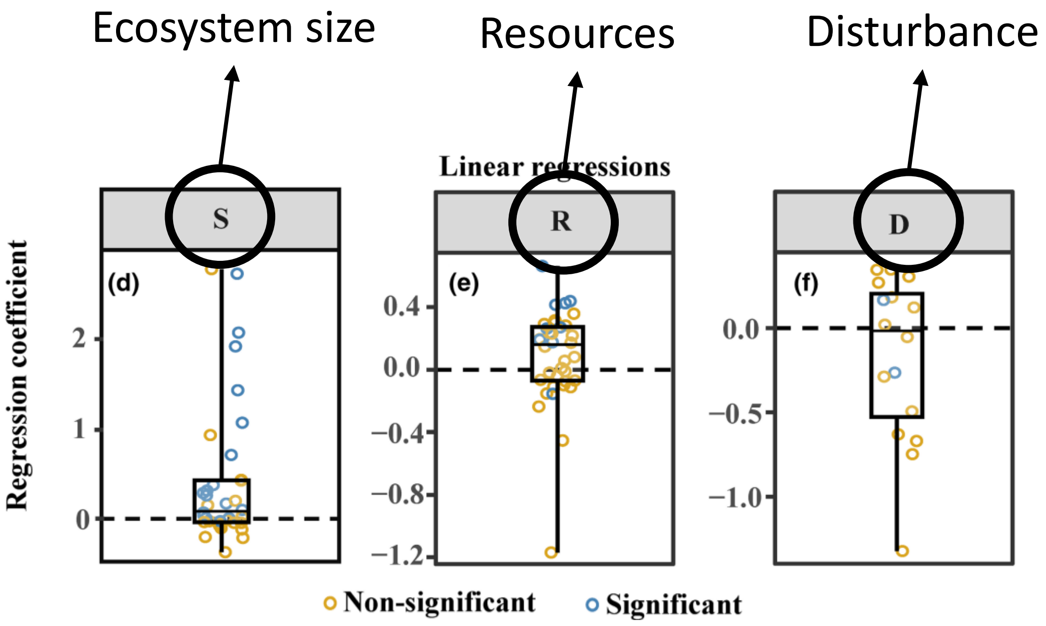
Young et al. 2013

What limits food chain length?
Several theories

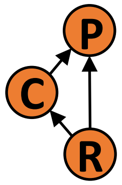


Guo et al 2023

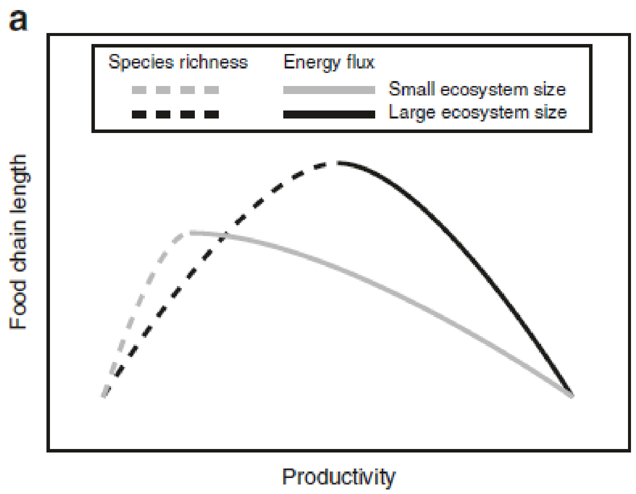
What limits food chain length?
Several theories



Guo et al 2023



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

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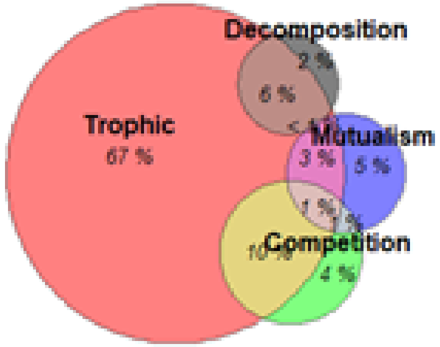
➢ **Historically focused on a few sets of network and species level properties**

➢ **A strong focus on food webs**

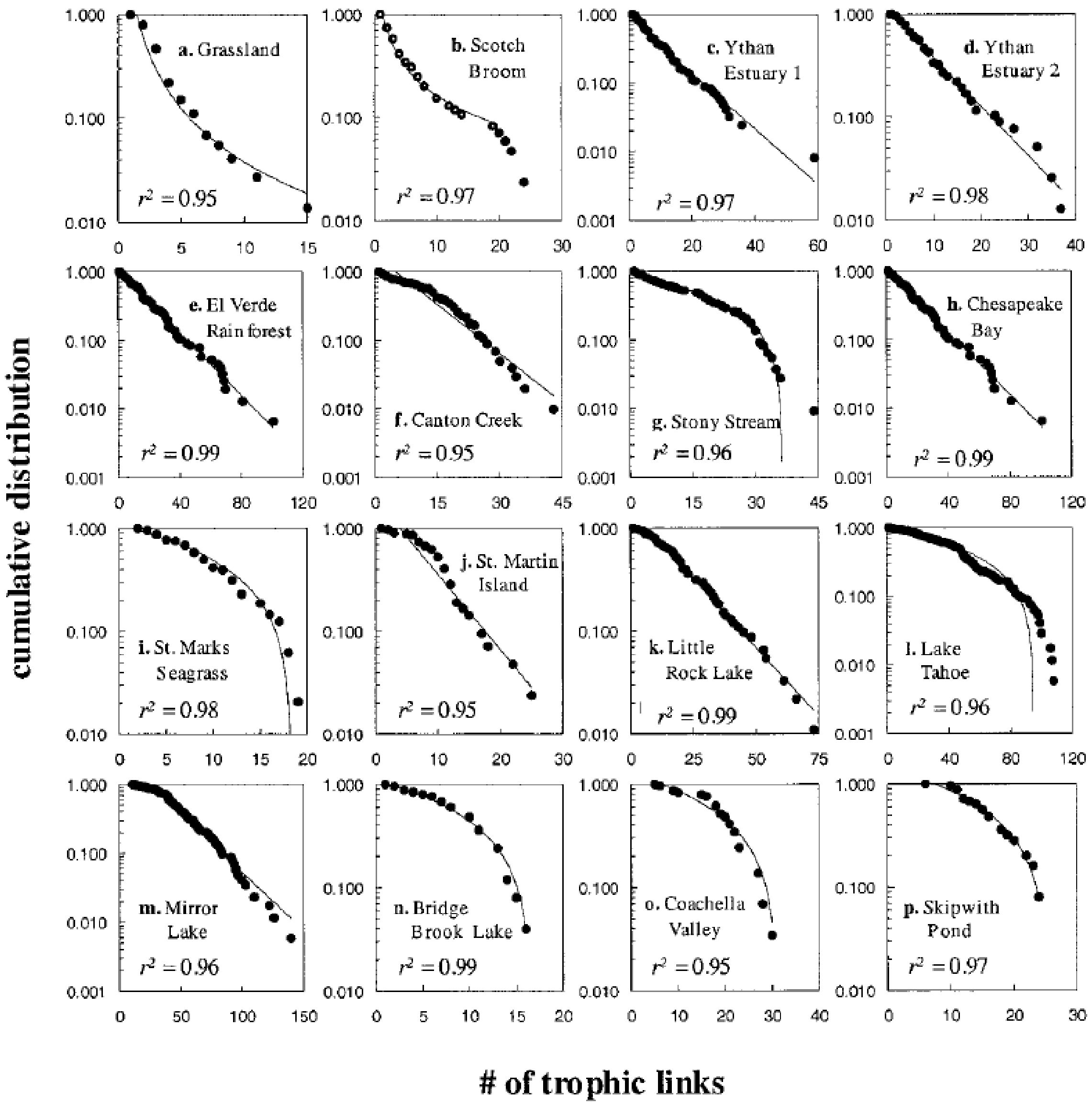


Analysing the structure of ecological networks: looking for general patterns?

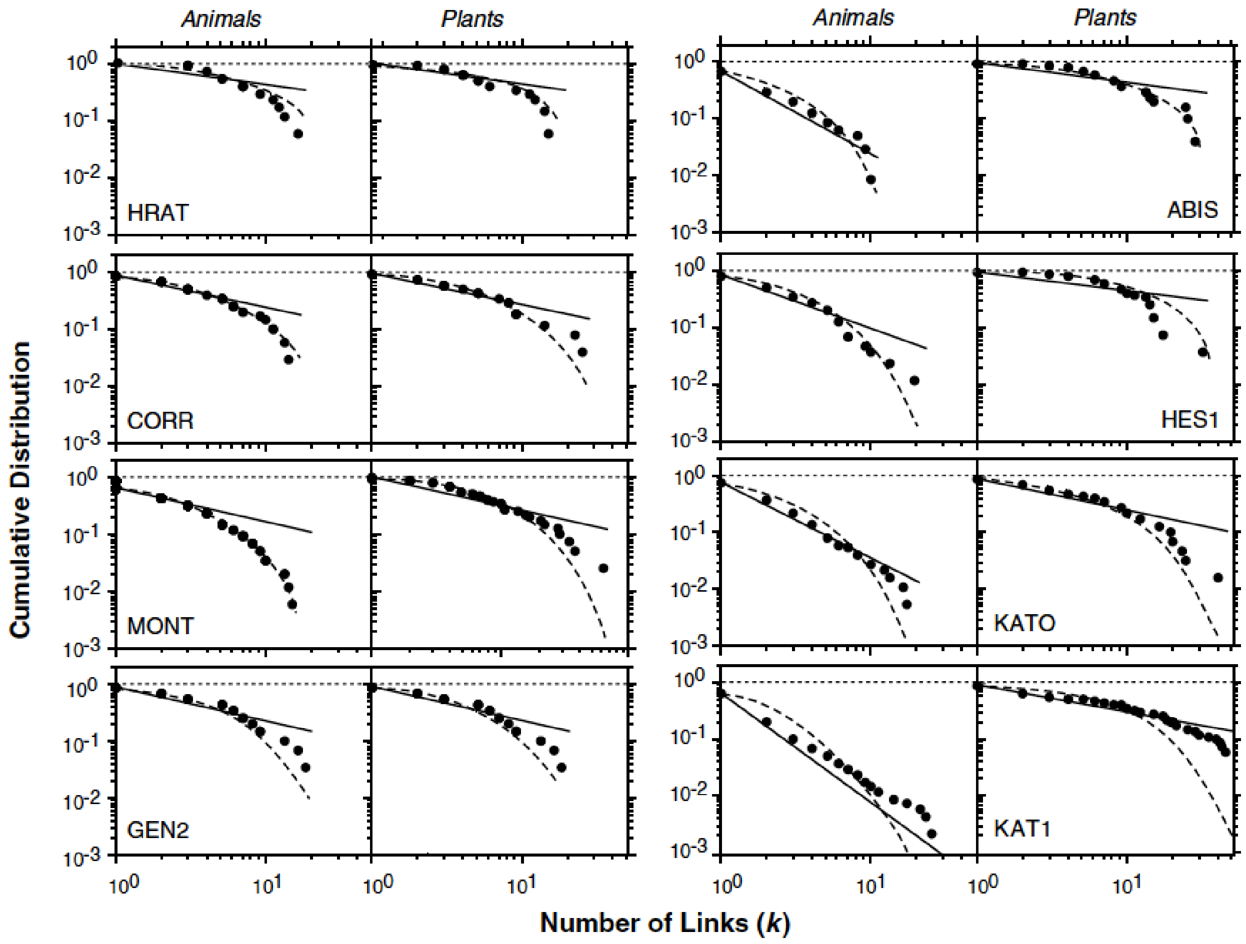
Part 2: examples of more recent patterns studied in ecological networks:

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

Degree distributions

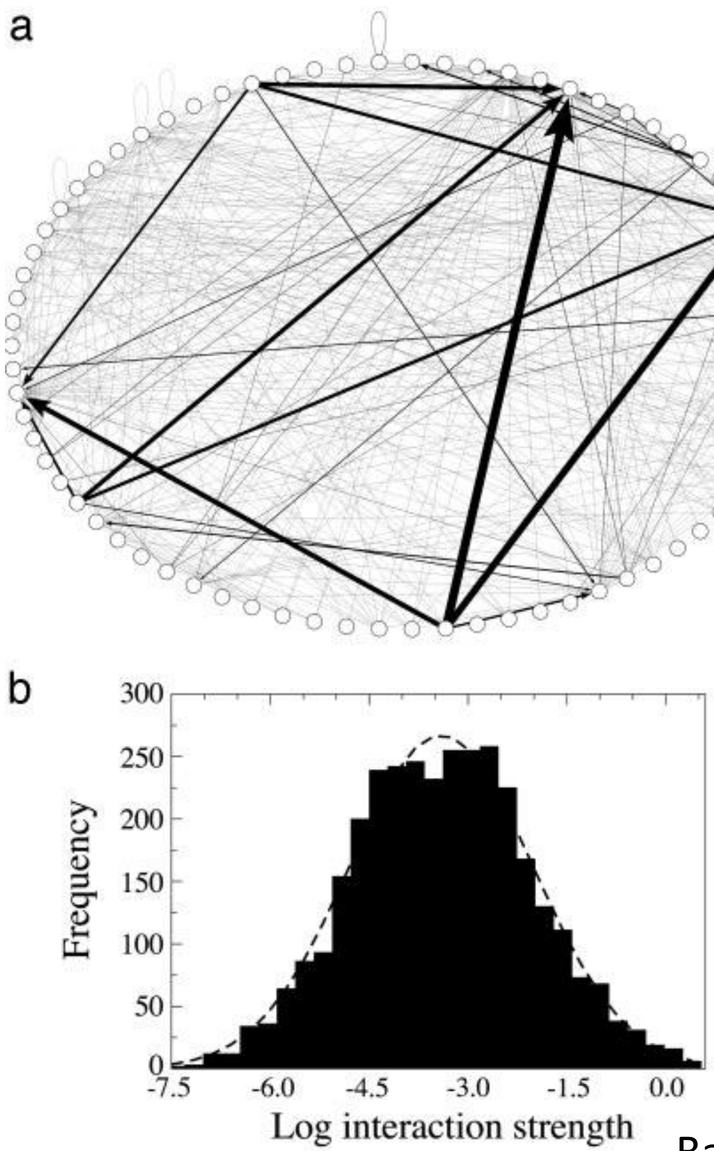


Dunne et al. 2002

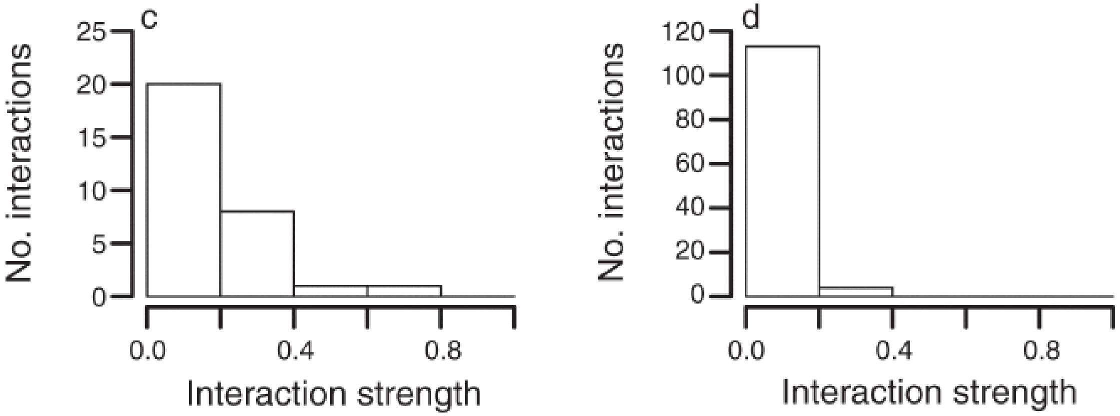


Jordano et al. 2003

Interaction strength distributions

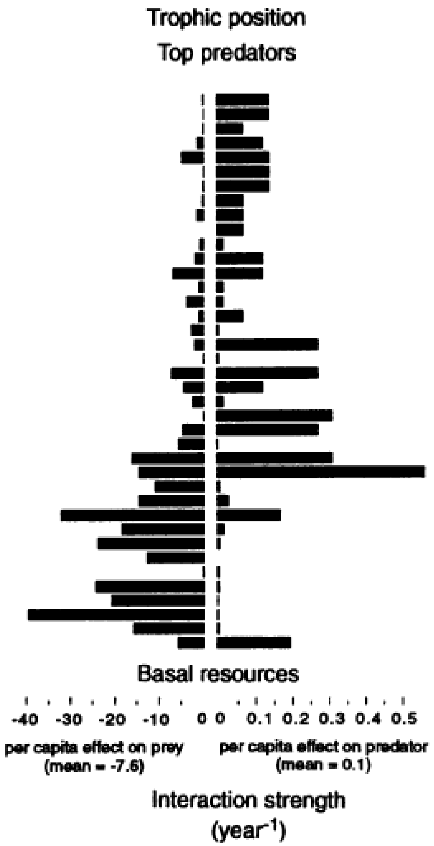


Bascompte et al. 2005



Vazquez et al. 2012

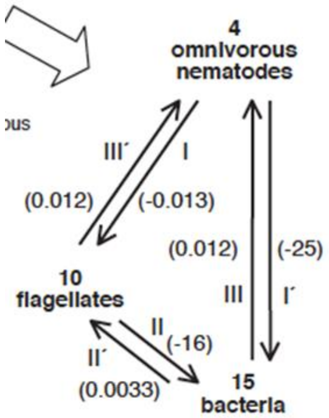
Interaction strength distributions: consequences on stability



