Implications of eco-evolutionary dynamics for the structure and functioning of ecological networks

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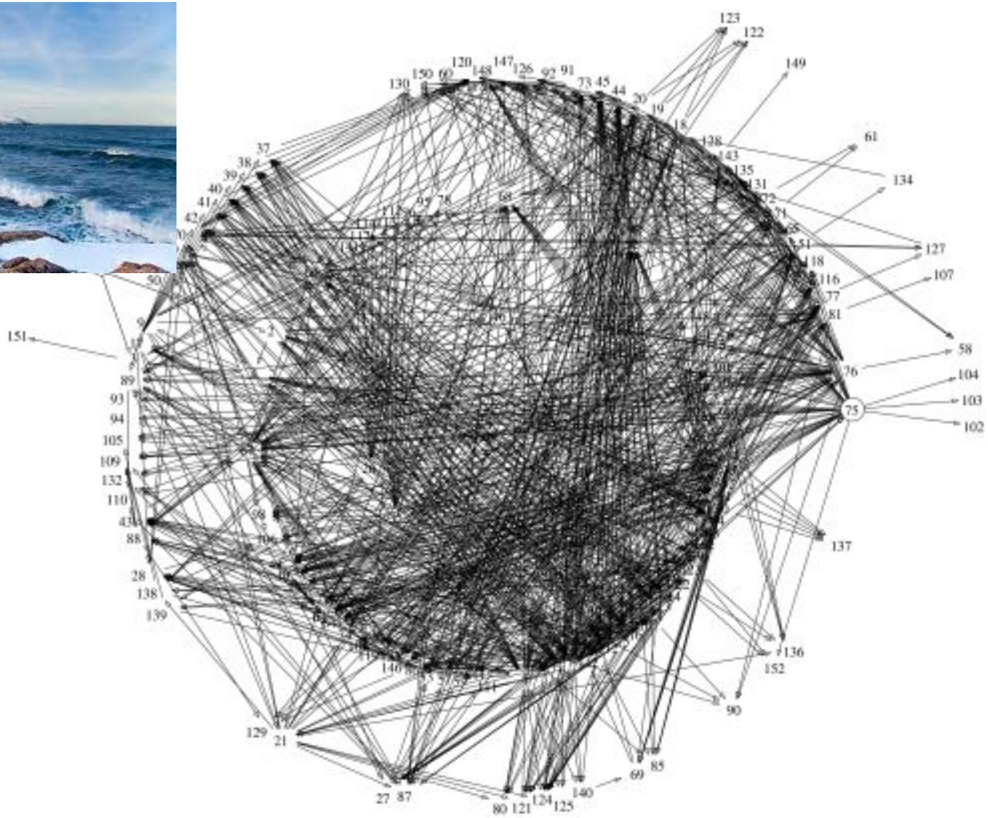
A look back on the diversity-stability debate



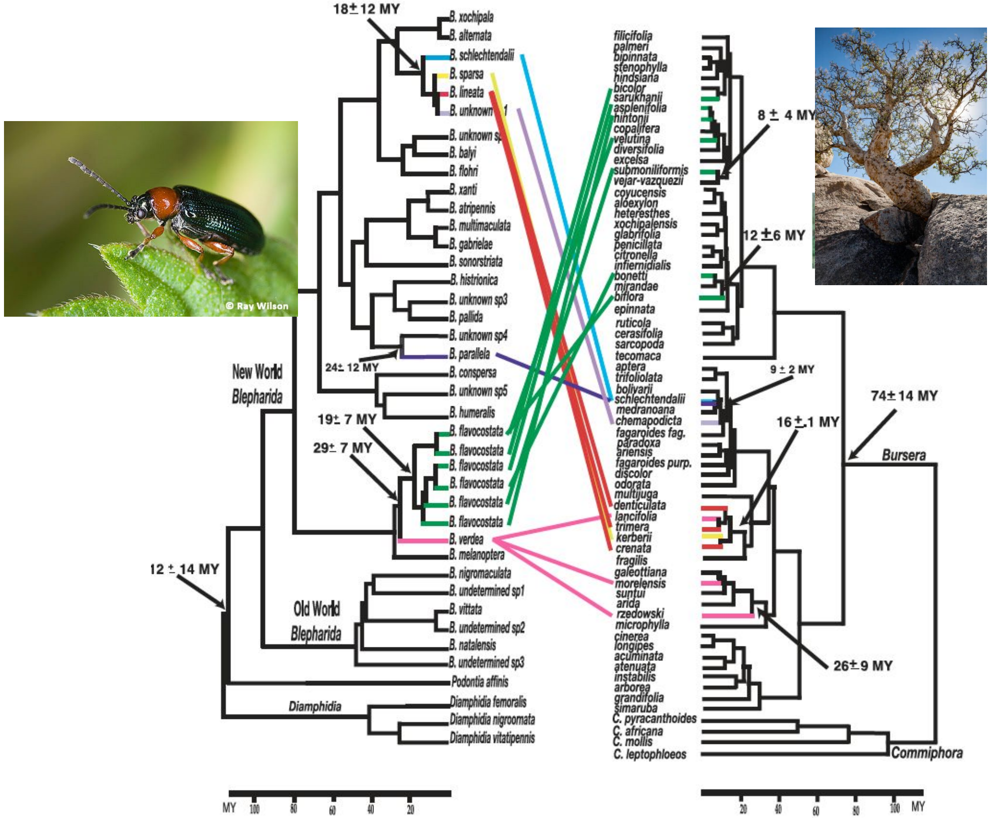
Bodini et al 2009

-Random approach (eg, May 1972): $$s\sqrt{kC} < 1$$

-Role of network structure:
*modularity (eg, Krause et al 2003)
*nestedness (Bascompte et al 2006)

-of the distribution of interaction strength (McCann et al 1998, Neutel et al 2002)

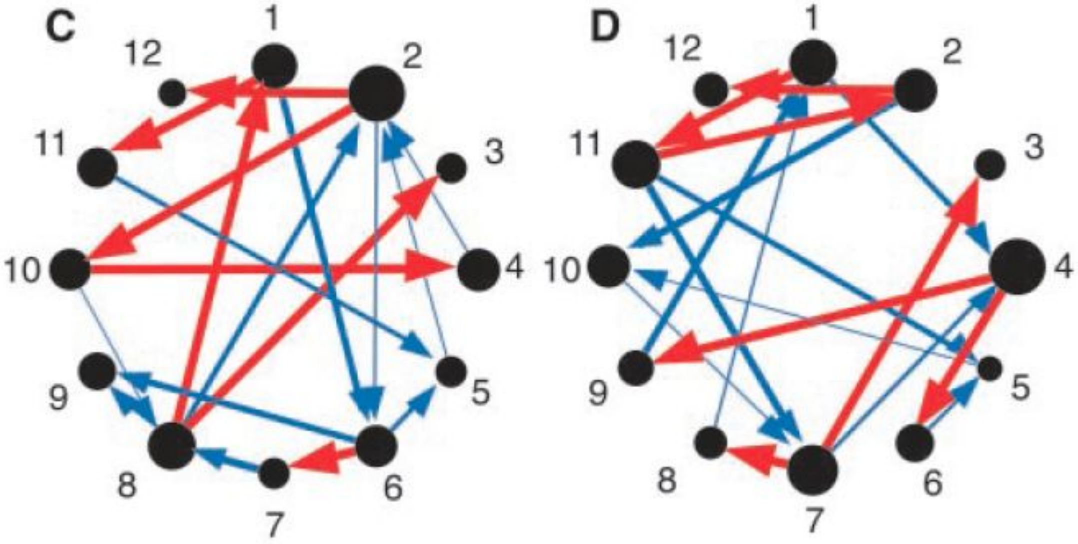
Evolution influences the possibility of interactions



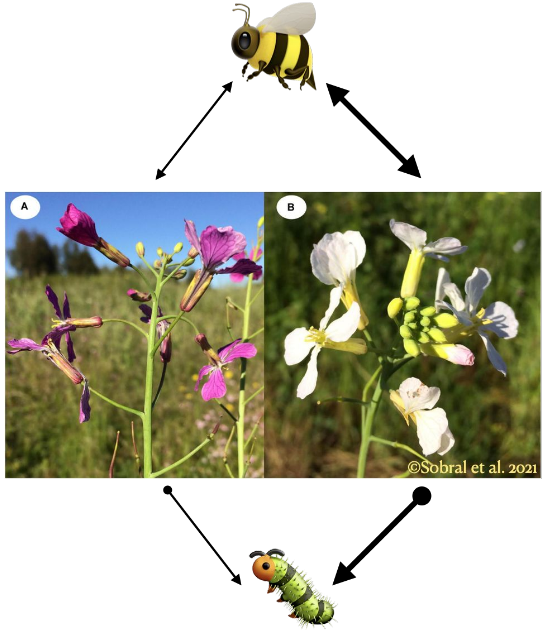
Prediction of interactions based on trait matching

Congruent diversification of plant defenses and herbivorous insects (Ehrlich & Raven 1964, here Becerra et al 2003)

Evolution influences interaction strength



Adaptive foraging of predators (eg, Kondoh 2003)



Intensity of antagonistic vs mutualistic interactions (Irwin & Strauss 2003)

Preliminary remarks & key questions

- Evolutionary dynamics likely affect all components of stability conditions
- Most eco-evolutionary works are on one species or small modules
    - How do these dynamics scale up at the network level?
- What kind of network structures emerge from eco-evolutionary dynamics? Relevance?
- Implications from a functional point of view?
- Implications for the resilience of networks in a disturbed world?

Plan

1. What phenotypic traits should we use?
2. Evolution of body size (mass) and emergent properties of trophic networks
3. Evolution of bipartite networks in mutualistic vs antagonistic interactions
4. Effects of global changes on network eco-evolutionary dynamics

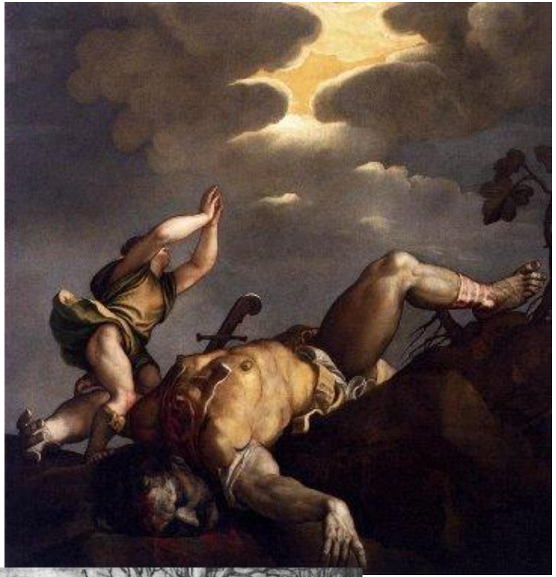
Choice of traits: a dichotomy

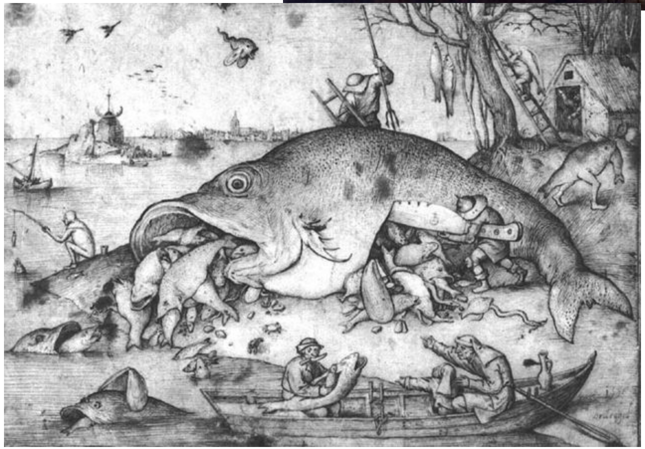
- "Statistical" approach: interactions based on a large number of traits (eg, webworld (Caldarelli et al 1998, Drossel et al 2000), matching model (Rossberg et al 2006))
- Coevolution of few traits (usually one) (Loeuille & Loreau 2005, Kondoh 2003, Allhoff et al 2015)