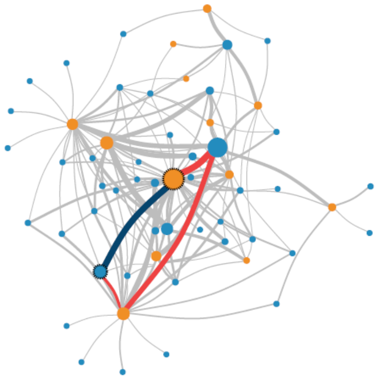
De Ruiter et al. 1995 Science

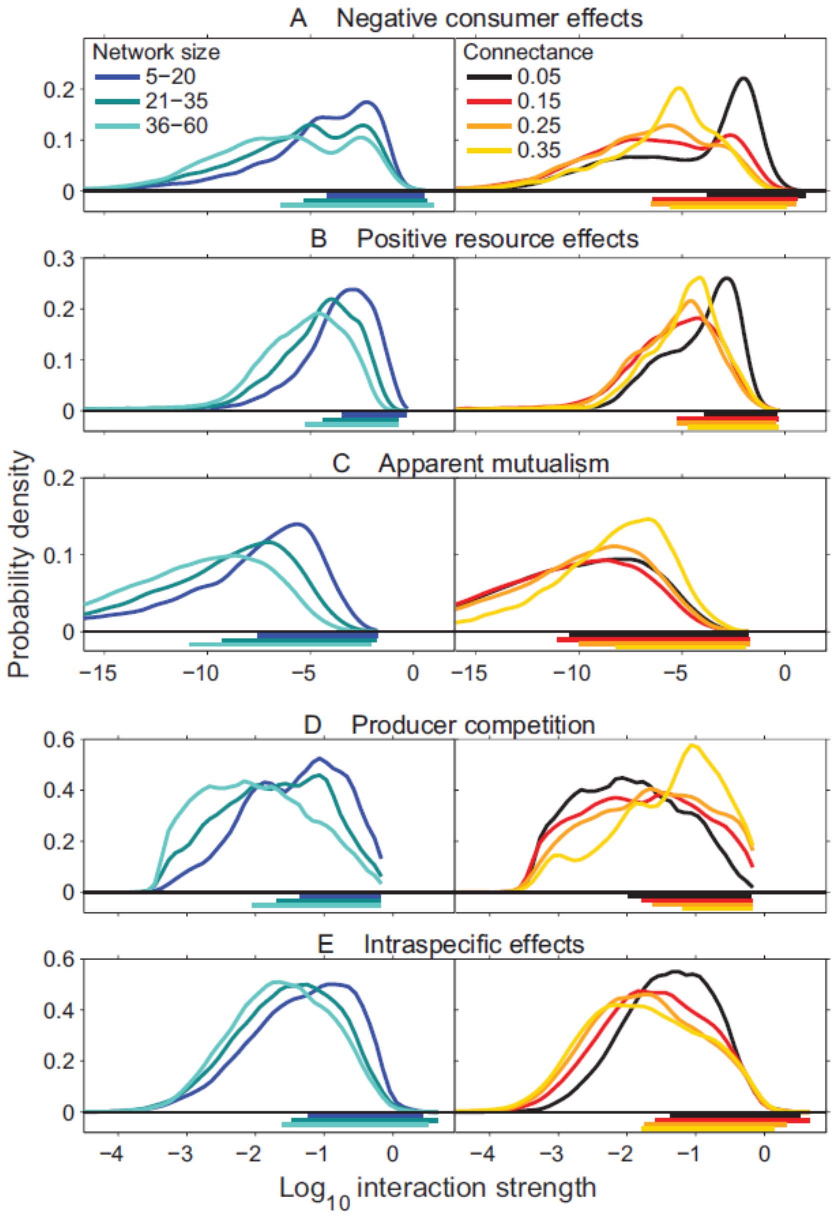
Stability in Real Food Webs: Weak Links in Long Loops

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



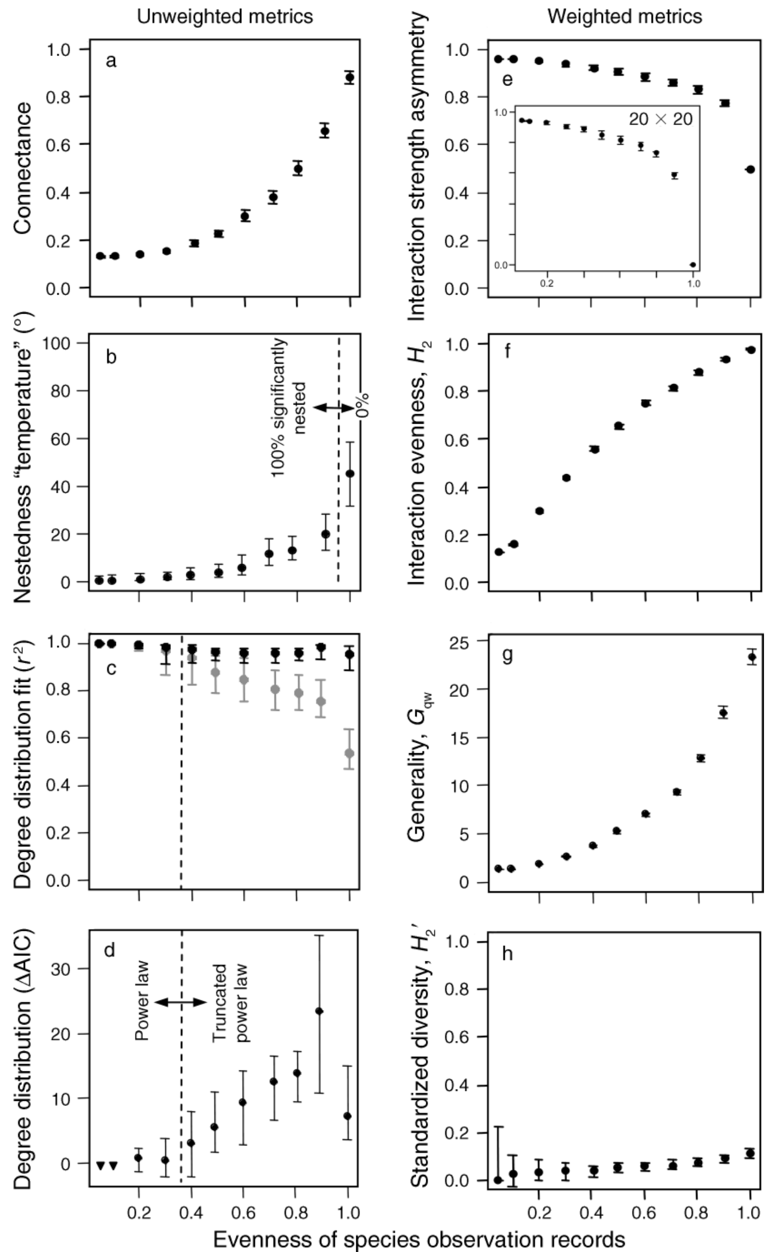
Neutel et al. 2002 Science





Iles & Novak 2016

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]

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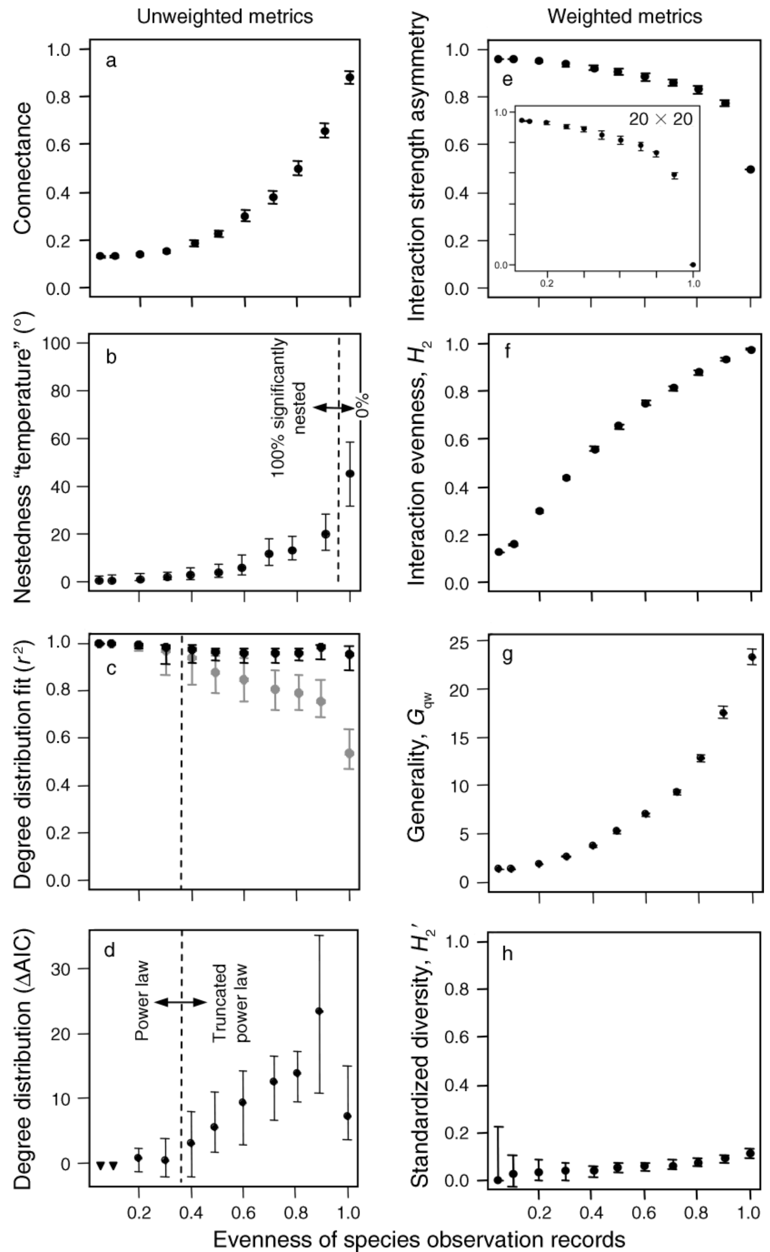

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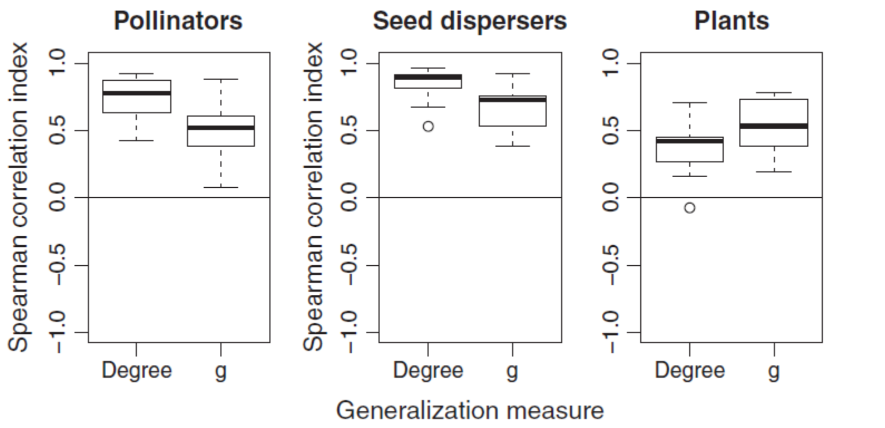
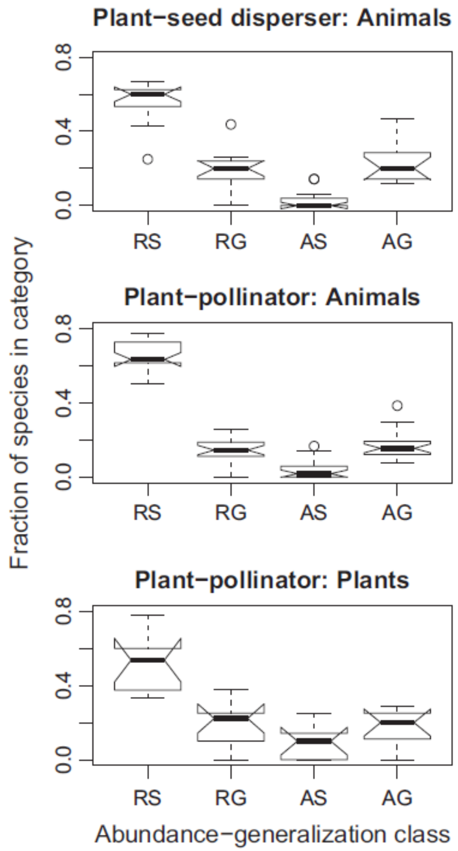
Ecology Letters, (2016) **19**: 4–11 doi: 10.1111/ele.12535

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

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GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 11 (2010) 185–195

Basic and Applied Ecology

www.elsevier.de/baae

INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

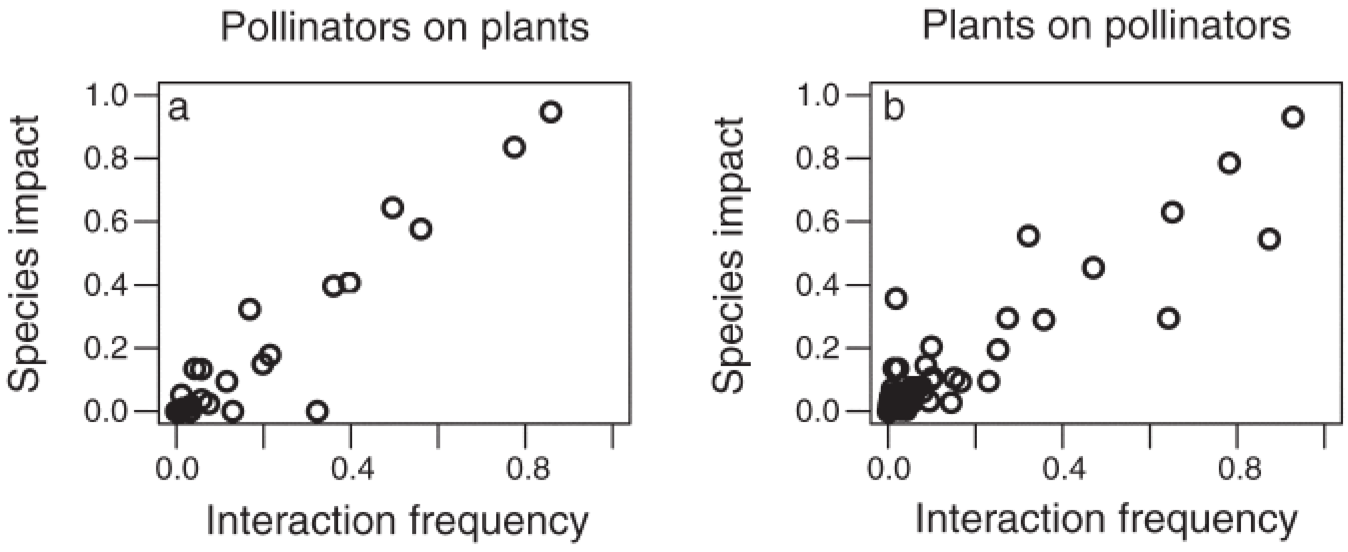
Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide

Nico Blüthgen*

Interpretations can be:

(1) *niche-based*, describing specialisation, trait (mis-)matching between species, niche breadth and niche overlap and their relationship to interspecific competition and species coexistence, or

(2) *impact-based*, focusing on frequencies of interactions between species such as predation or infection rates and mutualistic services, aiming to quantify each species' relative contribution to an ecological effect.



Vazquez et al. 2012

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

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- **Looking for groups**
- How networks vary in space and time
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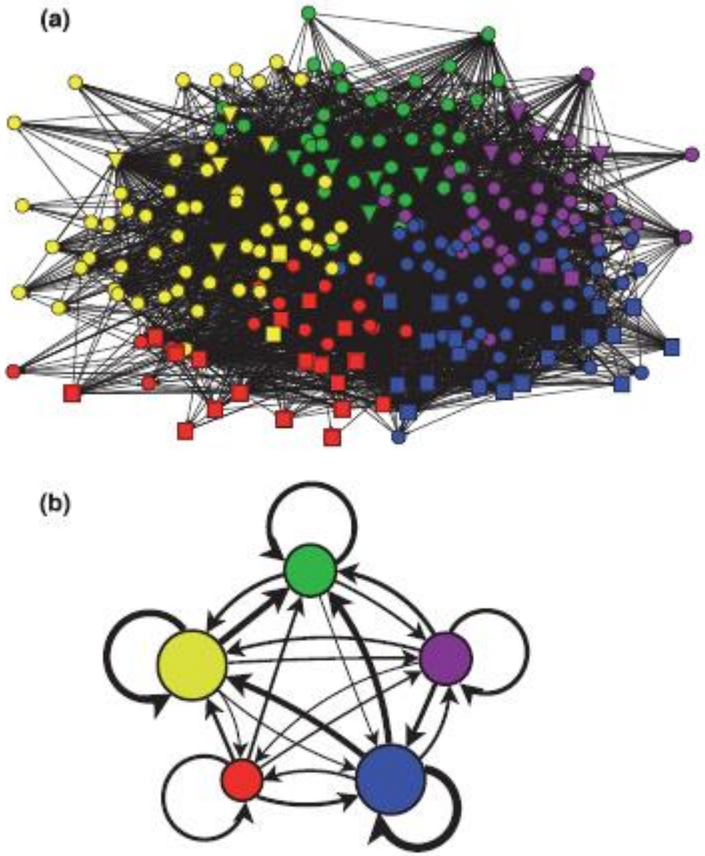
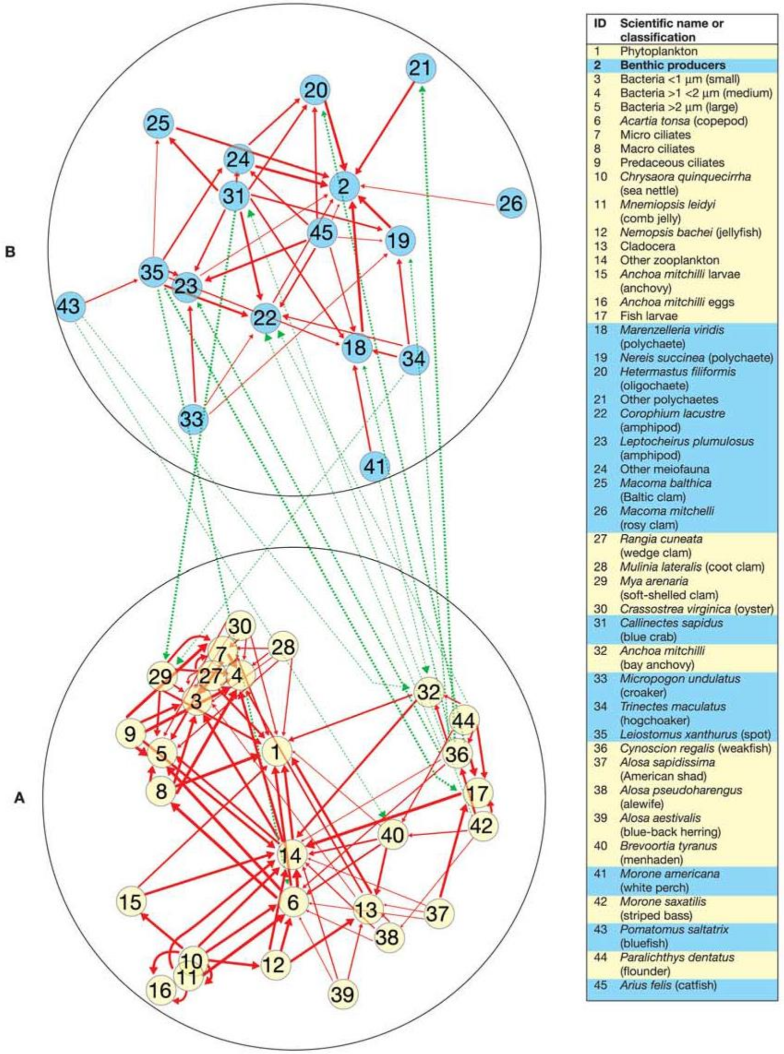
Modularity

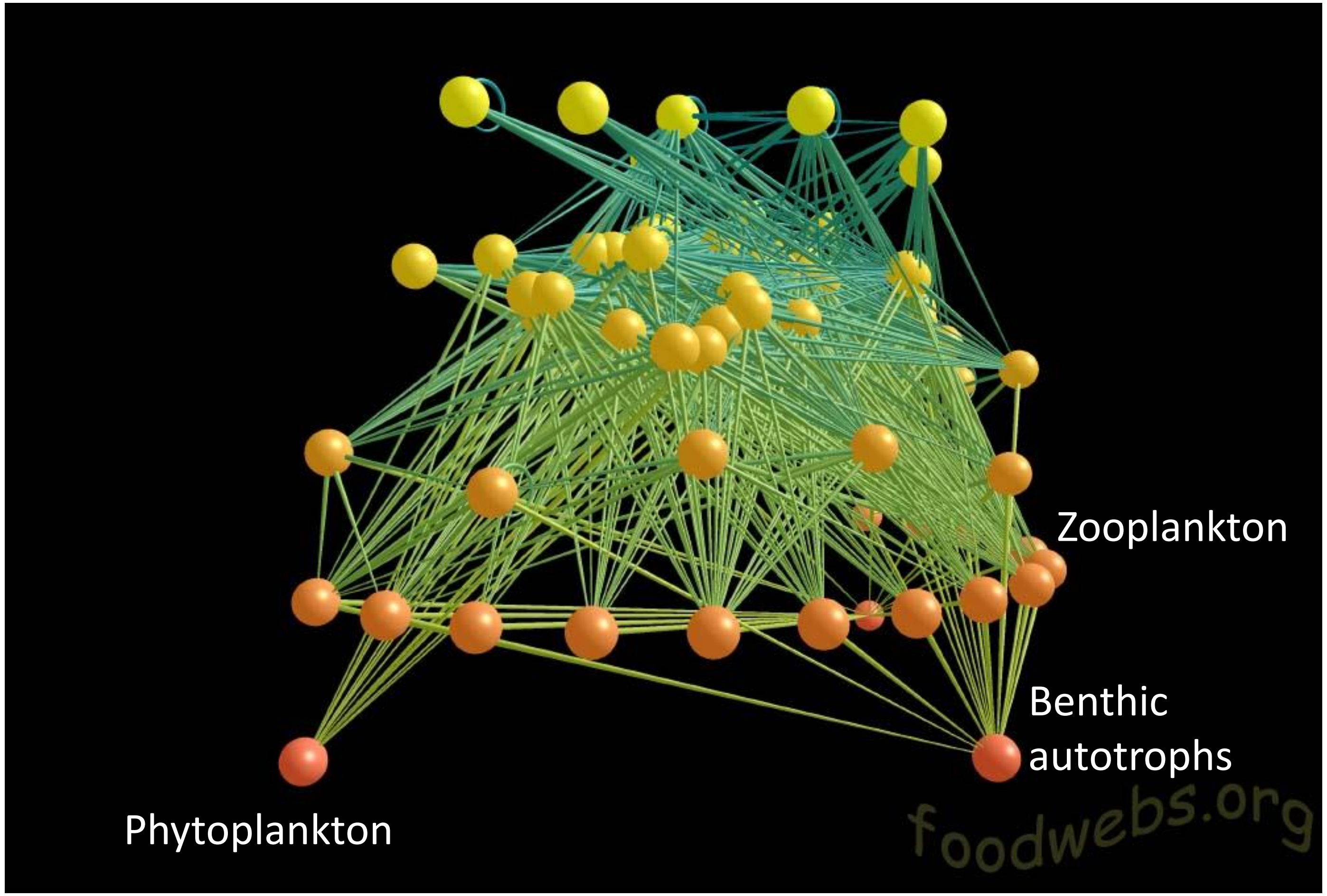


Caribbean food web
Rezende et al. (2009)



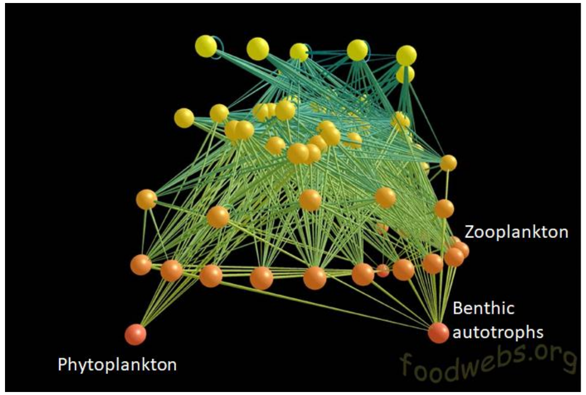
Chesapeake Bay food web
Krause et al. (2003)

The trophic group: a classical notion in food web ecology

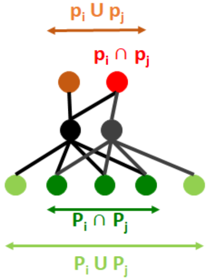


Which is the notion of group that best describes food web structure?

Trophic groups

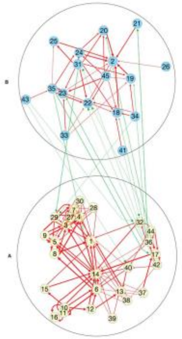


$$G(E) = \sum_{g=1}^{|E|} \frac{1}{|g|} \sum_{i,j \in G} (T(i,j) - E(T(i,j)))$$



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

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)

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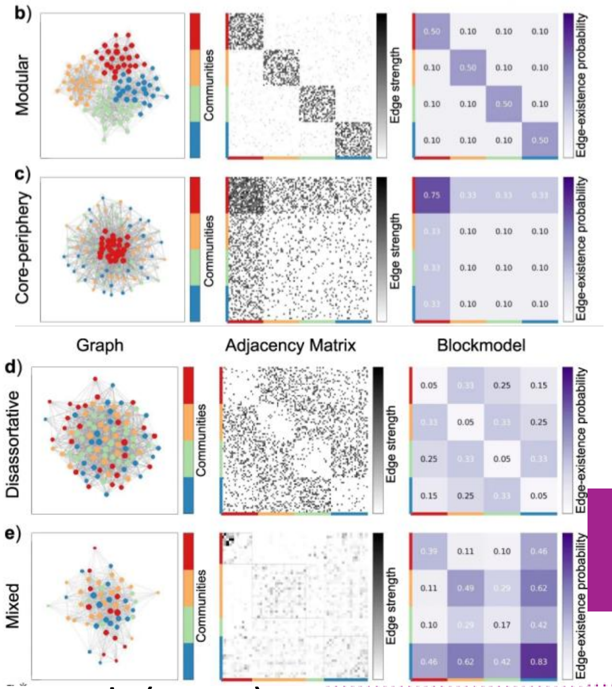
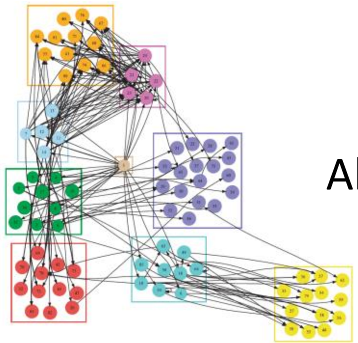


Faskowitz et al. (2018)

Stochastic block model

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



Allesina & Pascual (2009)

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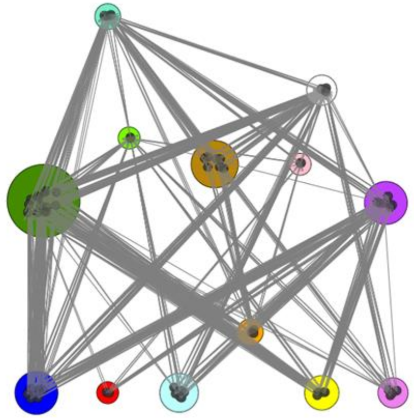
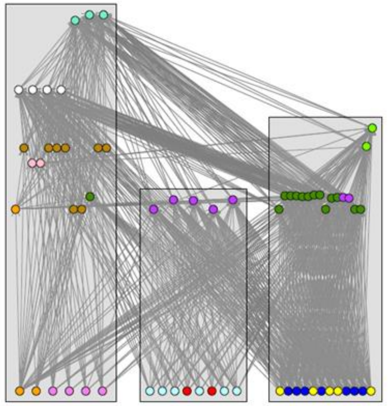
Gauzens et al. (2015)