A need to choose the most relevant trait! (see also Loeuille & Loreau 2009, Loeuille 2019)

The most usual suspect: body size

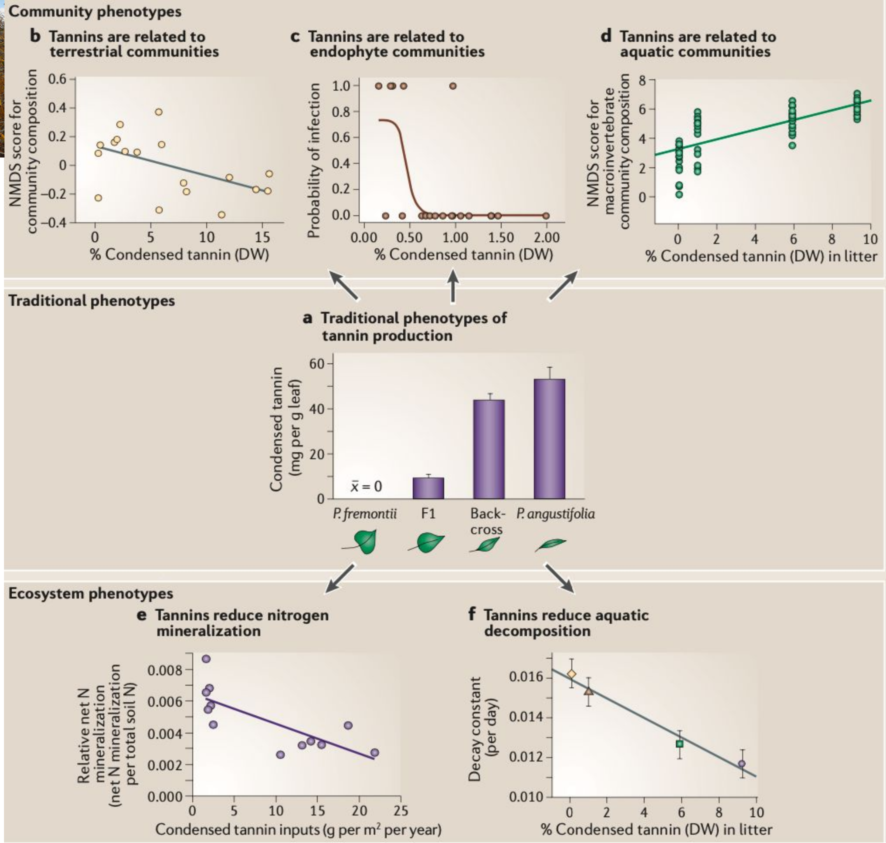
- Constrains many aspects of the species ecology (Peters et al 1983)
- Linked to metabolic demands (Brown et al 2004)
- As such constrains basic life-history traits, but also interspecific interactions
- Variations observed within (Branco et al 2020) or between species (Naisbit et al 2011)





Plant defenses

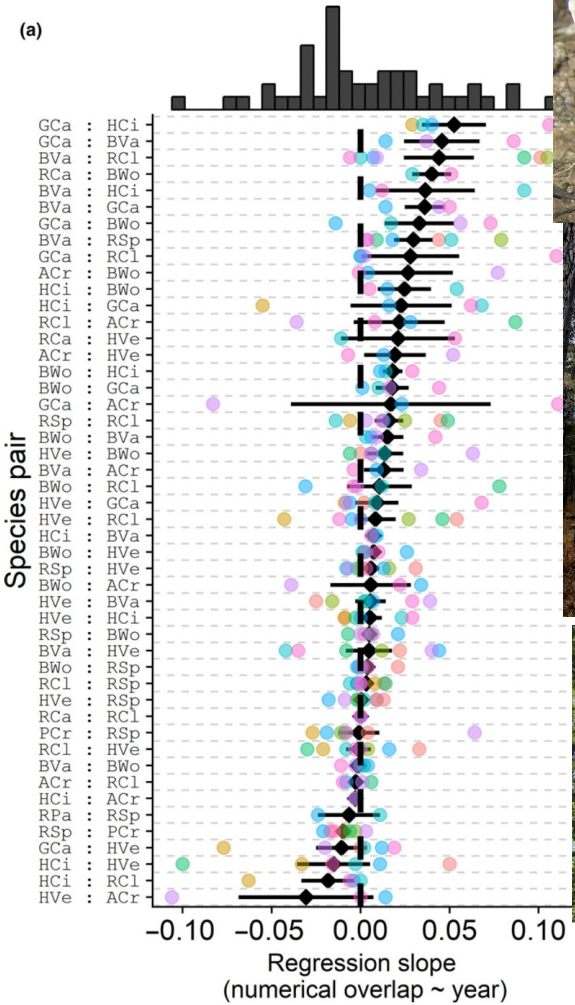
- Diversity and links with species diversity (Ehrlich & Raven 1964)
- Limit transmission of energy upward (White 2003, Loeuille & Loreau 2004)
- Defenses can be overturned and used as weapons (van der Meijen et al 1996, Renwick et al 2002)
- Side-effects on many structural and functioning aspects (Whitham et al 2003, 2006)



Whitham et al 2006

Species phenologies

- phenology: timing and periodicity of various steps of the life-cycle (eg, egg laying date, flowering period, migration date)
- Basic: interaction if active at the same time!
- All interactions are concerned! mutualism: pollination mismatch (Kudo & Ida 2013); competition based on phenology overlap (Carter et al 2018); predation: budburst-caterpillar-great tit-hawk (Both et al 2009)



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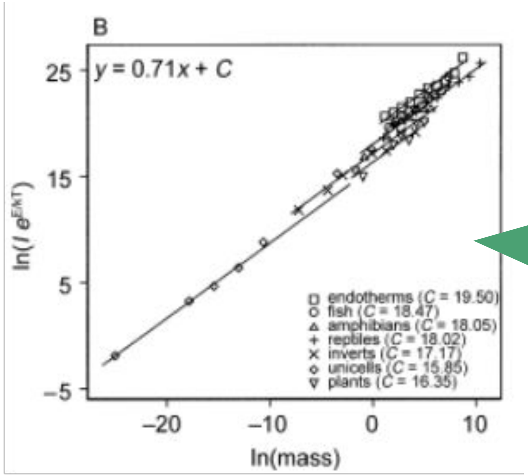
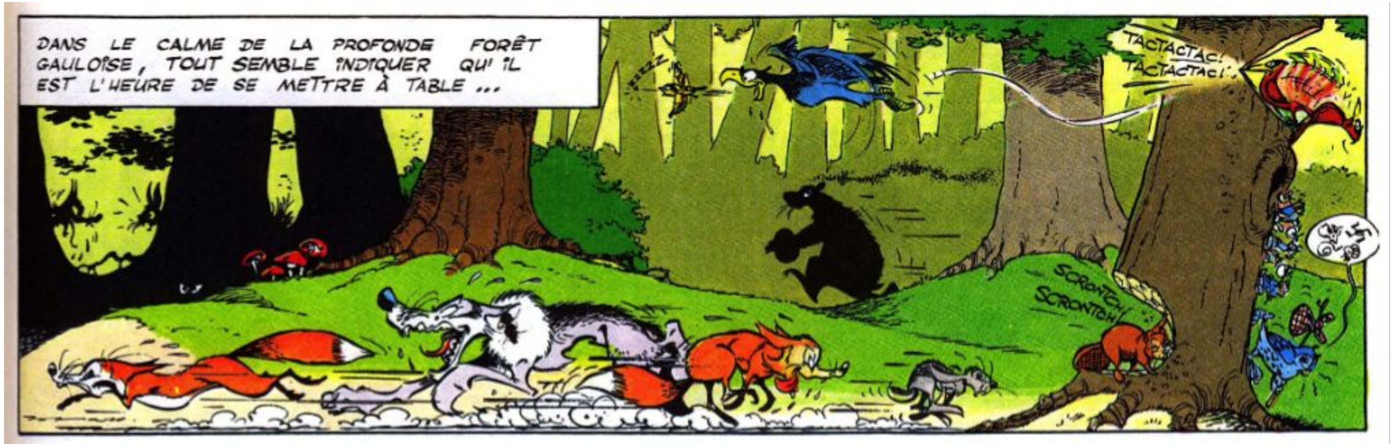


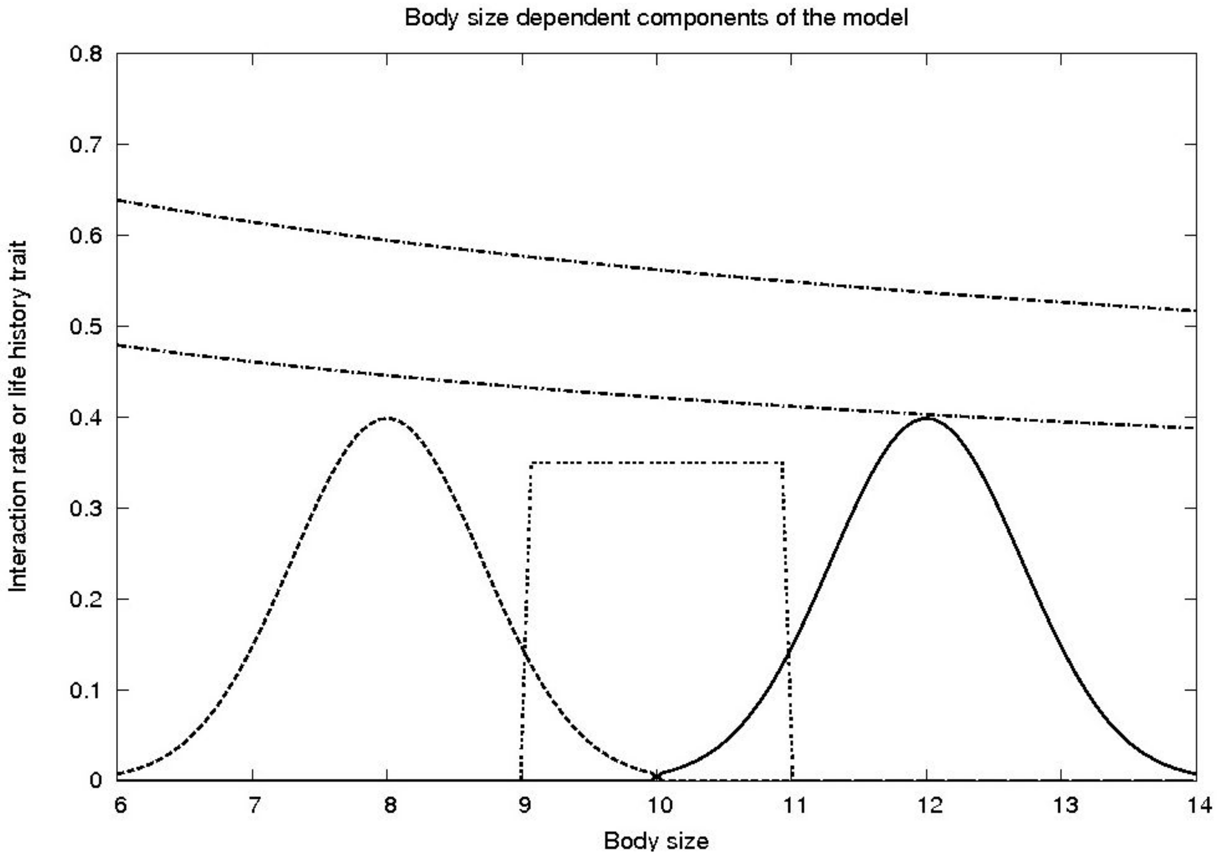
THV (eg, Brown et al. 2004)