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



Trophic groups

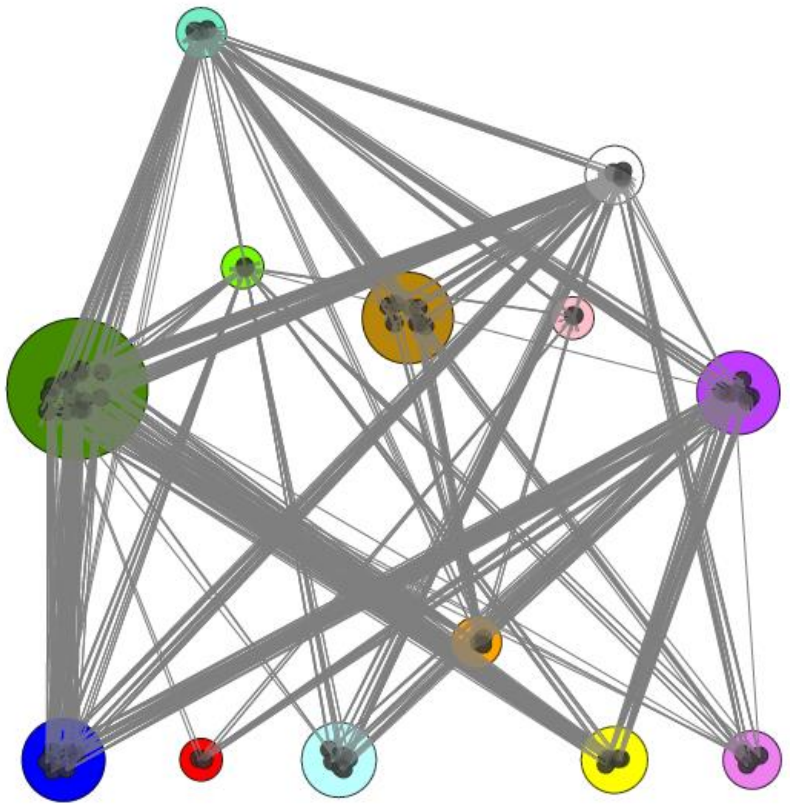


Modules

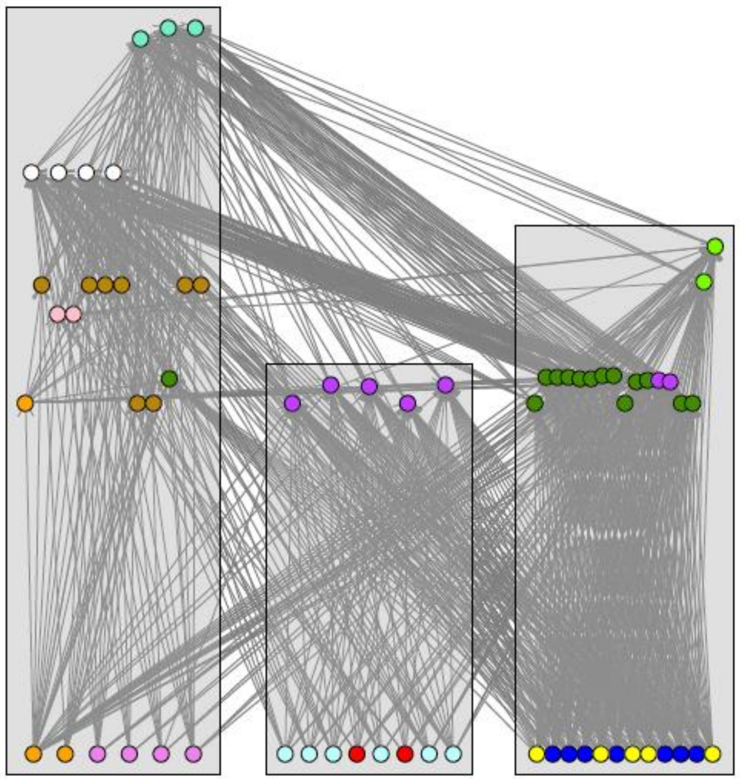
	species (links)	TG	AP	M	TG-AP overlap	module-AP overlap
Benguala [35]	29 (203)	7	7	3	0.841	0.397
Bridge Brooke Lake [36]	75 (553)	12	9	3	0.92	0.631
Carribean Reef [37]	249 (3313)	46	28	3	0.775	0.365
Chesapeake Bay [38]	33 (72)	13	7	3	0.745	0.428
Créteil Lake SI3	67 (718)	13	12	3	0.922	0.4738
Tuesday 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?

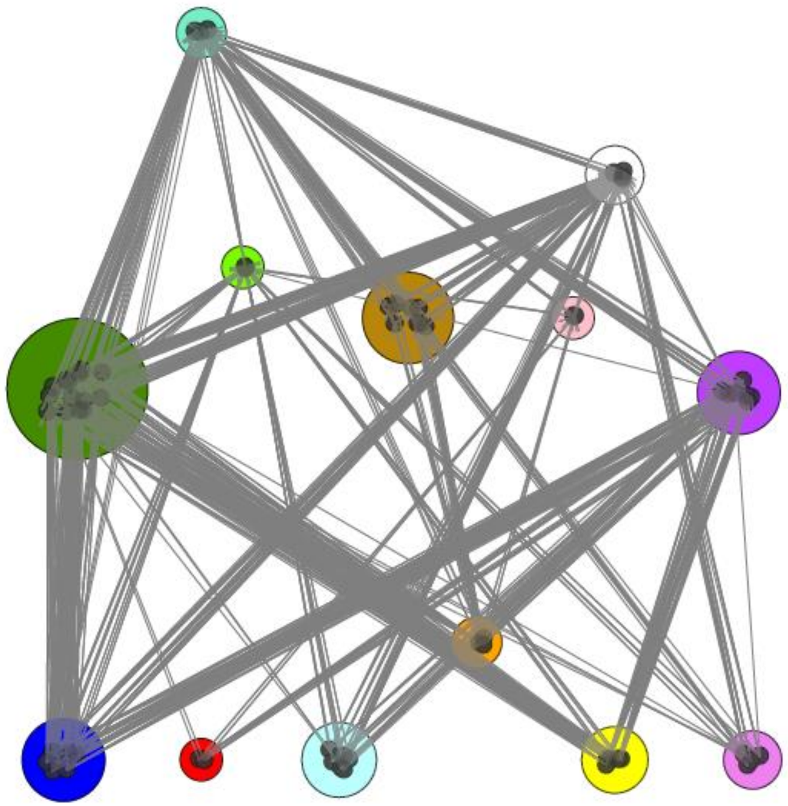


Trophic groups

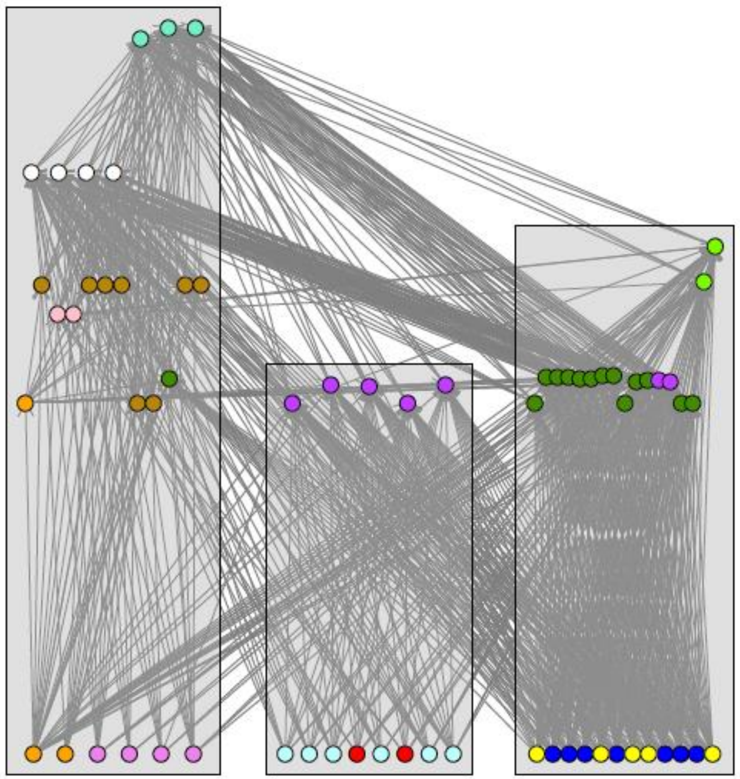


Modules

Groupes trophiques vs. modules?



Trophic groups

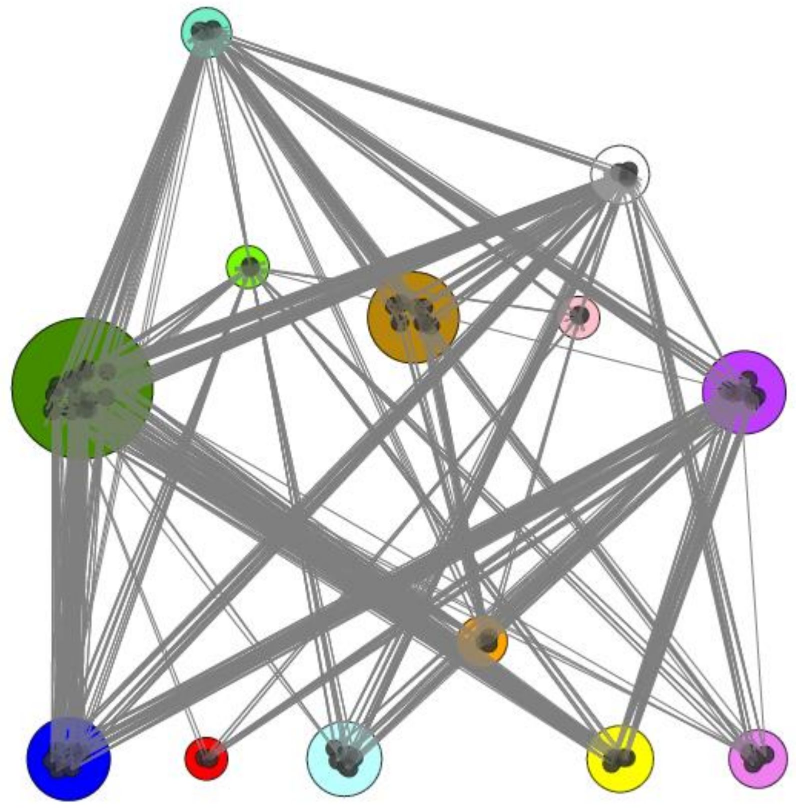


Modules

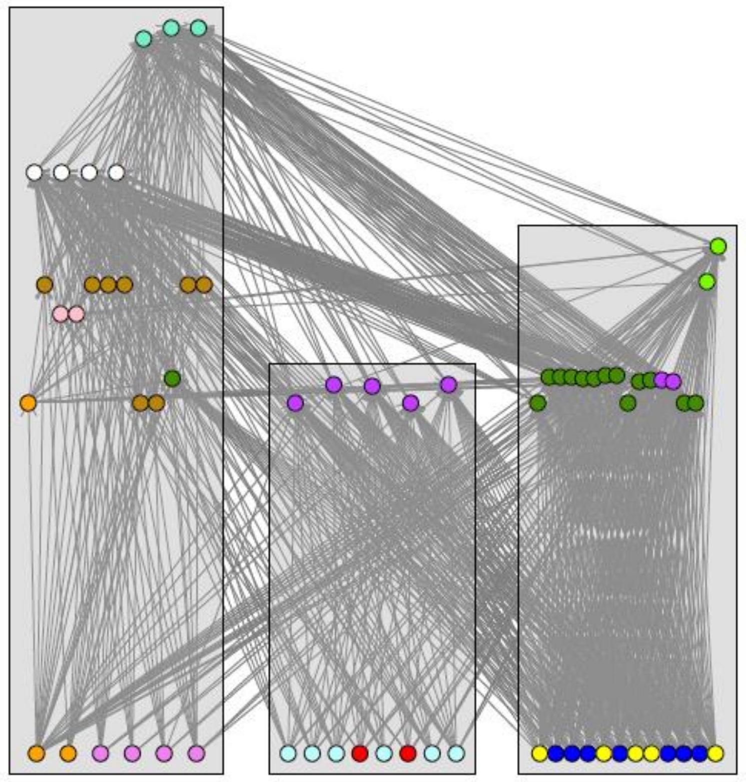
Diversity of module affiliation in trophic groups is significantly lower than random expectations (p<0.0001 for all 9 food webs)

Each trophic group belongs generally to a single module.

Groupes trophiques vs. modules?



Trophic groups



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

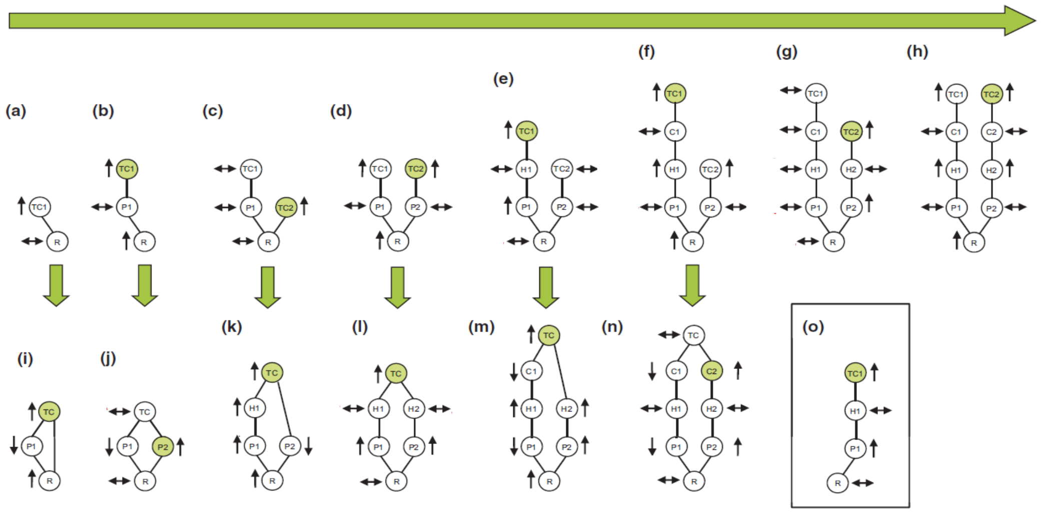
Food webs have a 2-level hierarchical structure:

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

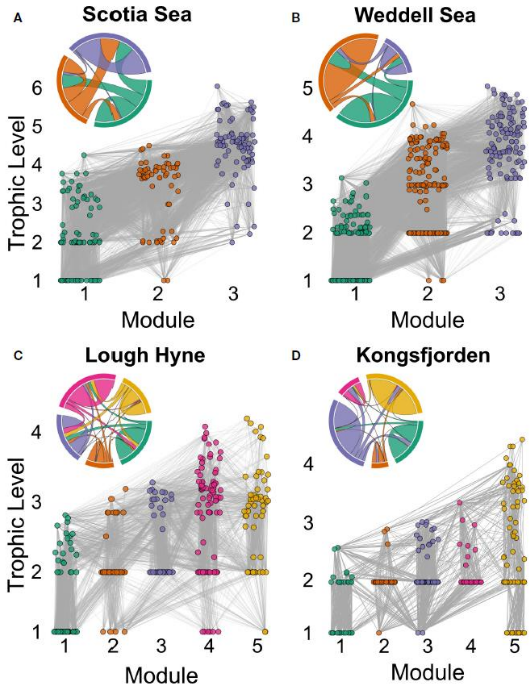
(2) trophic groups further partition these pathways into sets groups of species with similar trophic connections.

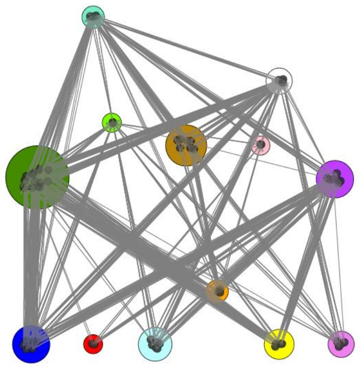
Modules and trophic groups thus provide complementary pictures of food-web structure

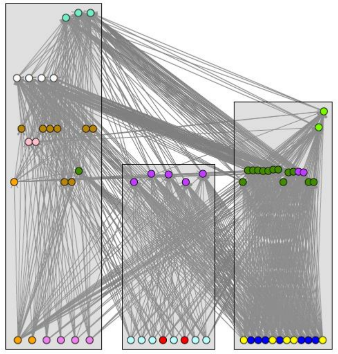
Predicting cascading effects in food webs?



- Bottom-up and top-down effects strongly depend on network structure







- Importance of energy chanels and trophic groups?

Eskuche-Keith et al. 2023

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

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

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

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%)."

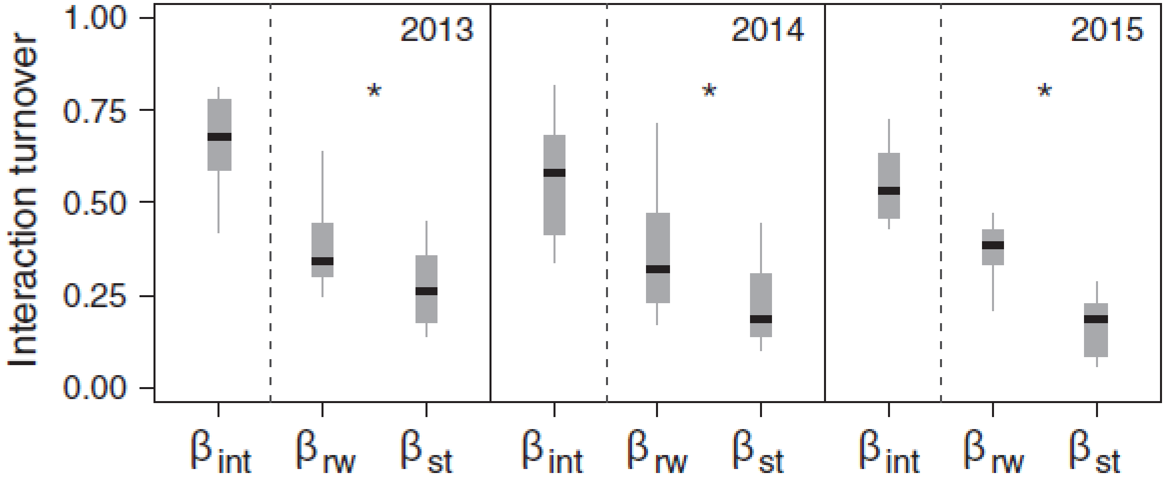
Petanidou et al. 2008

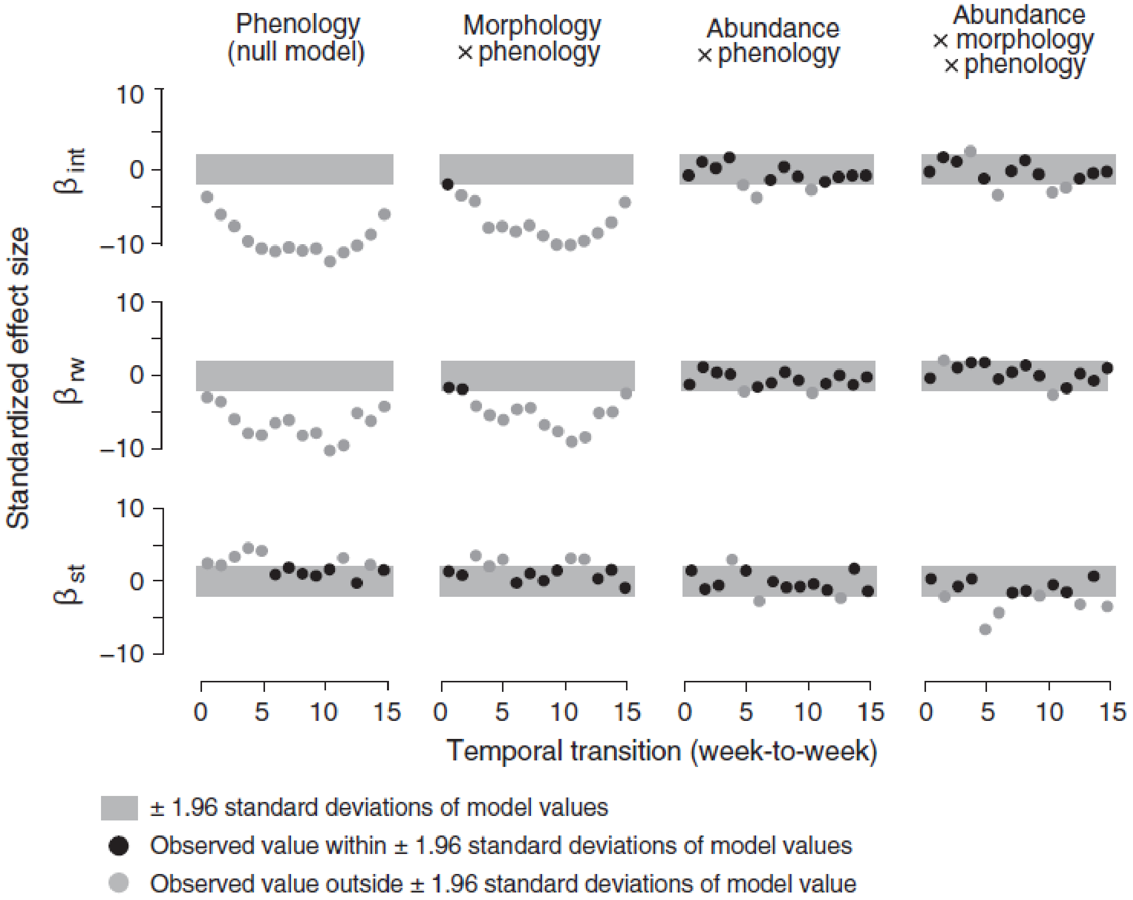
Network beta-diversity in time

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



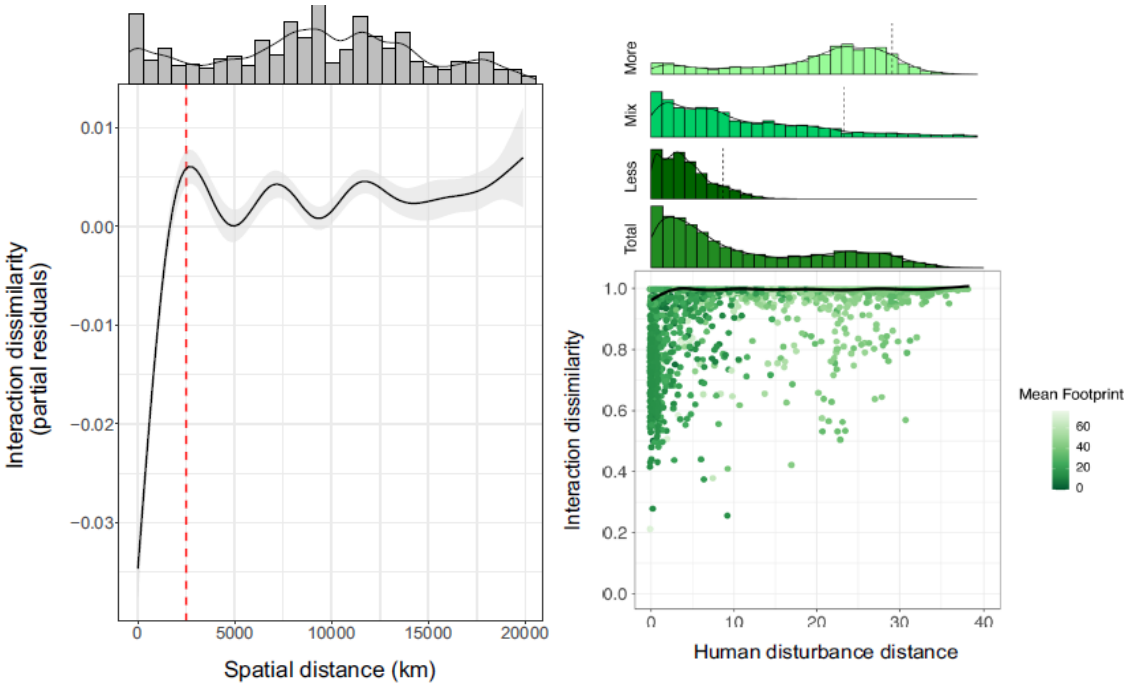


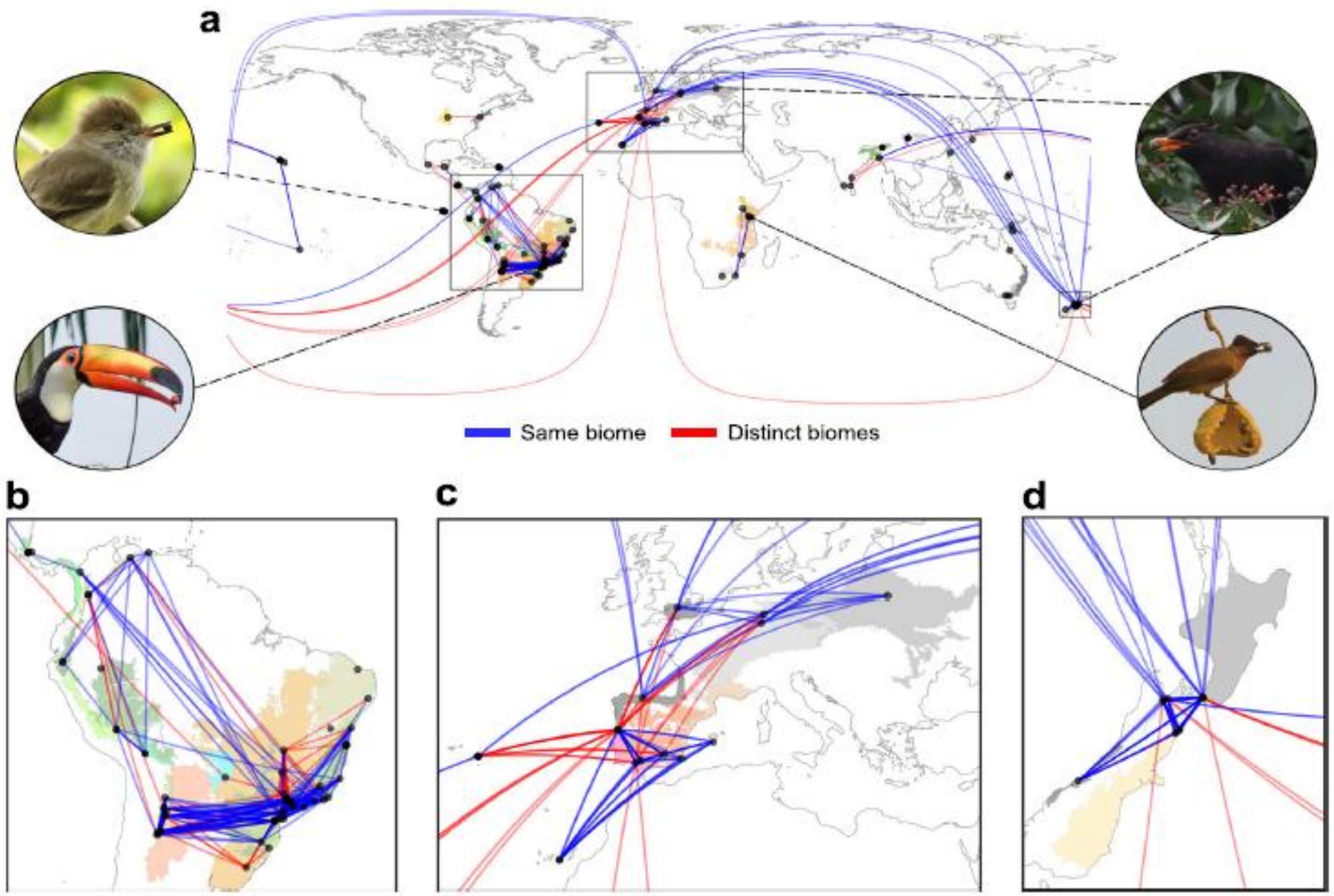
Network beta-diversity in space

Article https://doi.org/10.1038/s41467-022-34355-w

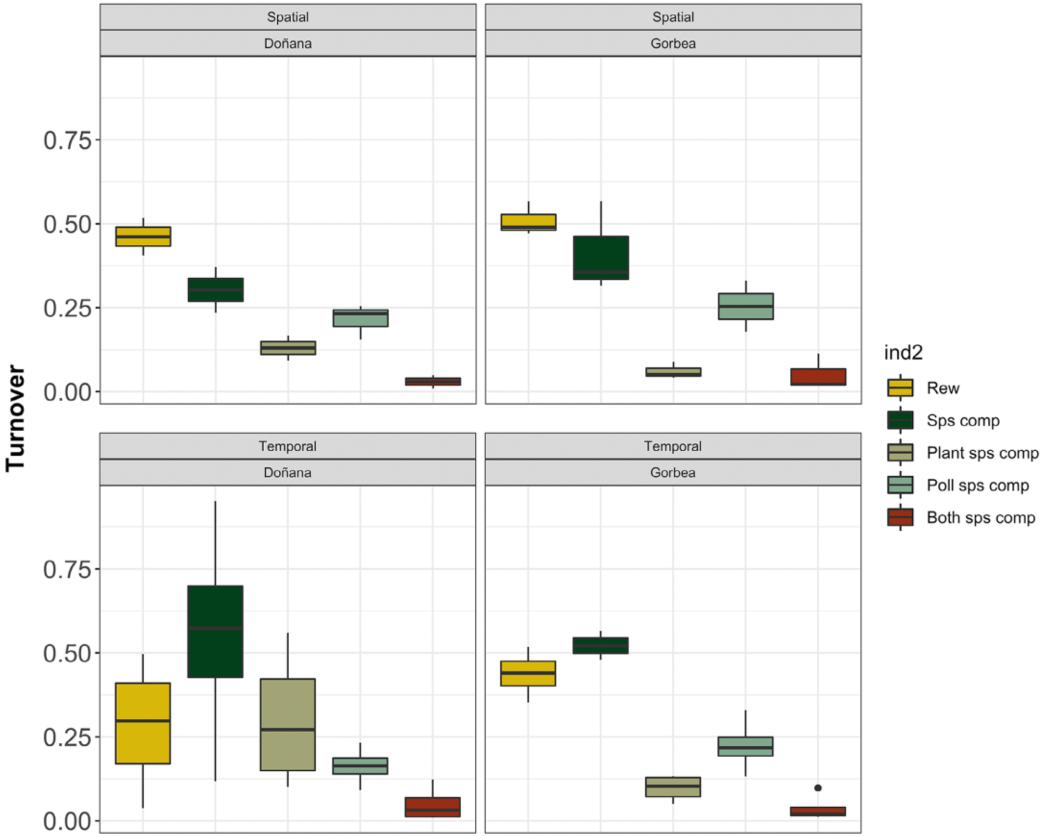
Global and regional ecological boundaries explain abrupt spatial discontinuities in avian frugivory interactions

Martins et al. 2022

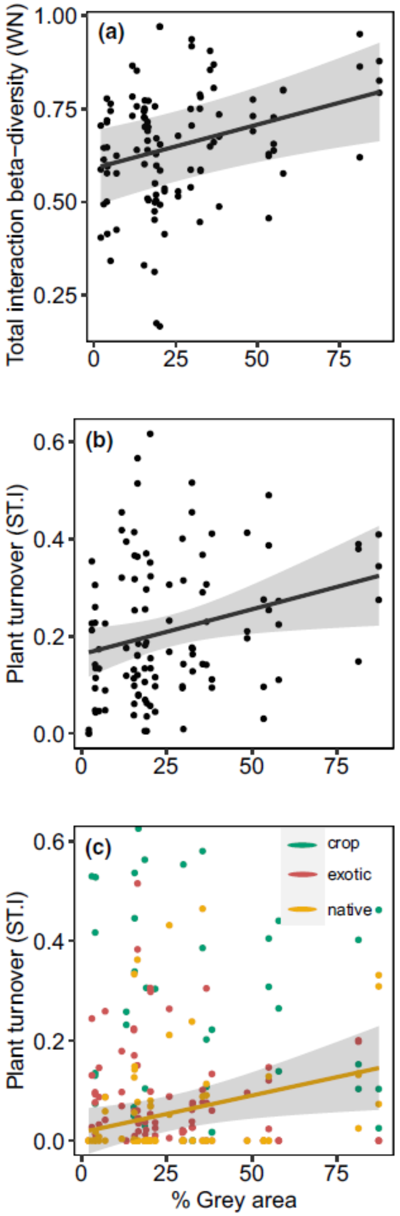


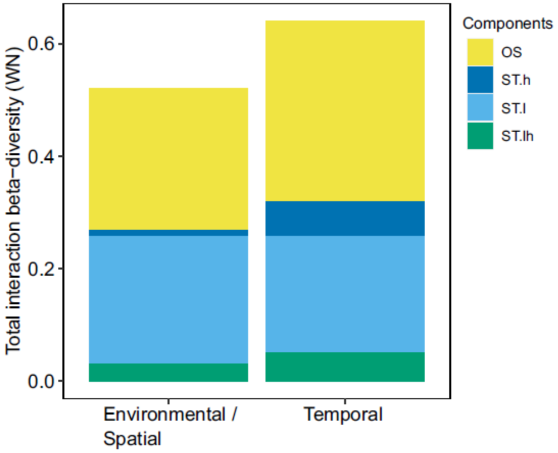


Beta-diversity of networks in space and time



Magrach et al. 2023





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?