Body size

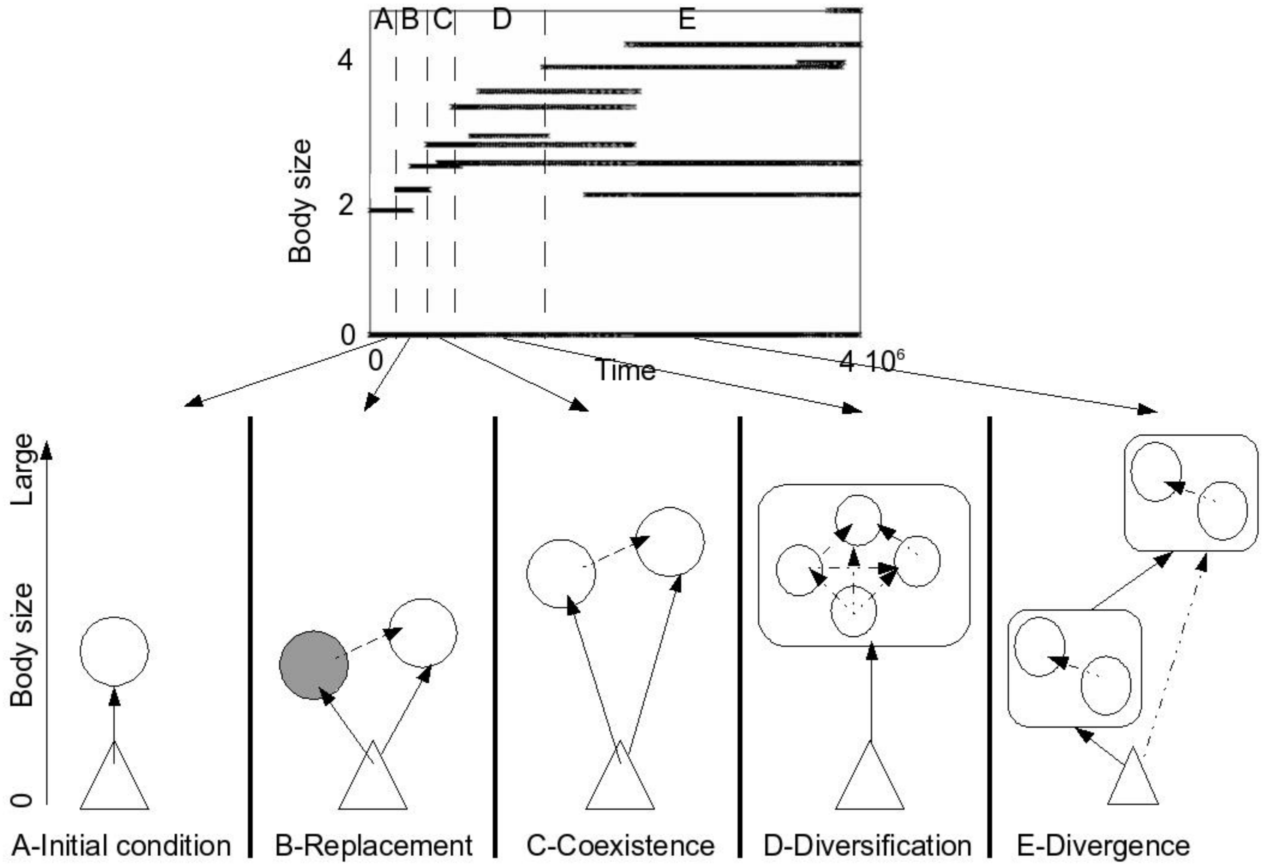
Competition (eg, Bowers & Brown 1982)



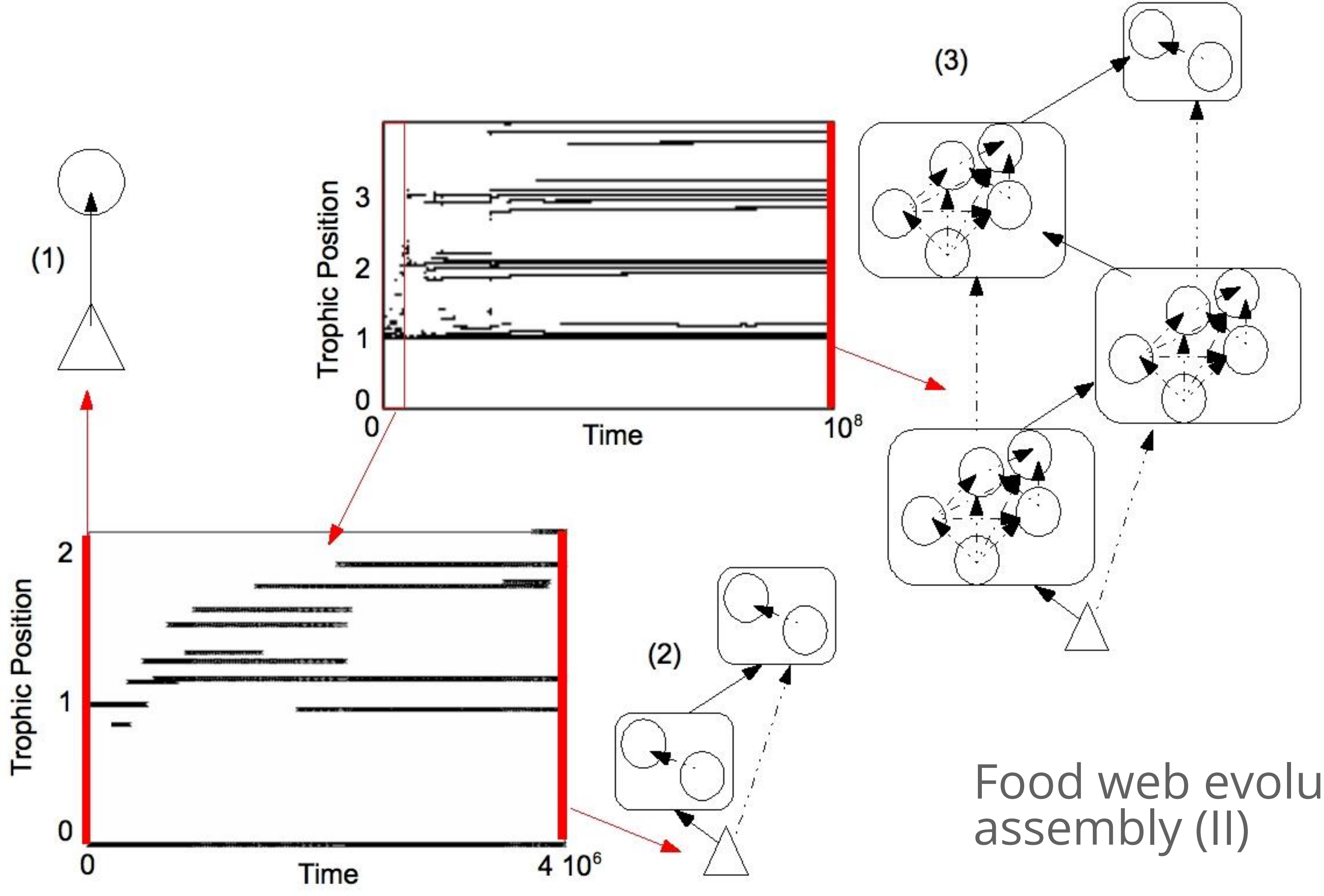
Trophic interactions (eg, Naisbit et al 2011, Brose et al 2006)



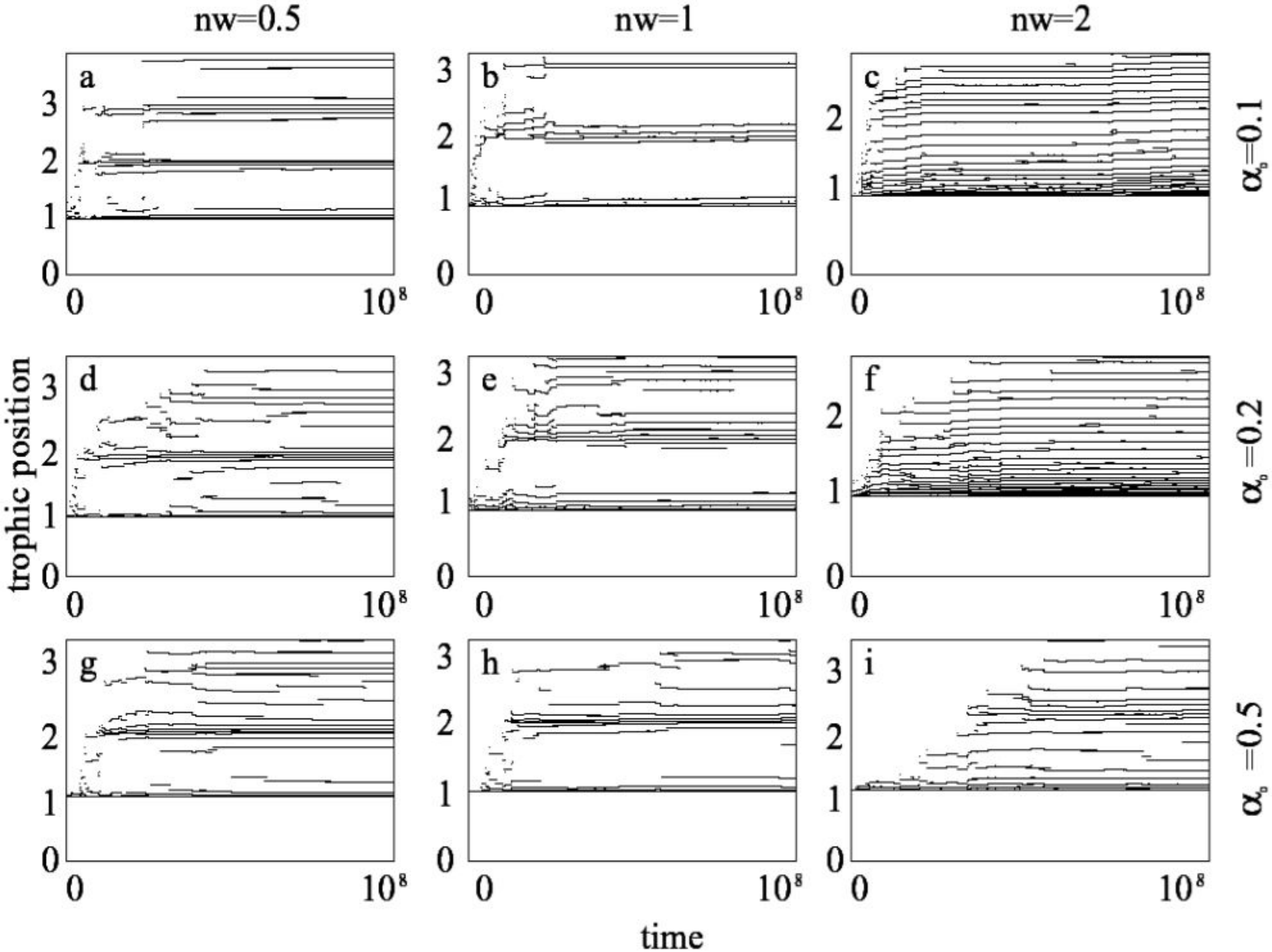
Body size in the model (Loeuille & Loreau 2005)