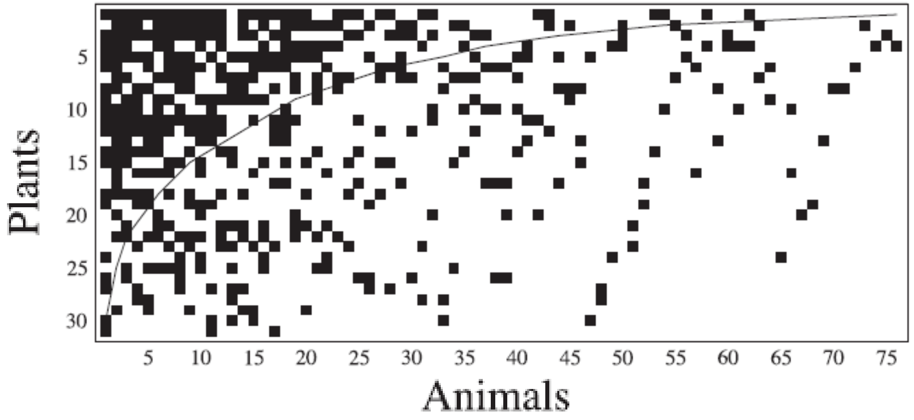
- Need to understand how species traits, abundances, environmental conditions affect such variations in space and time

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

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

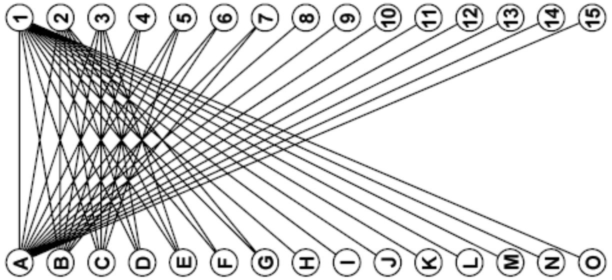
- Distribution of degrees and interaction strengths
- Looking for groups
- How networks vary in space and time
- **Comparing networks of different interaction types**

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

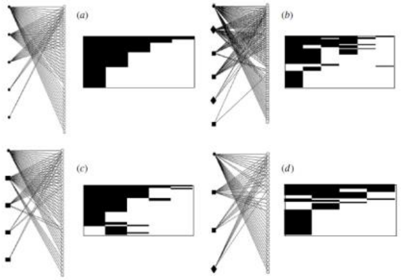
Bascompte et al. (2003)

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?

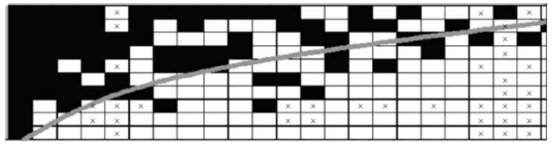
Paulo R. Guimarães Jr[1,2], Cristina Sazima[1], Sérgio Furtado dos Reis[1,*] and Ivan Sazima[1]



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

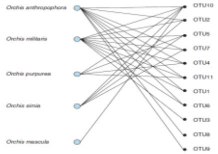
The Nested Assembly of Plant Facilitation Networks Prevents Species Extinctions

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

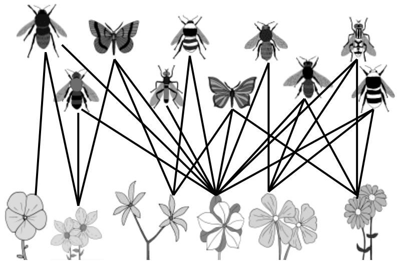
Low specificity and nested subset structure characterize mycorrhizal associations in five closely related species of the genus *Orchis*

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

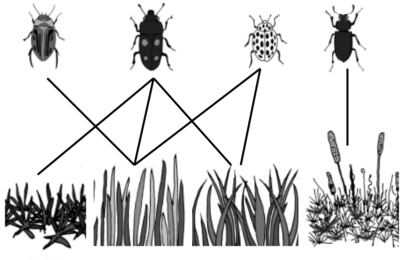


Comparing mutualistic and antagonistic webs: the example of plant-pollinator and plant-herbivore webs

Mutualistic



Antagonistic

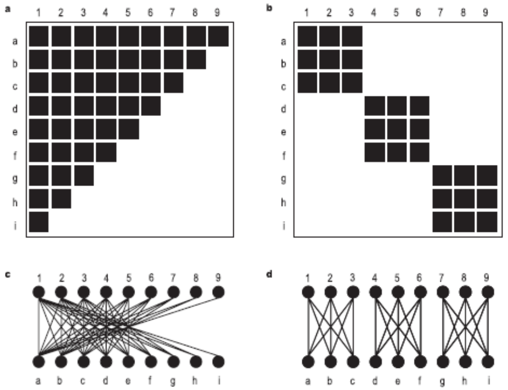


42 plant-pollinator webs

27 plant-herbivore webs

Higher connectance
Nested

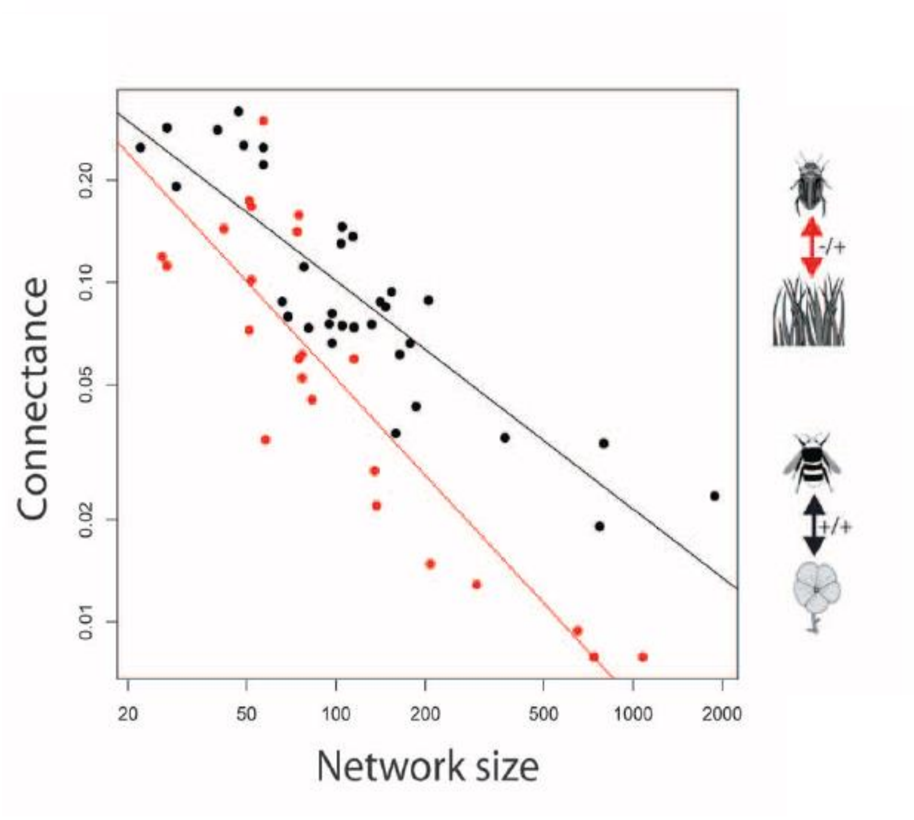
Bascompte et al. 2003



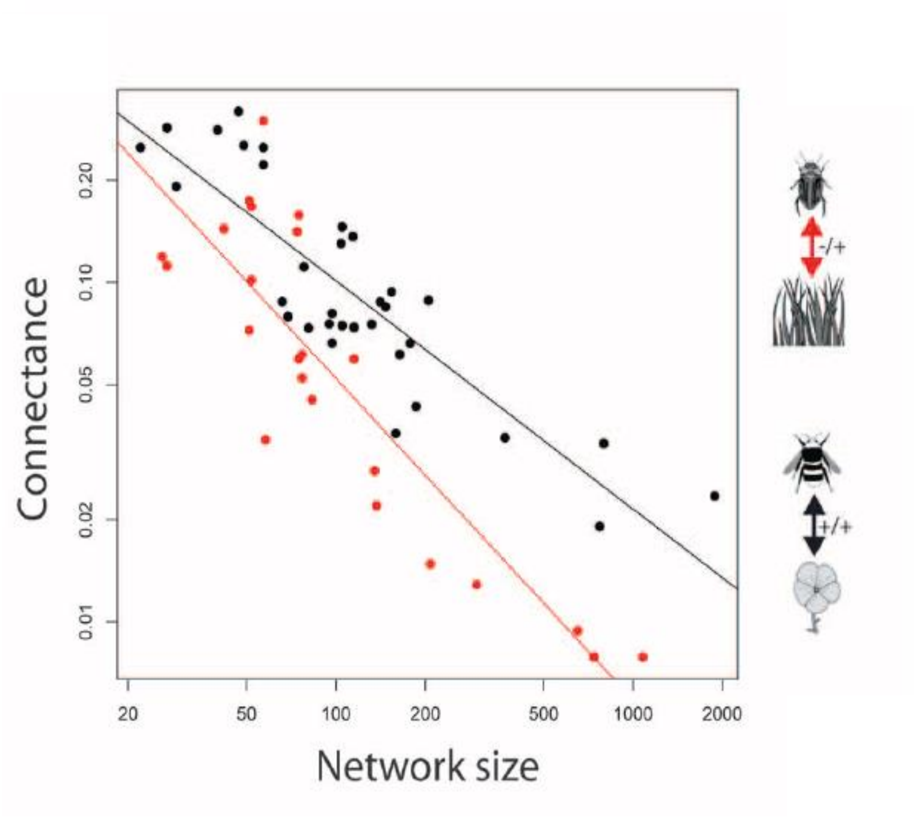
Lower connectance
Compartmented

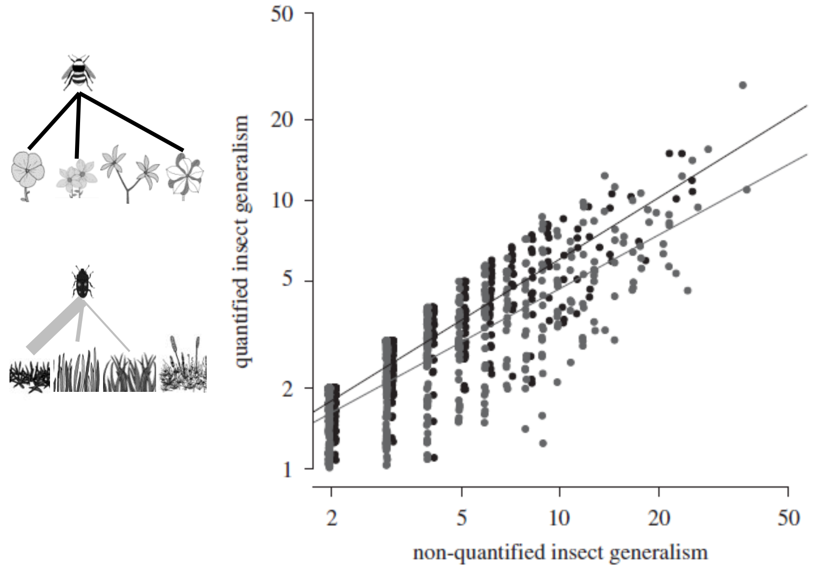
Lewinsohn et al. 2006

Connectance and interaction type



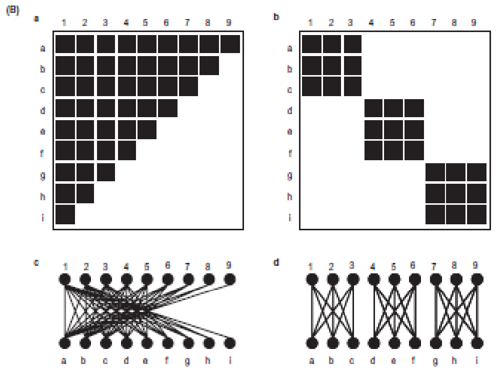
Connectance and interaction type

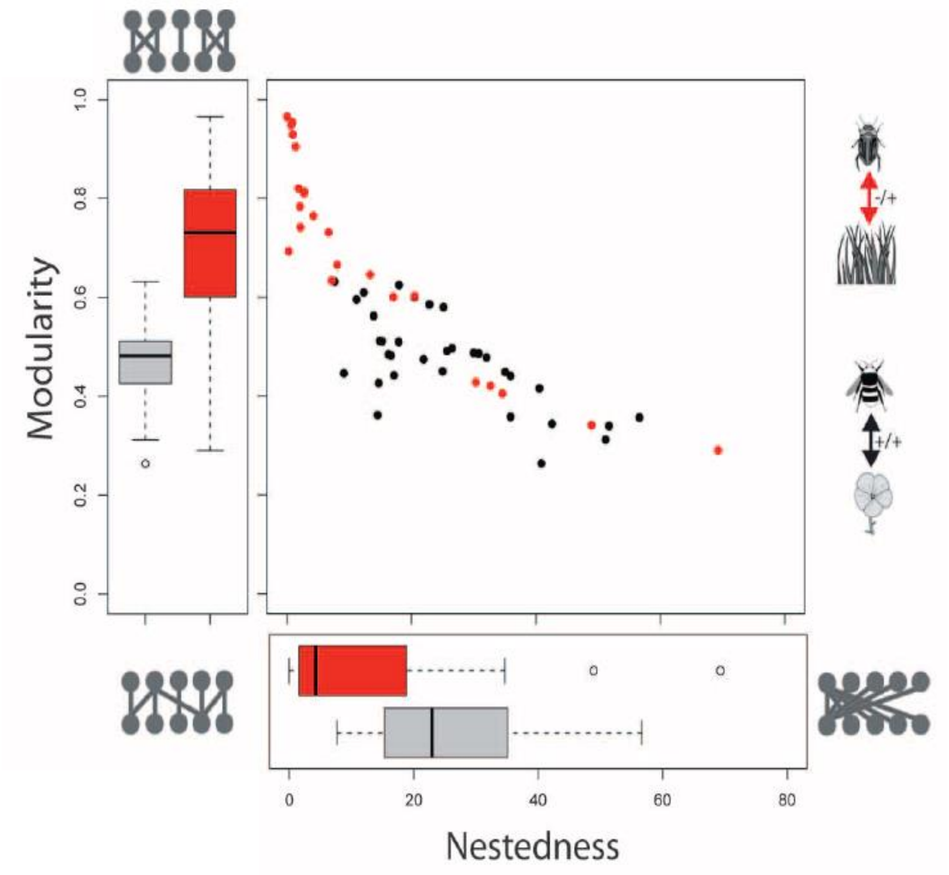




Fontaine et al. (2009) *Proc. R. Soc. B*

Nestedness and modularity





Thébault & Fontaine (2010) *Science*

Niche conservatism of mutualistic and antagonistic interactions

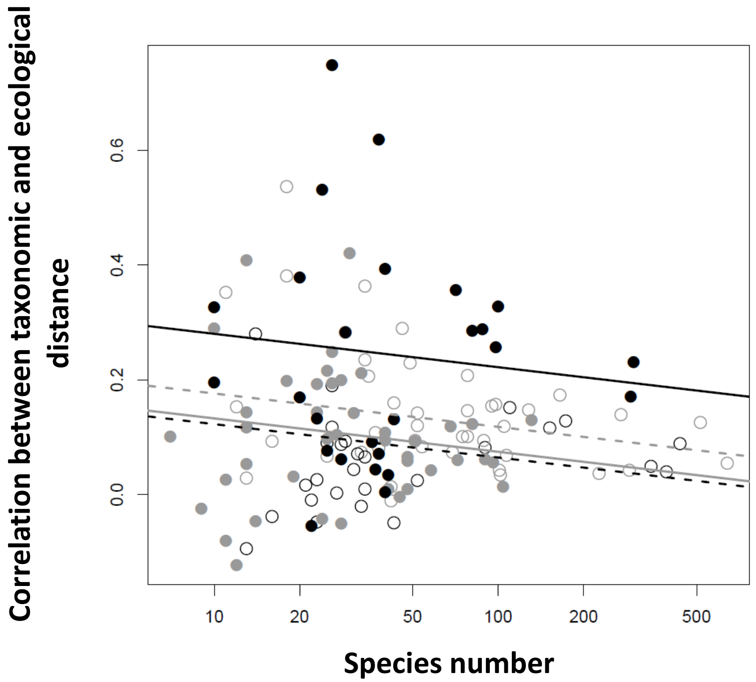
Niche conservatism: tendency of related species to share interaction partners