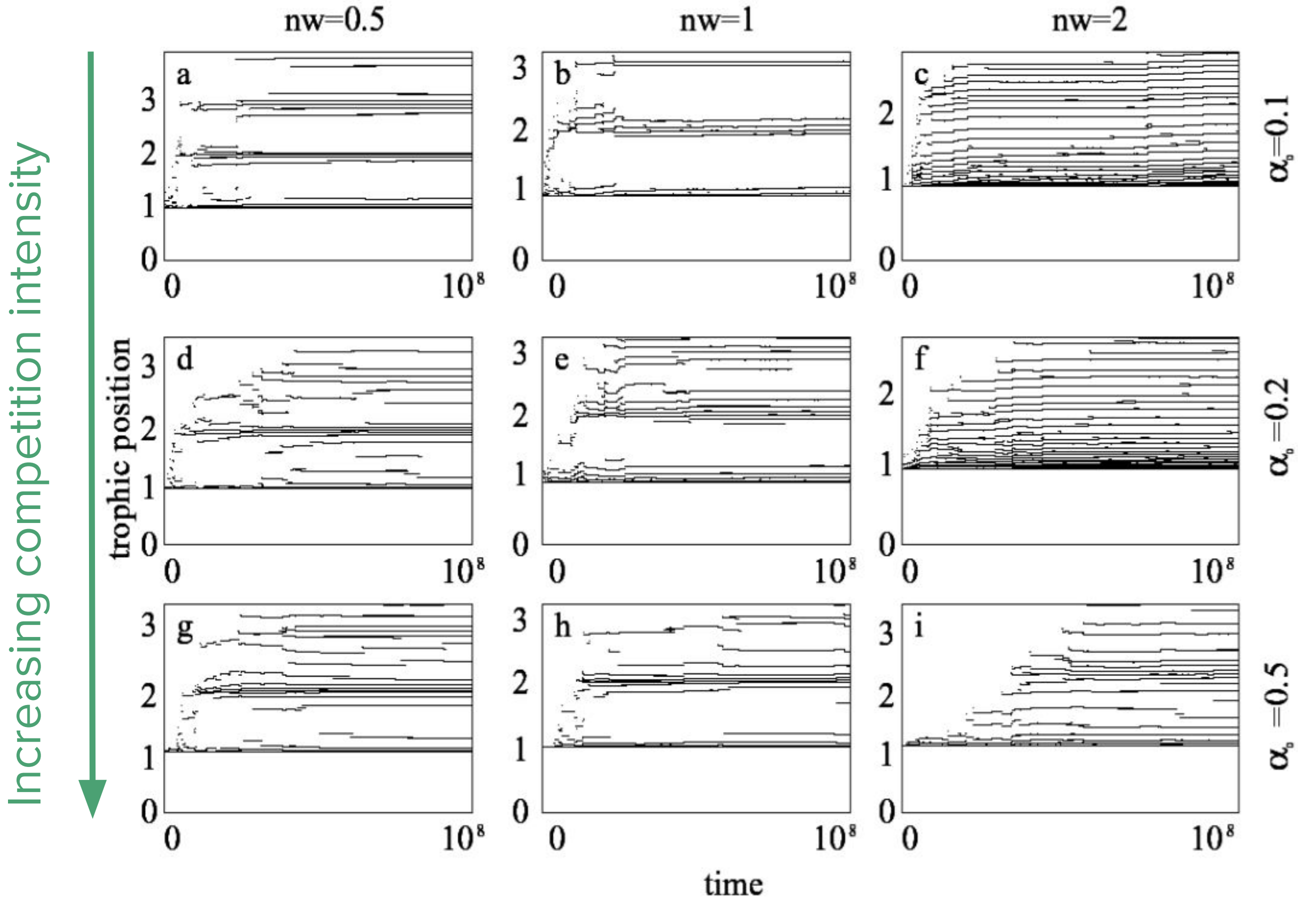
Food web evolutionary assembly



Food web evolutionary assembly (II)



Variability of possible trophic structures



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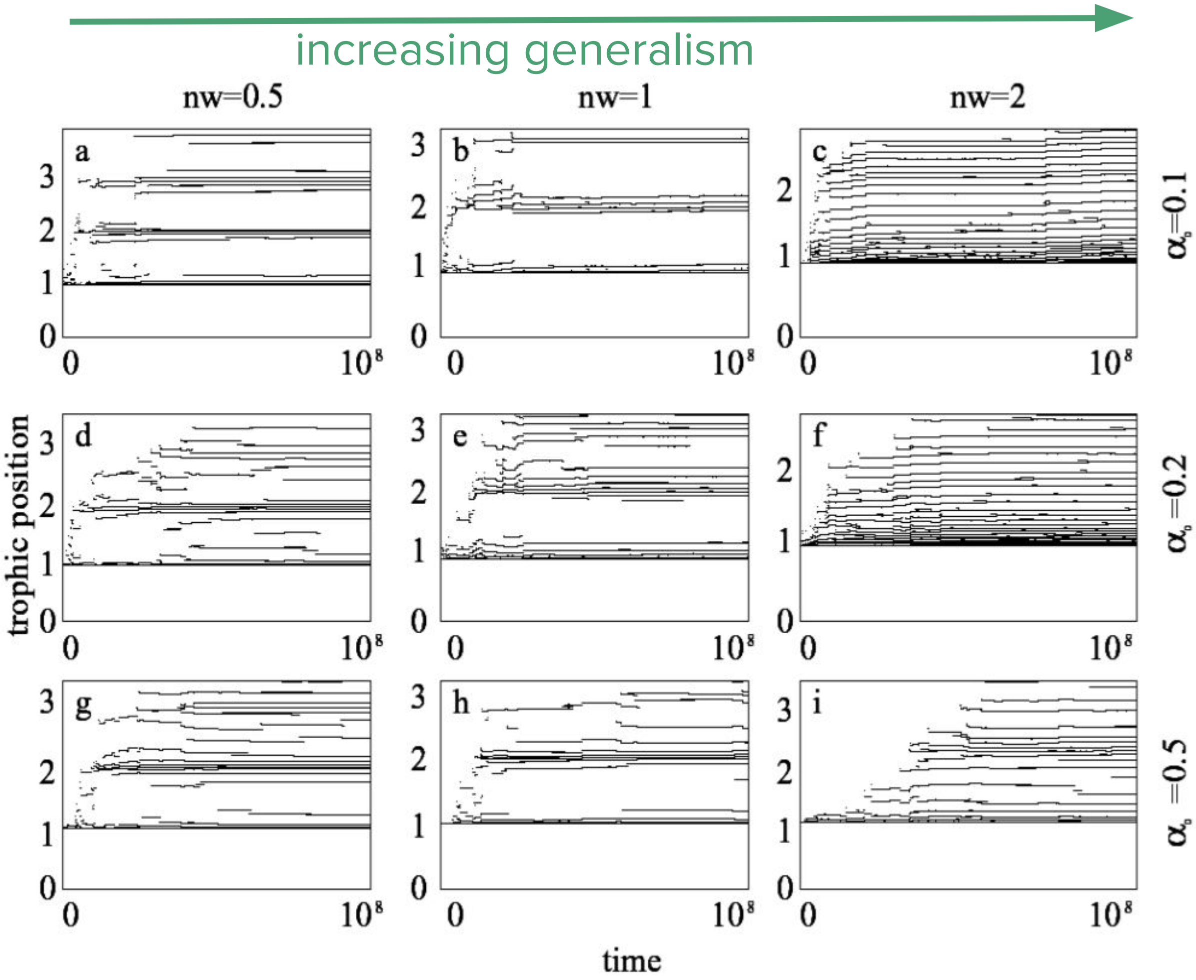
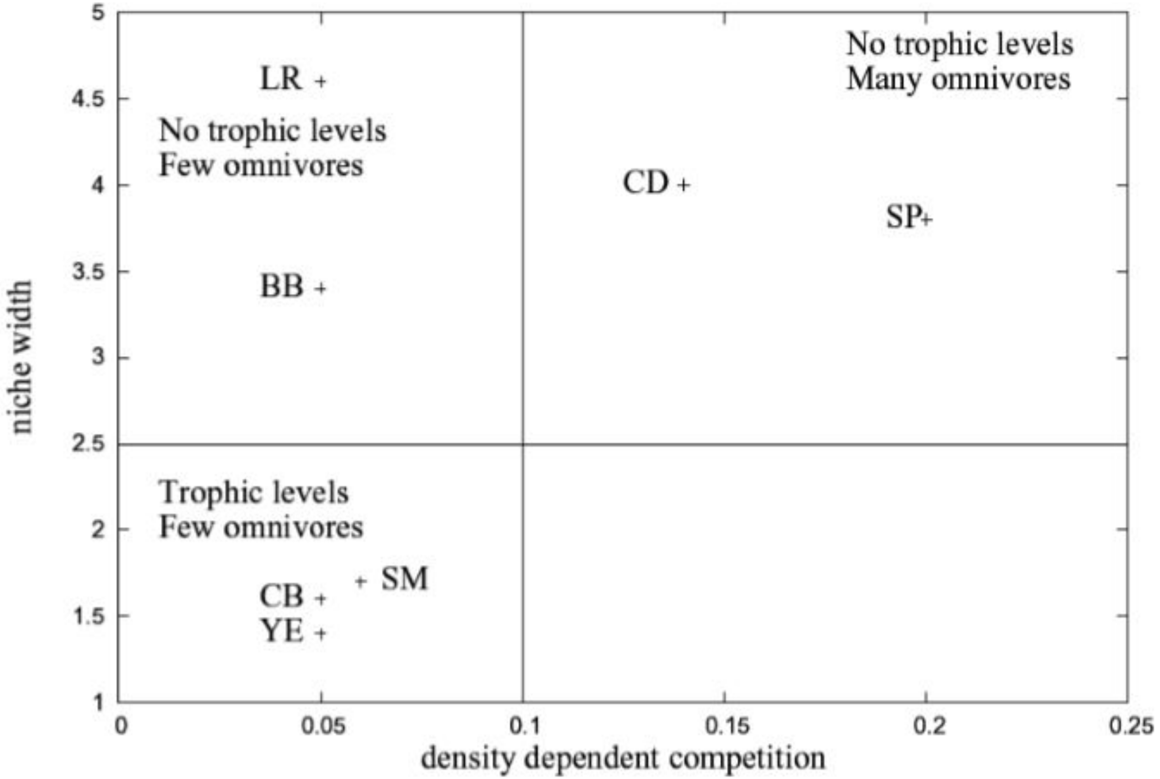


Variability of possible trophic structures

Some comparison with empirical data



-Connectance

-Food chain length

-proportion of omnivores

-% of top, bottom and intermediate species

Some other possible uses of this model

- Discussing allometric theory (eg, energetic equivalence rule: Loeuille & Loreau 2006)
- Discussing the effects of variation of temperatures on trophic structure (Stegen et al. 2012)
- Coevolution of body size and feeding niche width (Ingram et al. 2009, Allhoff et al. 2015)
- Linking diversification and diversity maintenance (Brännström et al. 2011)
- Effects of climate change
- Effects of species harvesting

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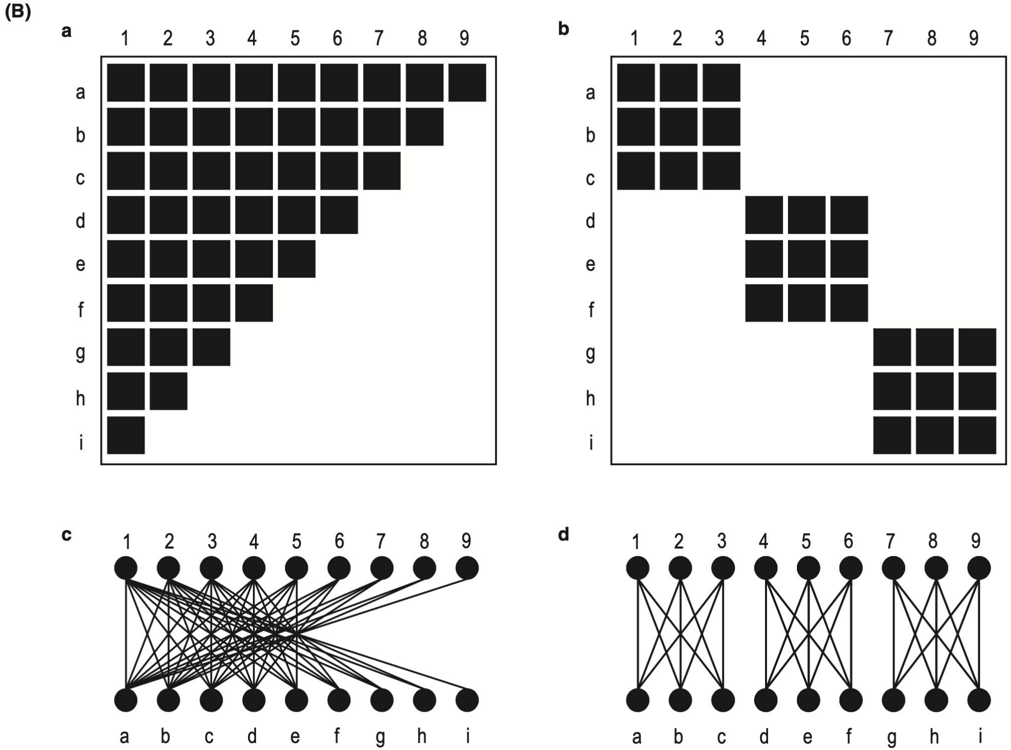
Contrasted structures of antagonistic vs mutualistic networks

Fontaine et al. 2011

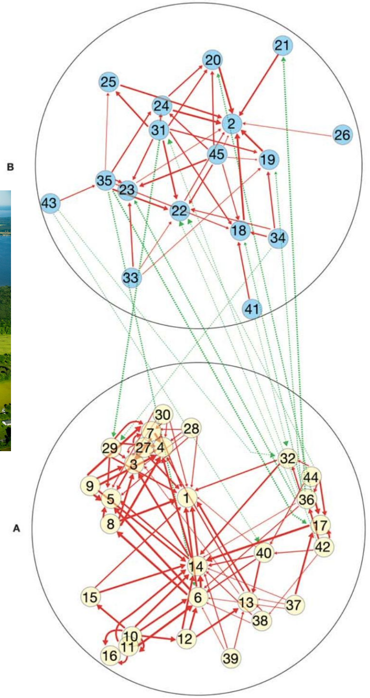


Mutualistic networks as typically nested

Antagonistic networks as typically modular

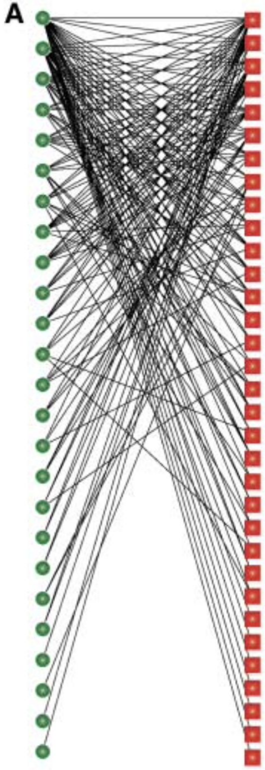
Some empirical examples

benthic



pelagic

Chesapeake Bay food web
(Ulanowicz & Baird 1989, Krause et al. 2003)



Mutualistic network,
Cazorla
Bascompte et al. 2006

Ecological dynamics and resulting structures

Thébault & Fontaine 2010

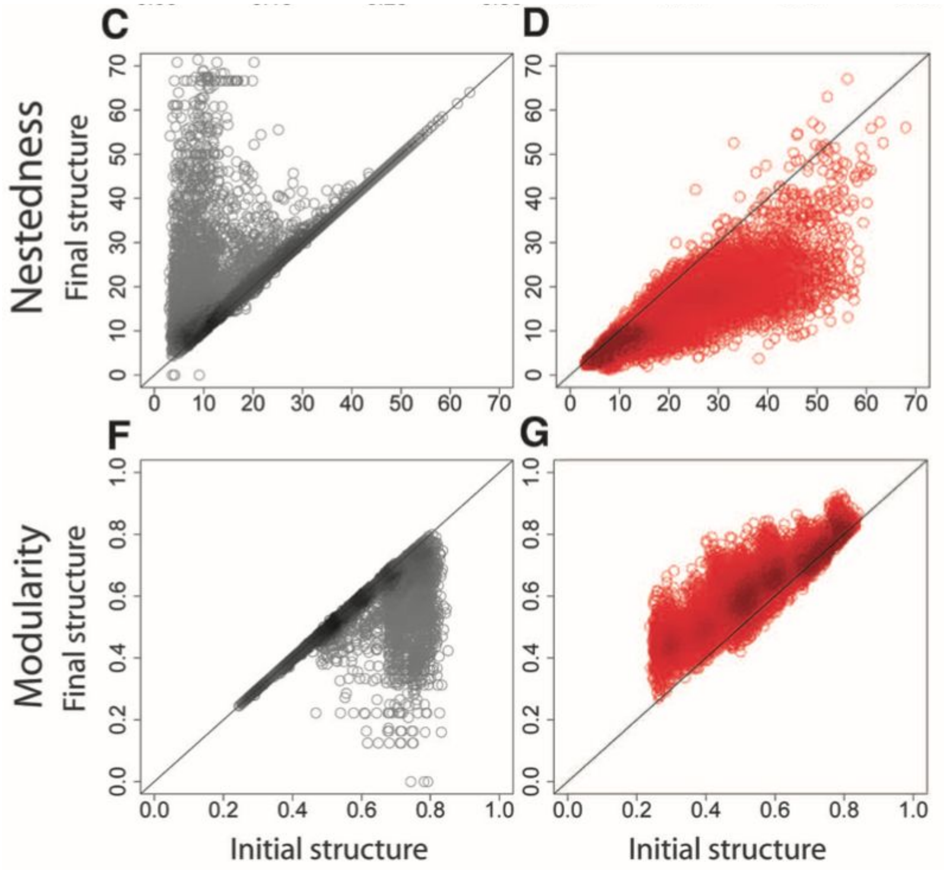
$$\frac{dP_i}{dt} = r_{Pi}P_i - I_{Pi}P_i^2 + \beta\sum_{j=1}^{Na}\frac{c_{ij}A_jP_i}{\alpha_{ij}^{-1} + S_{ij}}$$

$$\frac{dA_i}{dt} = r_{Ai}A_i - I_{Ai}A_i^2 + \sum_{j=1}^{Np}\frac{c_{ji}A_iP_j}{\alpha_{ji}^{-1} + \sum_{k,\alpha_{ki}>0}P_k}$$

- c_{ij} and c_{ji} define the type of network
- Intraspecific competition, type II functional response
- Initial diversity is varied (24 to 80 species), as well as connectance (0.05 to 0.2), nestedness and modularity
- Final state of the network

Emerging structures

Thébault & Fontaine 2010



- Mutualistic
- Antagonistic

Mutualistic networks tend to become more nested in time

Antagonitic networks tend to become more modular

Matching empirical patterns

Coevolution and emergent structures

- Coexistence based on ecological dynamics may be unstable from an evolutionary point of view (Edwards et al 2018)
- Nestedness and modularity depend on the evolved degrees of specialization
- Specialization and coevolution are intimately linked
- Coevolution of mutualistic interactions leading to nested systems?
- Coevolution of antagonistic interactions leading to modular systems?

Model structure


Maliet et al. 2020

Individual based model

2 guilds: (A) (eg, plants) (B) (eg, animals)

4000 cells on a torus, each cell occupied by 1 ind A and 1 ind B

During each time step

An individual is killed, replaced by an individual within the grid (mutation possible)

Probability of choosing an individual biased by fitness

Mutualisme

$$W_A(x_A, x_B) = \frac{1}{r_A - 1} + e^{-||x_A - x_B||^2 \times (\alpha_A^2/2)}$$

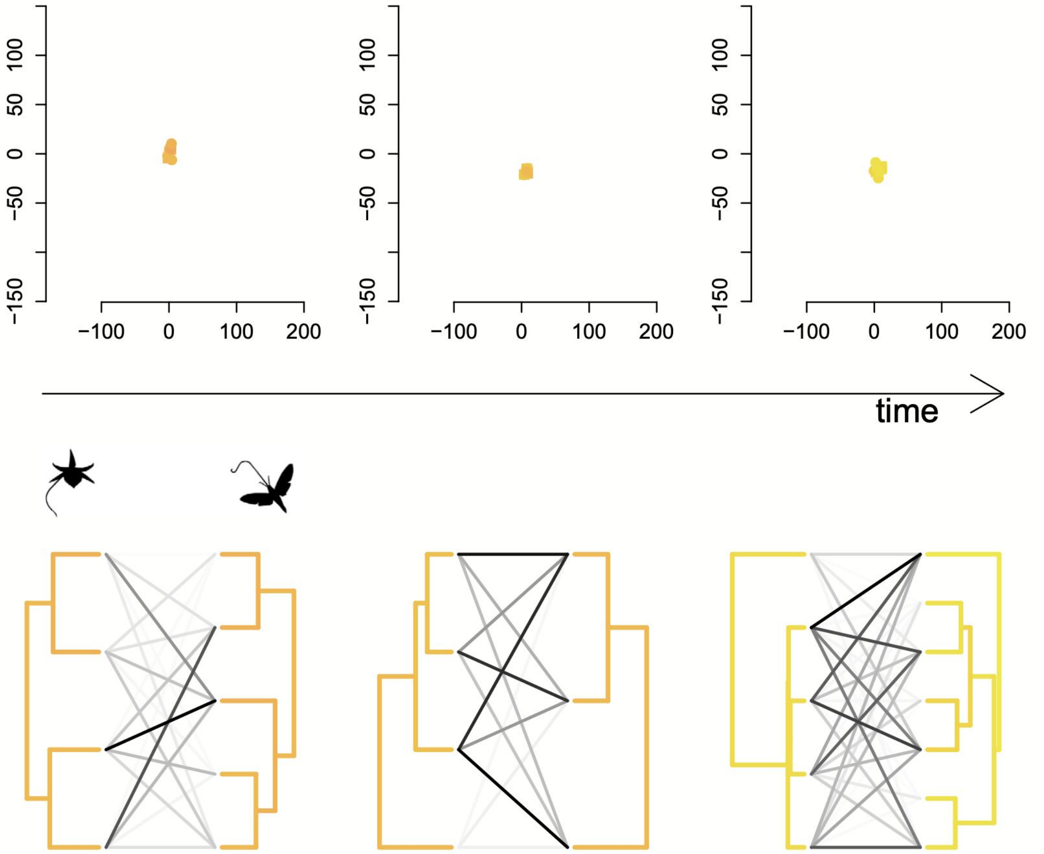
$$W_B(x_A, x_B) = \frac{1}{r_B - 1} + e^{-||x_A - x_B||^2 \times (\alpha_B^2/2)}$$