Niche conservatism of mutualistic and antagonistic interactions

Niche conservatism: tendency of related species to share interaction partners

Proportions of networks of each type with a significant correlation between taxonomic and ecological distance matrices:

	Pollination networks	Herbivory networks
Insect side	0.80	0.43
Plant side	0.51	0.58

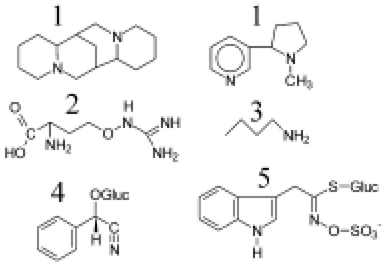


Fontaine & Thébault 2015

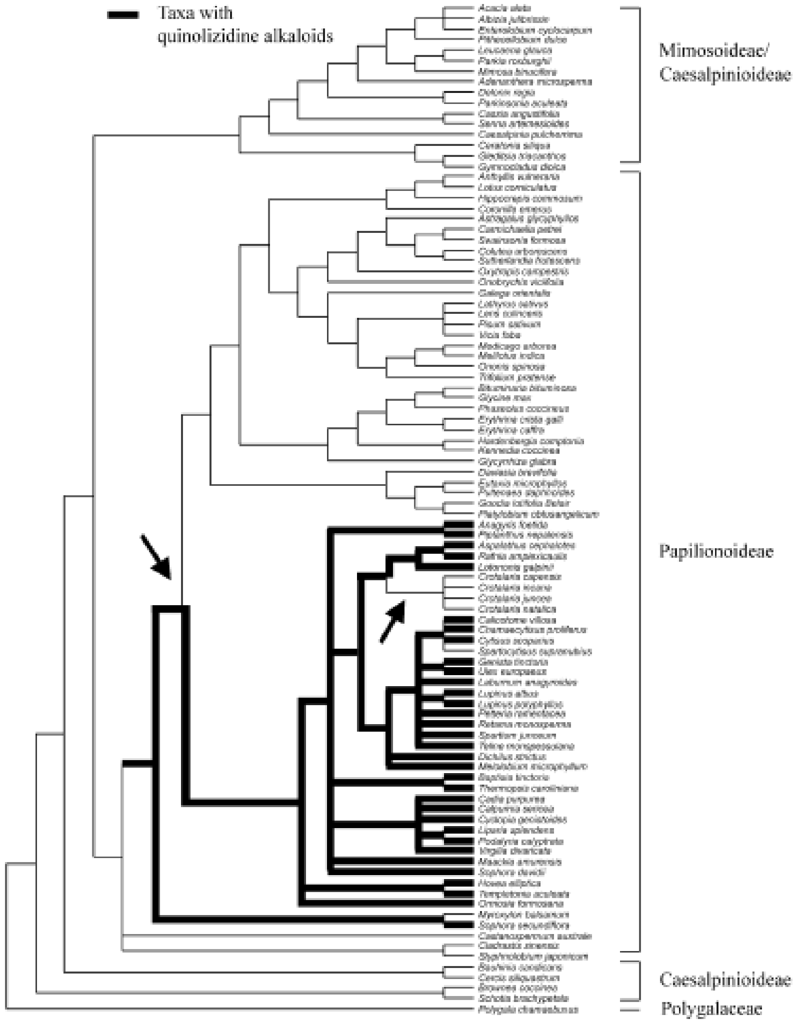
The structure of plant-insect networks partly depends on the type of interaction considered (mutualism or antagonism)

What could explain these different structures?

- Different plant traits involved in these interactions



Wink (2003)



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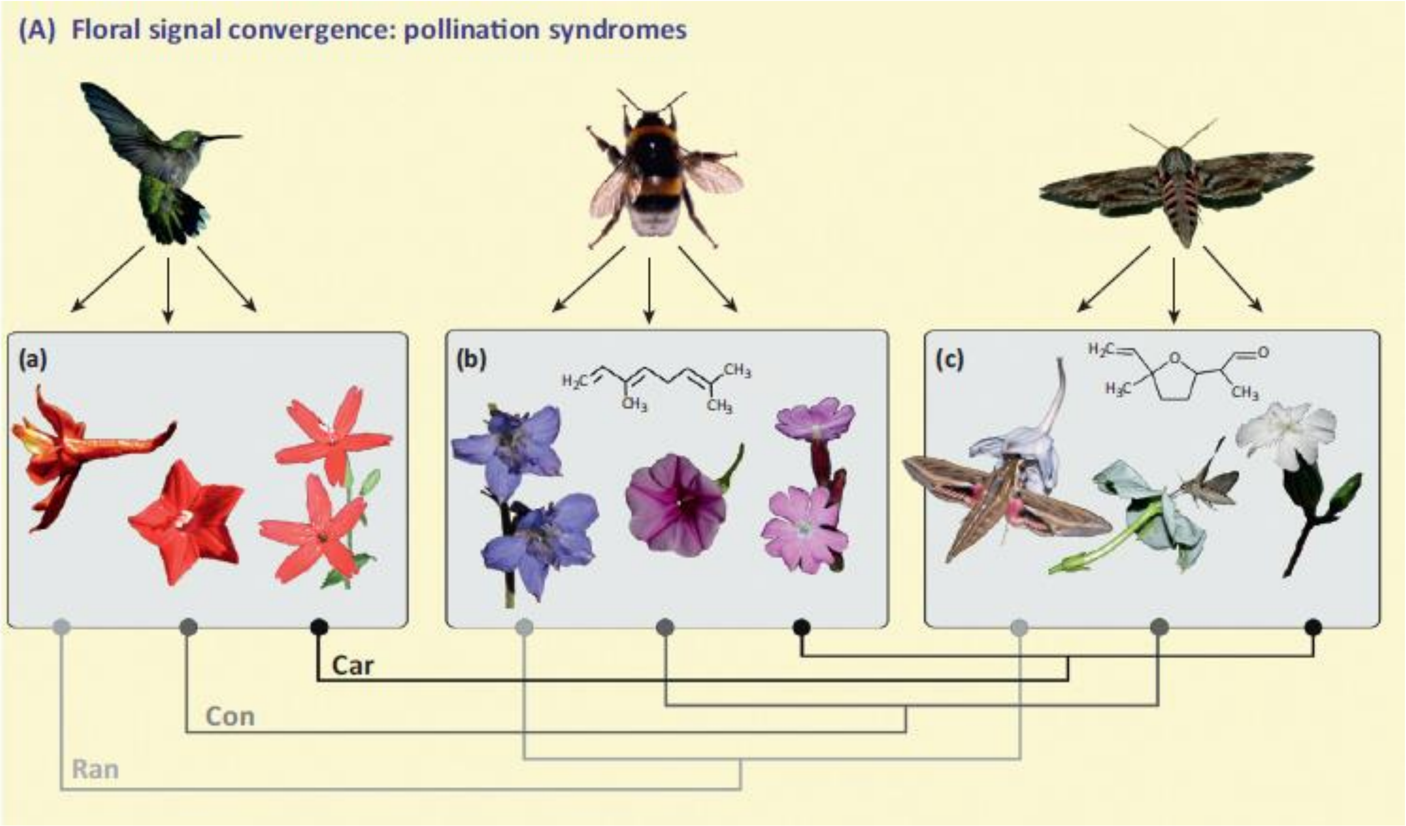

Schiestl and Johnson (2013)

What could explain these different structures?

- Evolutionary and neutral processes

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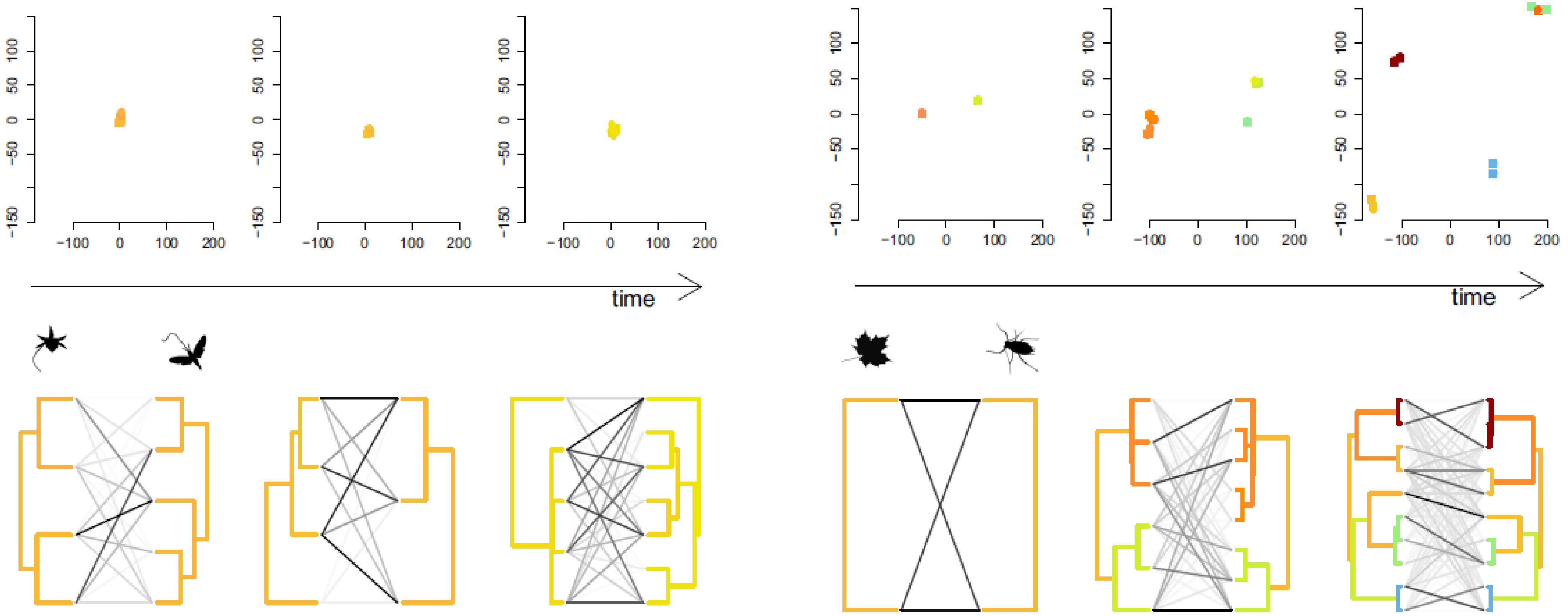
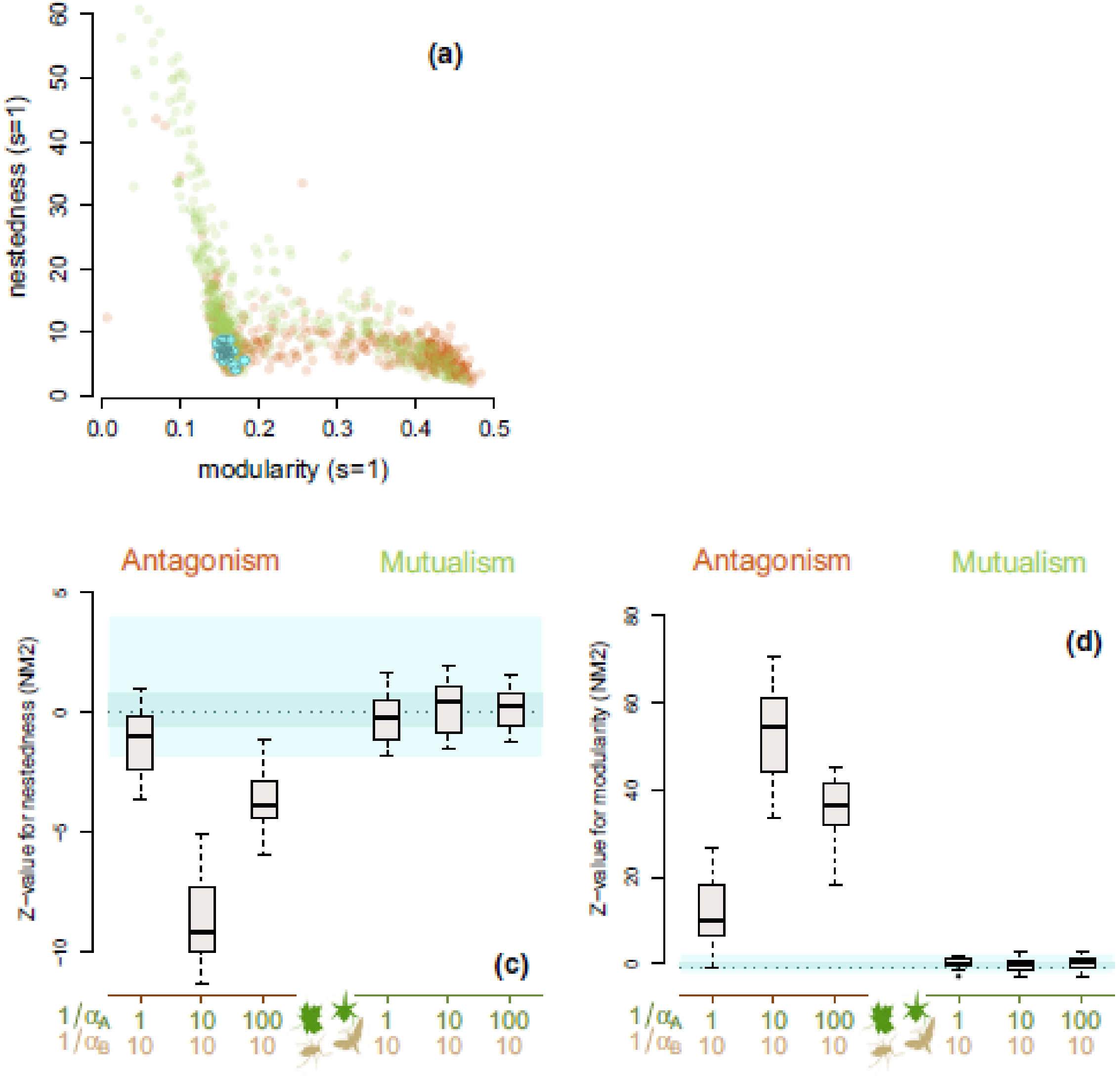
- Evolutionary and neutral processes



Maliet et al. (2020)

What could explain these different structures?