Antagonisme

$$W_A(x_A, x_B) = \frac{1}{r_A - 1} + 1 - e^{-||x_A - x_B||^2 \times (\alpha_A^2/2)}$$

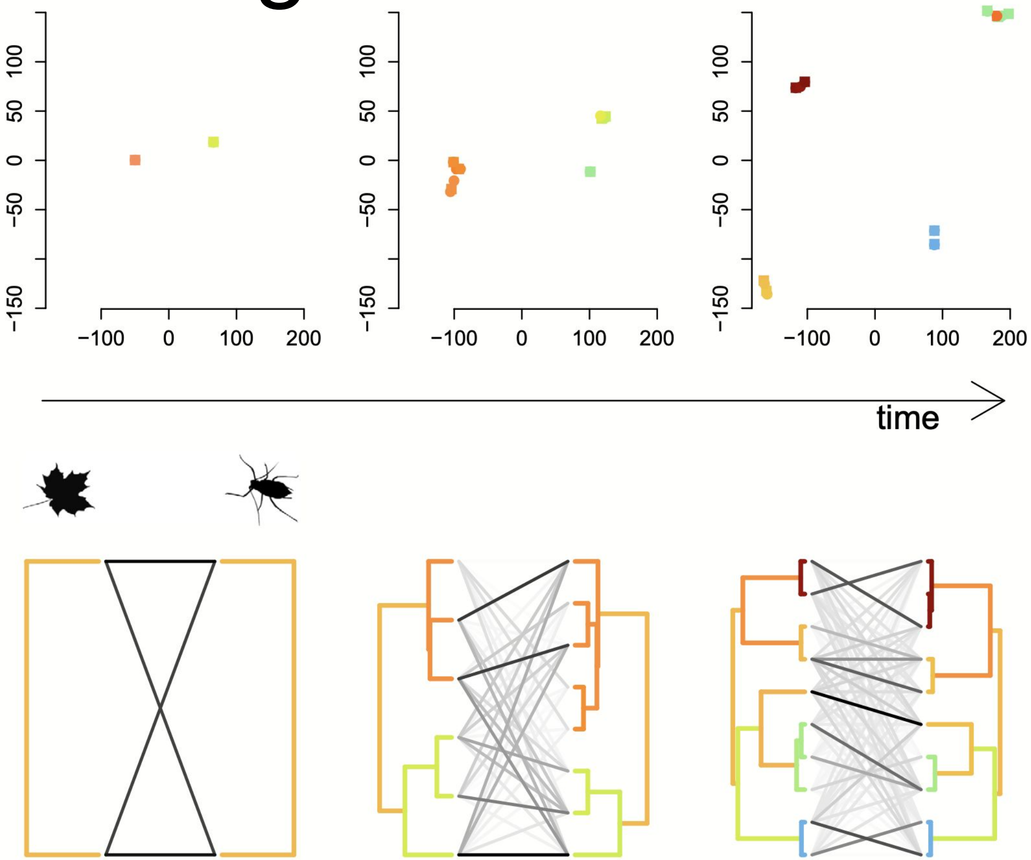
$$W_B(x_A, x_B) = \frac{1}{r_B - 1} + e^{-||x_A - x_B||^2 \times (\alpha_B^2/2)}$$

Coevolutionary emergence of mutualistic networks



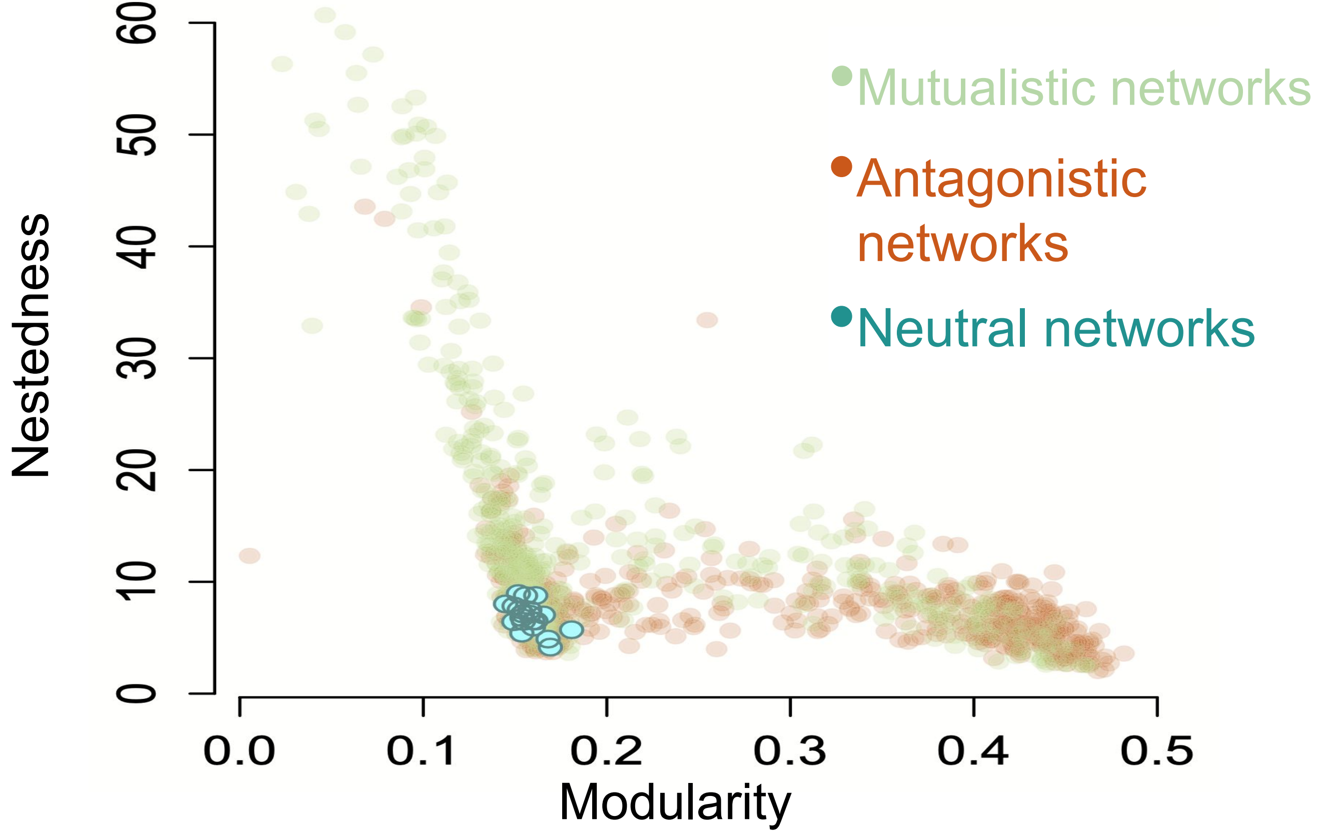
Maliet et al.
2020

Coevolutionary emergence of antagonistic networks



Maliet et al. 2020

Comparing evolved networks



Maliet et al. 2020

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Evolutionary response to global changes

- Has now been observed in many instances (Bonnet et al. 2022)
- Not really surprising from a theoretical point of view:

  $\Delta z = h^2 S$ (Lush 1937, Lande 1979)

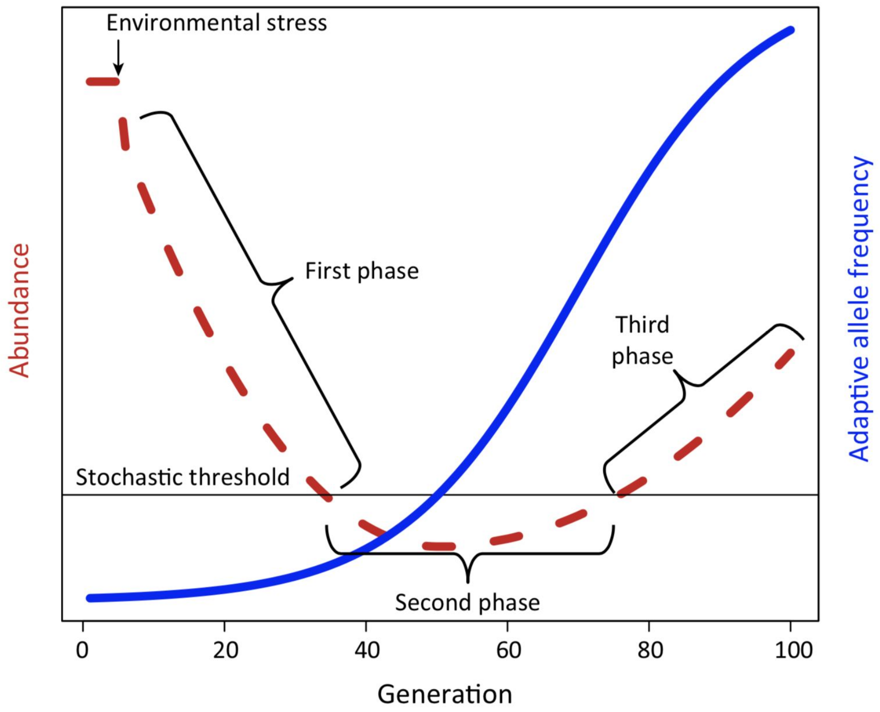
- Is the evolutionary response strong enough to matter? (Hairston et al. 2005)
- If it matters, will it be systematically positive?

age and size at maturity, (eg Olsen et al. 2004)

Evolution of phenologies (Nussey et al. 2005, Jonzen et al. 2006, Phillimore et al. 2010, Franks et al. 2007)

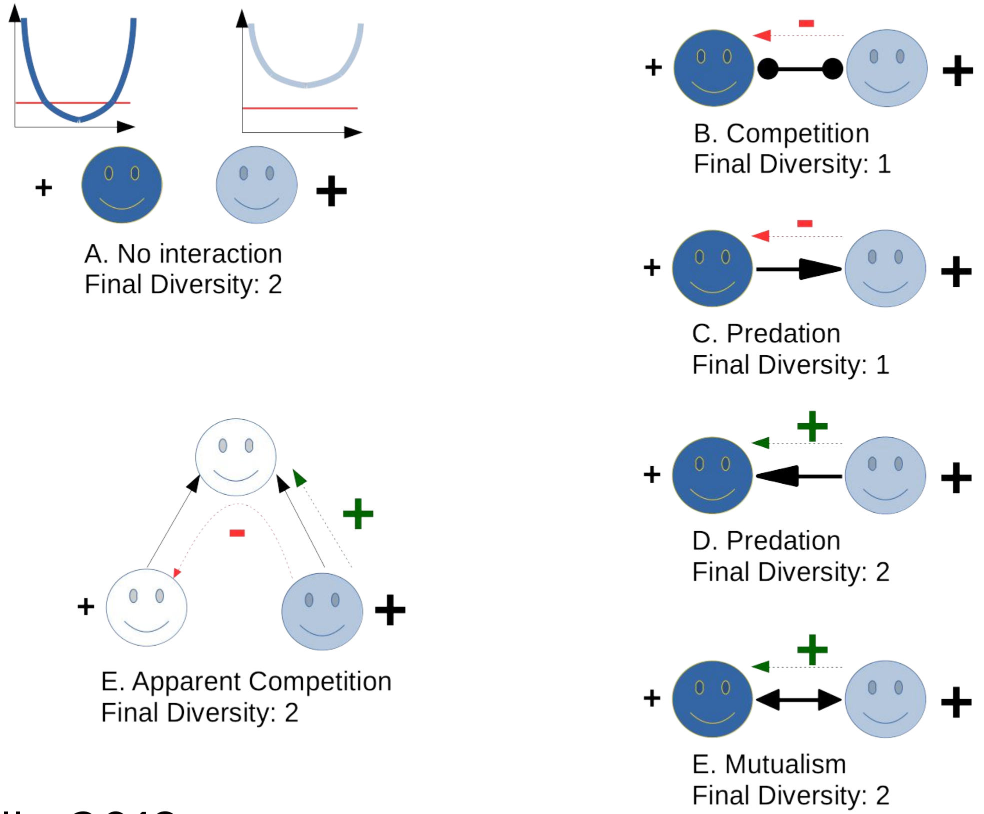
Evolution & resilience of coral reefs (Pandolfi et al. 2011)

Species declines and possible evolutionary rescue



- Gomulkiewicz & Holt 1995 (1 species quantitative genetic model): race between population decline and adaptation
- Does occur in nature: resistance to antibiotics, to pesticides (Carlson et al. 2014)
- Large population size, short generation time, large genetic variabilities
- Intensity of disturbance

Bringing Evolutionary rescue in a network context



(A) Species separated, evolutionary rescue (div=2)

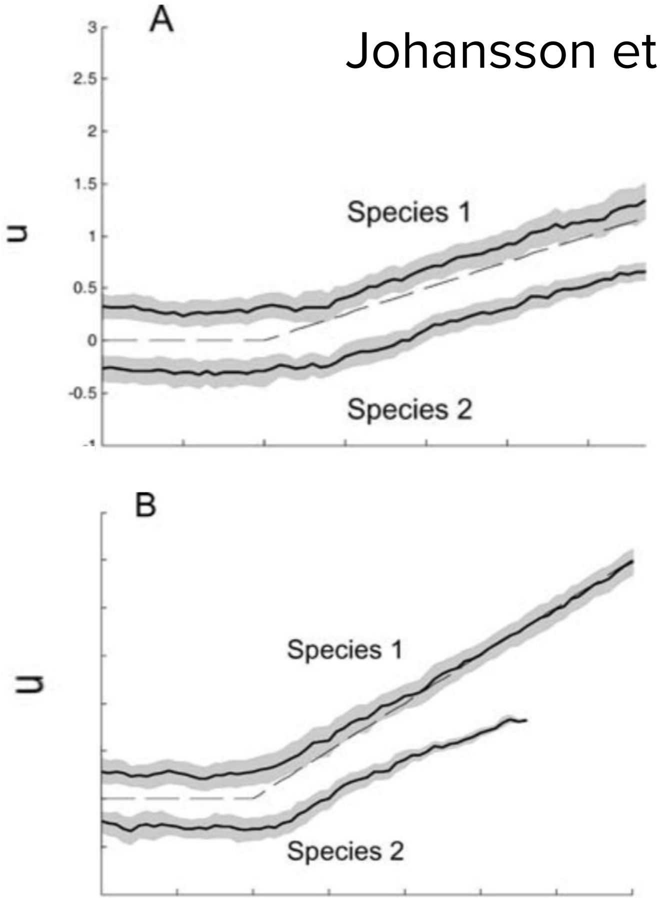
(B) (to (E)) depending on ecological interaction, variations in diversity

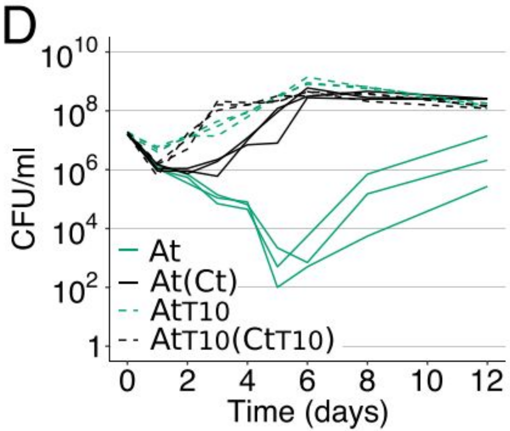
ER+indirect ecological effects: species with high genetic diversity as keystones?

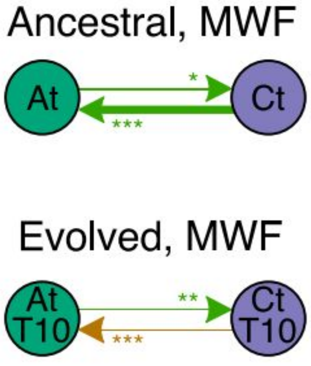
Loeuille 2019

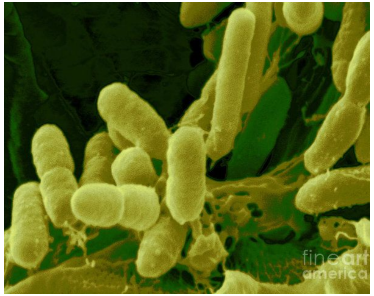
How it could work out

Johansson et al. 2007





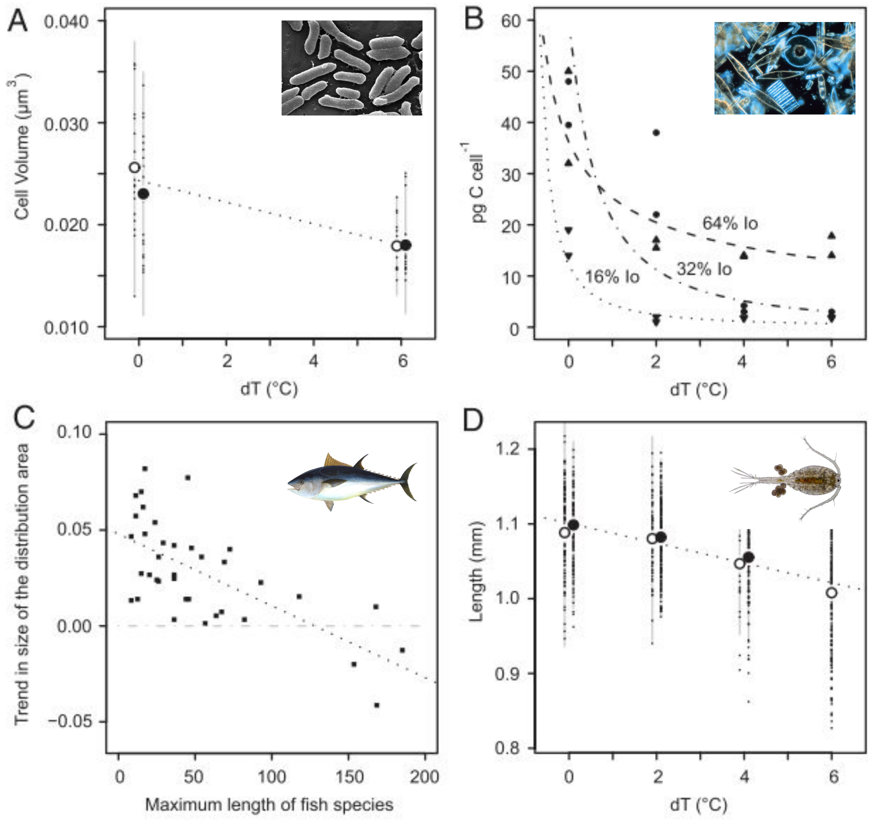




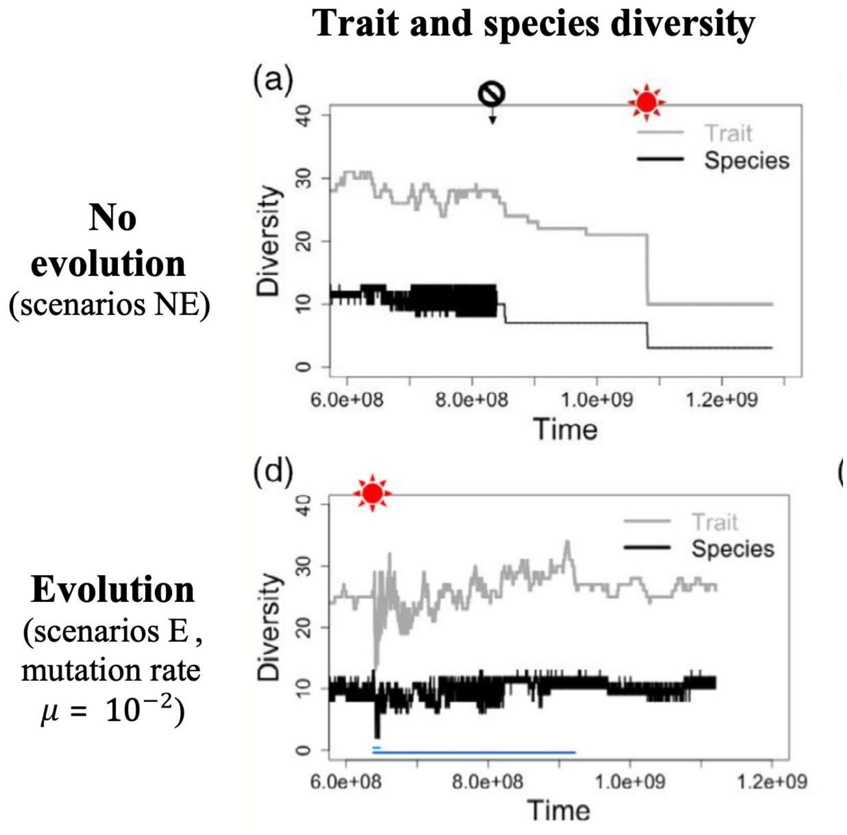
Piccardi et al. 2019

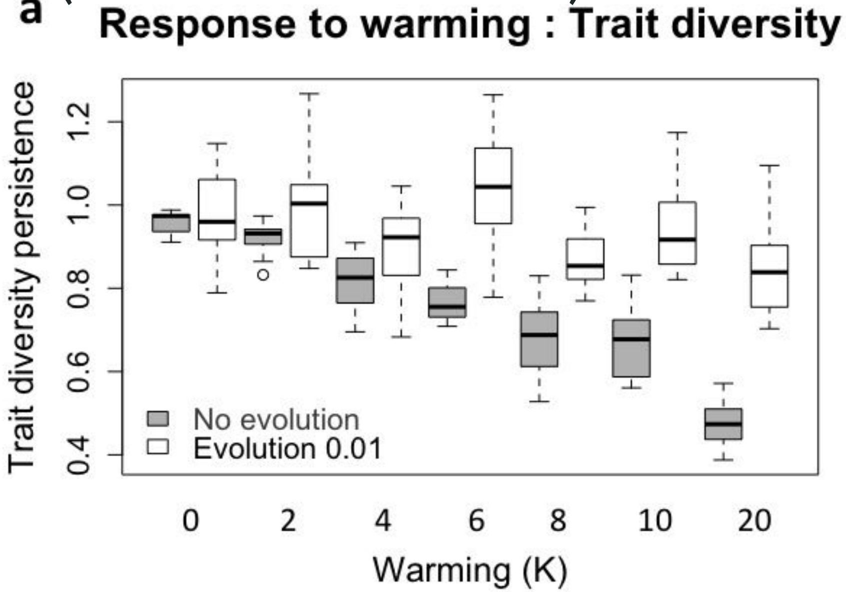
Selection of smaller body sizes under climate warming

- General observation of smaller body sizes (eg, Daufresne et al. 2009)
- True at different scales (within populations, but also among species)
- Viewed as a general rule (Sheridan & Bickford 2011)
- However, exceptions exist (eg, O'Gorman et al. 2017)
- Implications for ecological interactions?