- Evolutionary and neutral processes



Maliet et al. (2020)

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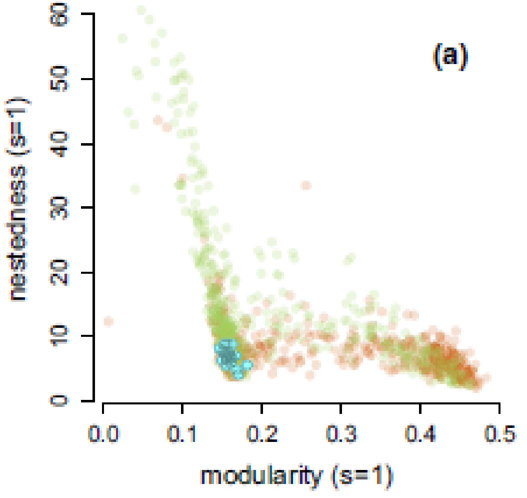
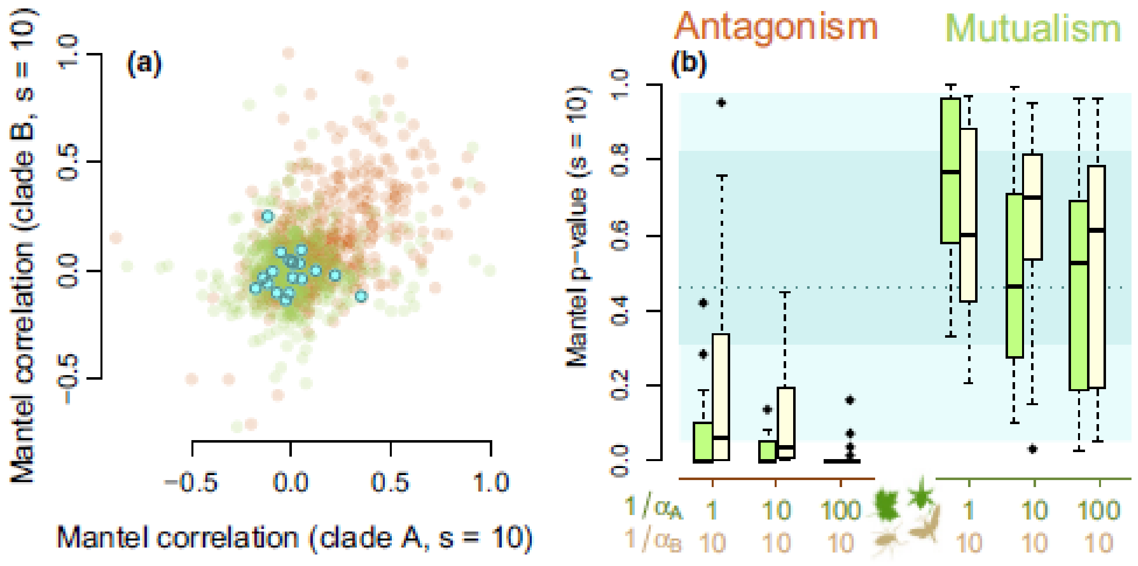
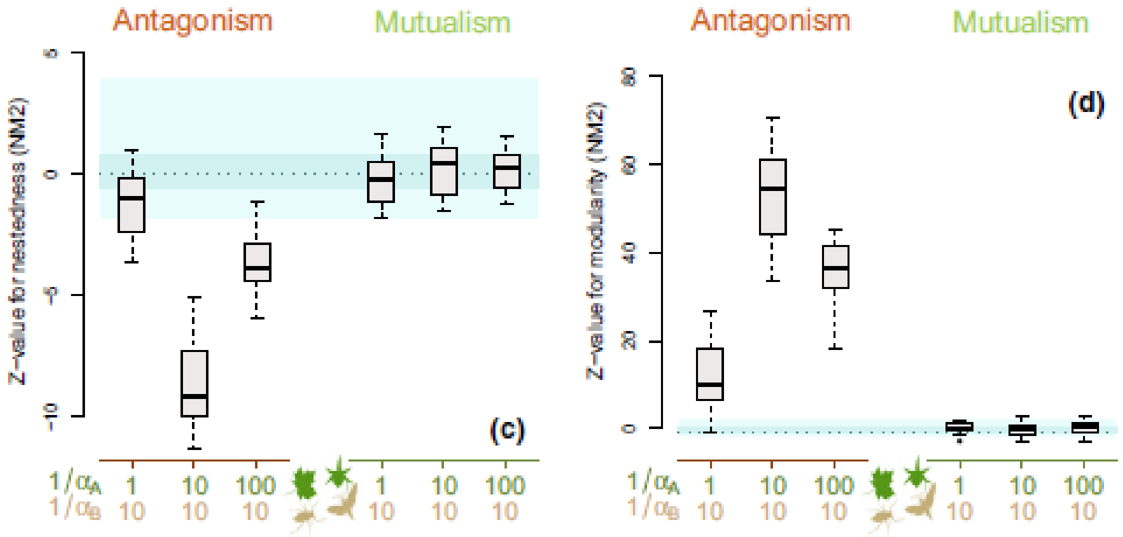






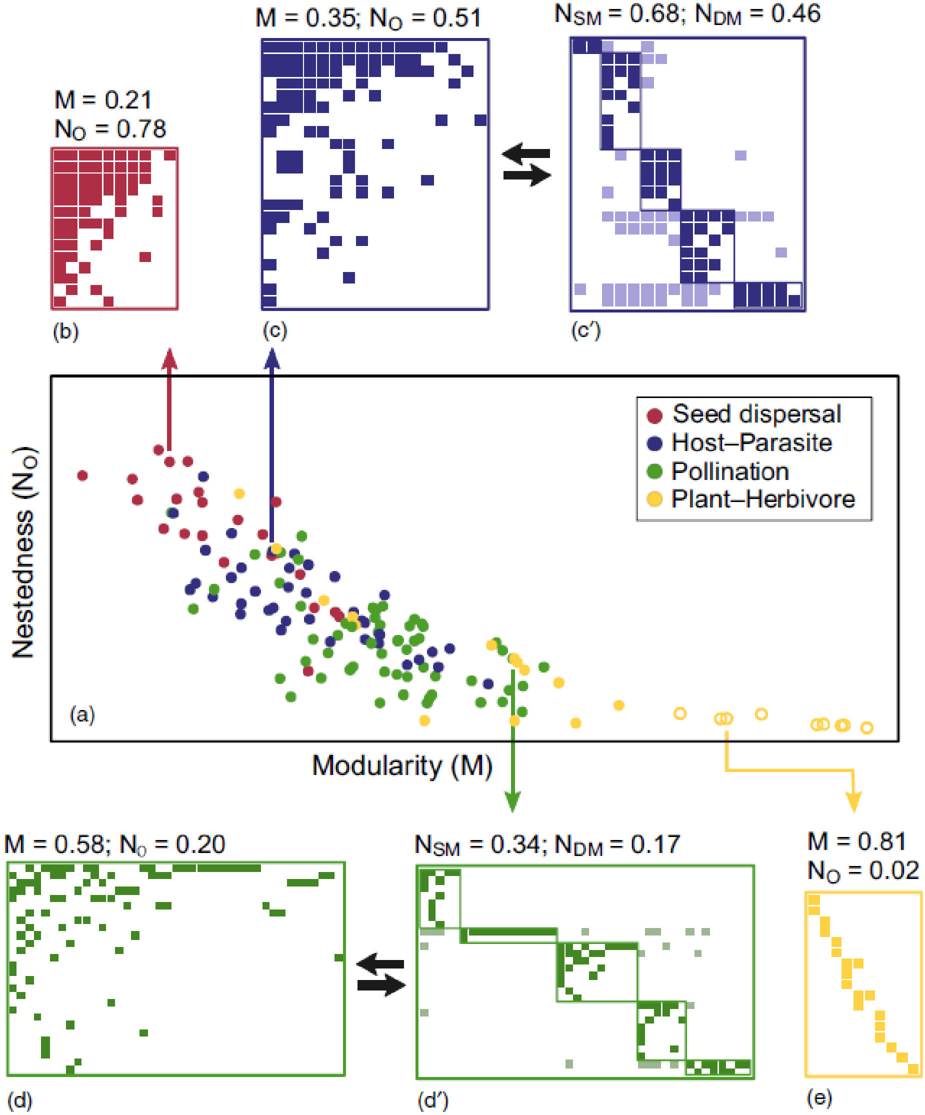
Maliet et al. (2020)

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

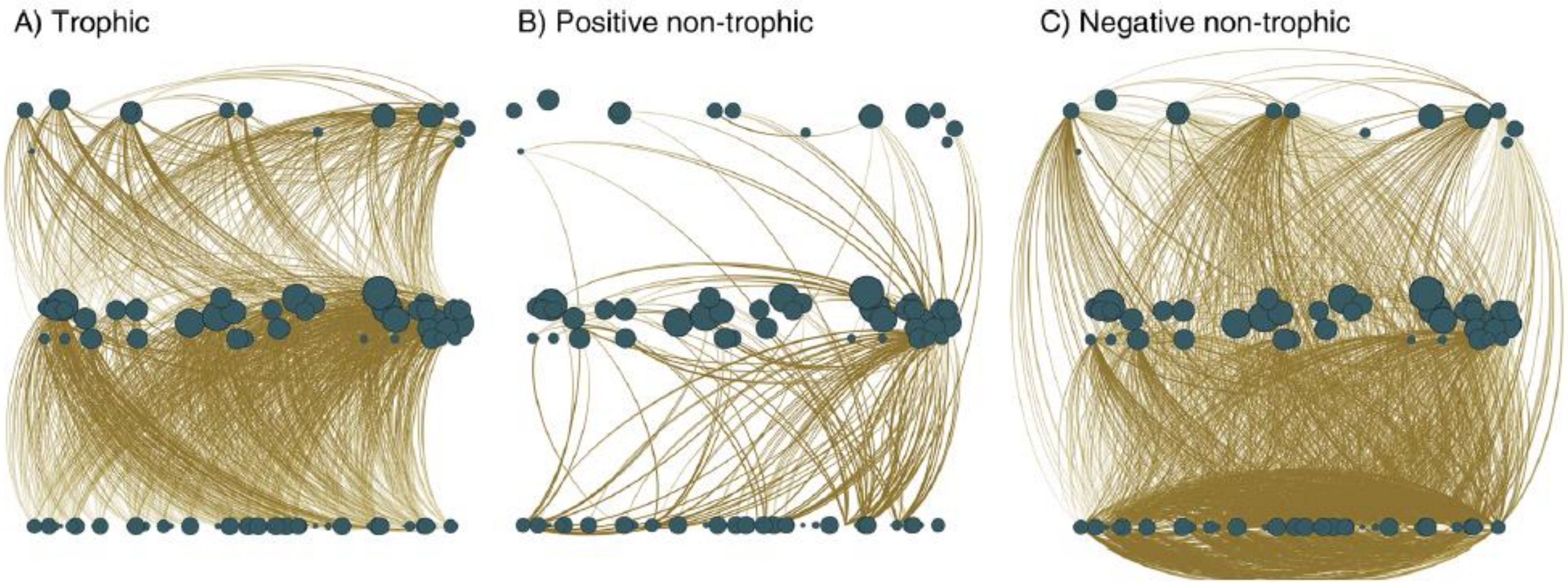


Pinheiro et al. (2022)

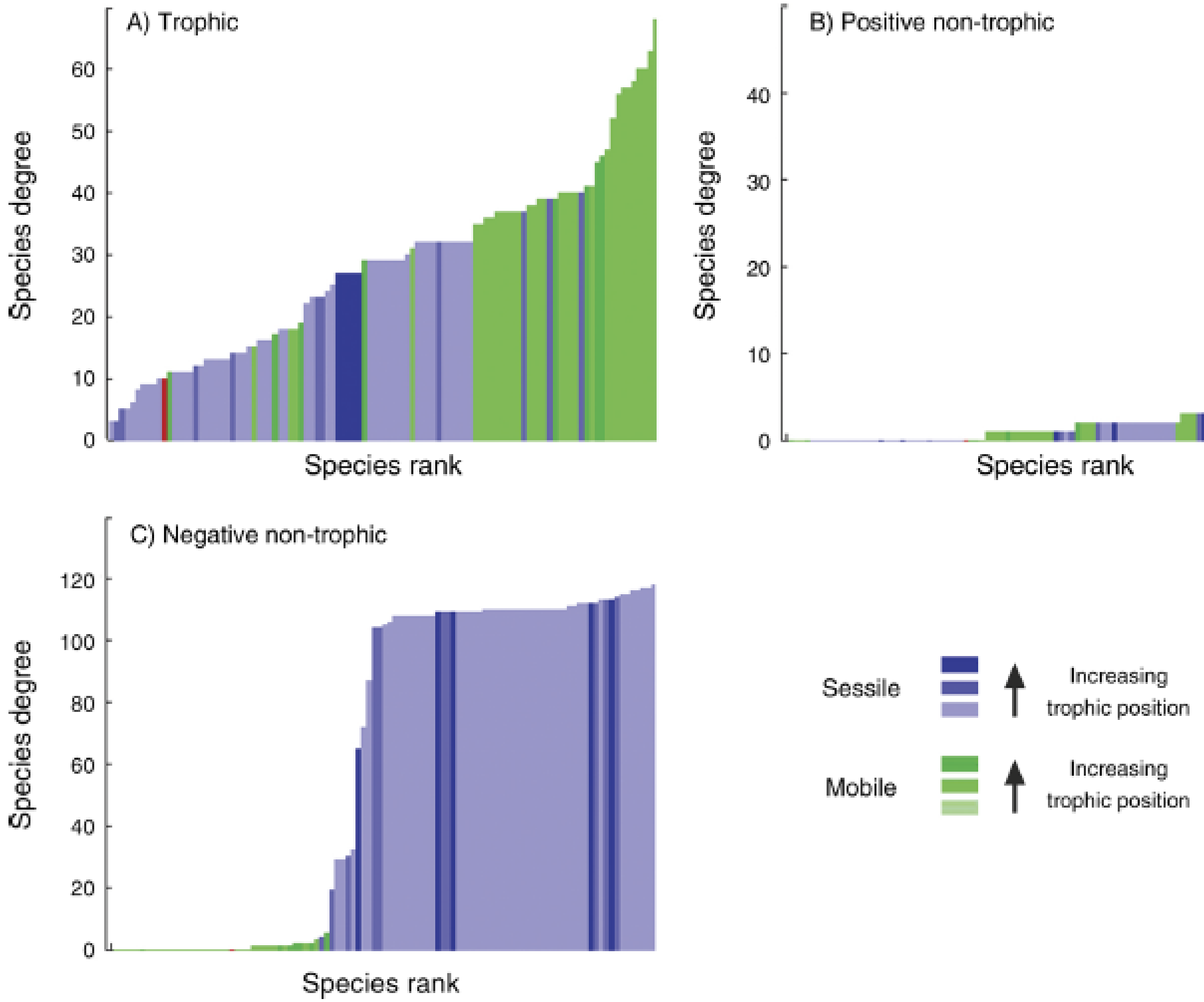
Does the structure of ecological networks differ between different types of interactions? Conclusion and perspectives

- 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?