Effects of warming on complex evolved food webs (Yacine et al 2021)





- Long term, diversity is maintained by evolution
- However: (i) Large short term turnover of traits/species; (ii) large sizes (top trophic levels) collapse

On the exploitation of food webs

- Expected ecological outcomes:

  (1) Species decrease, possible extinction (primary extinction); extinction of interactors

  cf fish stock overexploitation (88% of stocks (EU), likely underestimated (Thurstan et al 2010)

  (2) Extinction of interactors (secondary extinctions)

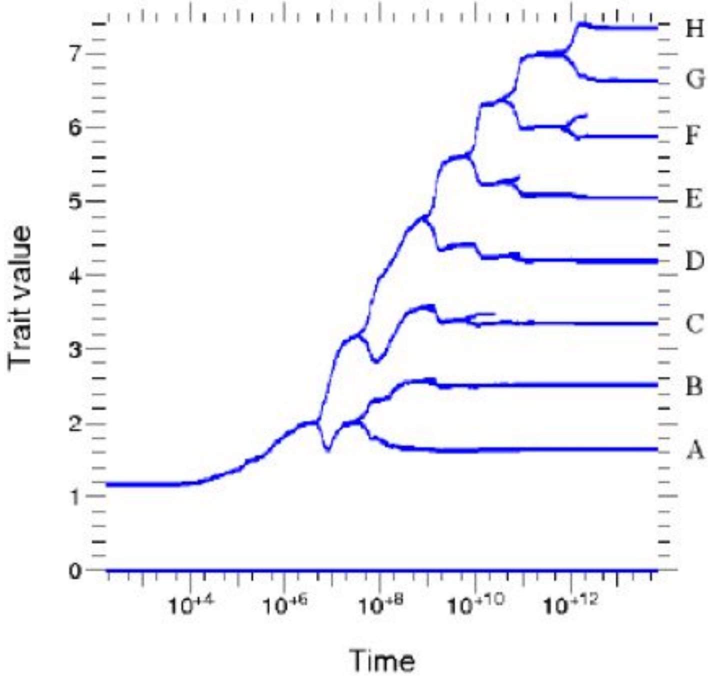
- Expected evolutionary outcomes?

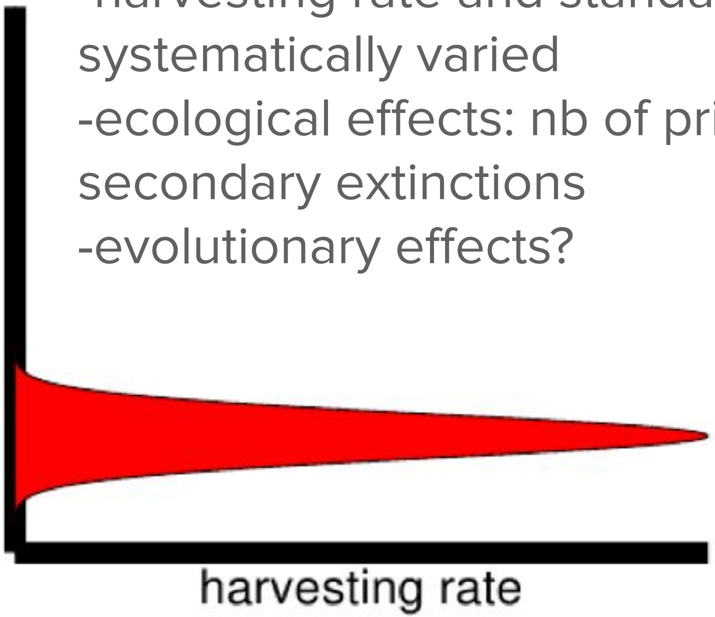
Eco-evolutionary dynamics in exploited food webs

Trophy hunting:
Selects smaller ornaments (eg, Coltman et al 2003)
And smaller sizes as a side-effect

Fishing:
-size quota or trophy: smalls are favored
-intense: early maturity selected, small adults as a side effect (Olsen et al 2004)

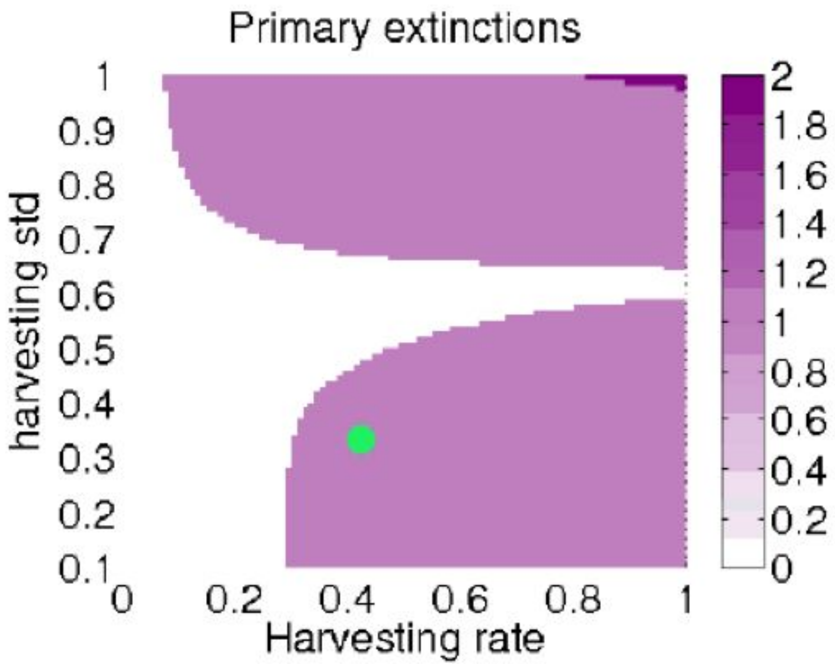
Implications from a network point of view?

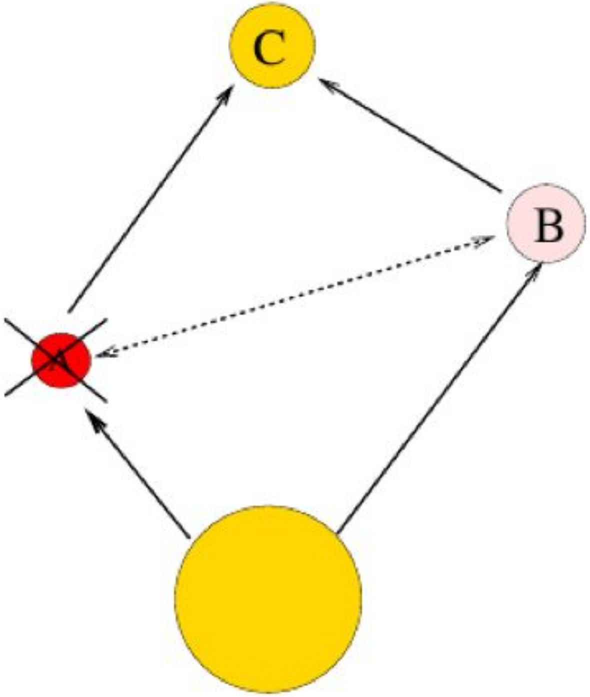




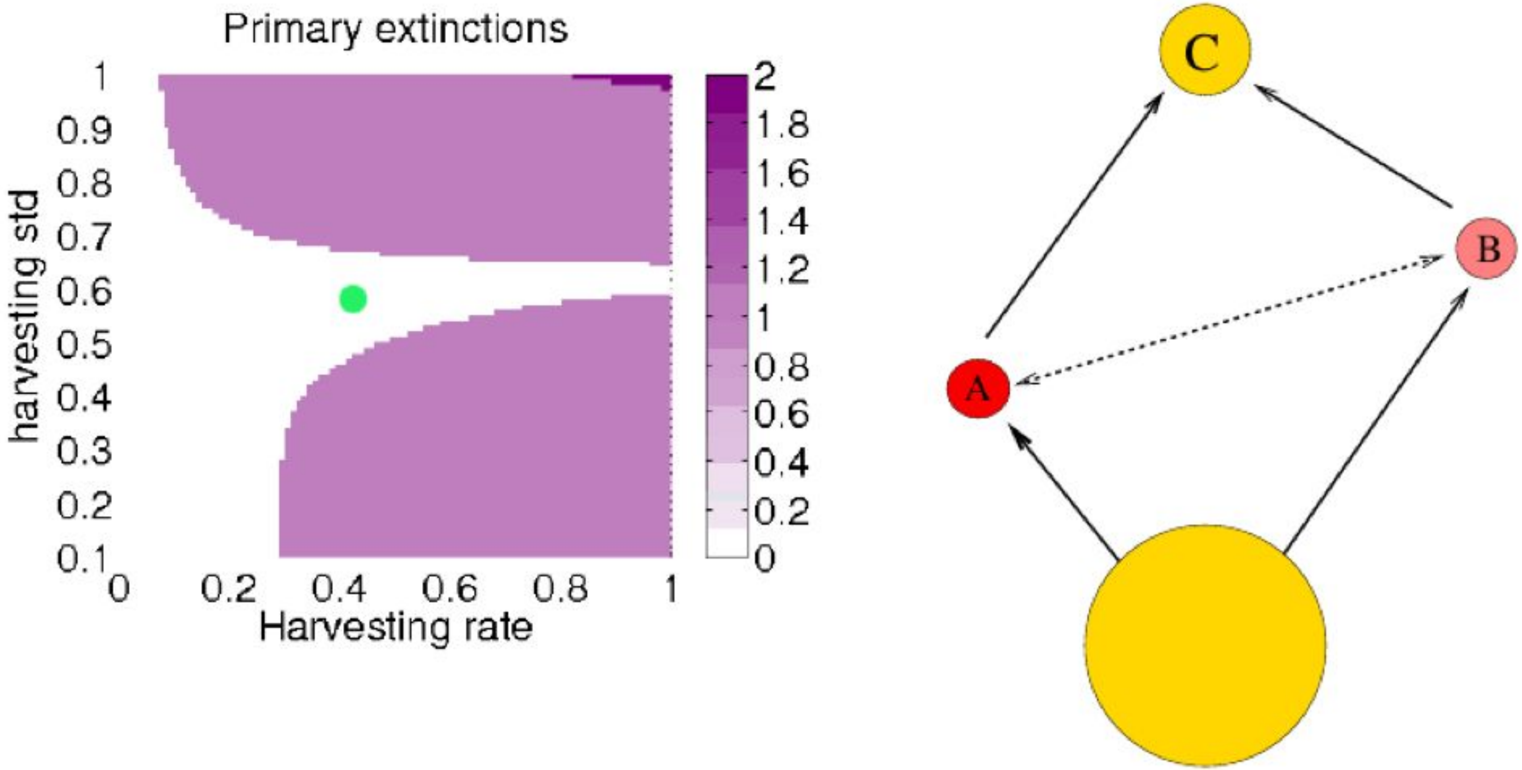
-Exploitation centered on smallest, largest, or median size
-harvesting rate and standard deviation systematically varied
-ecological effects: nb of primary and secondary extinctions
-evolutionary effects?

Simulation scenarios





Exploiting the basal species



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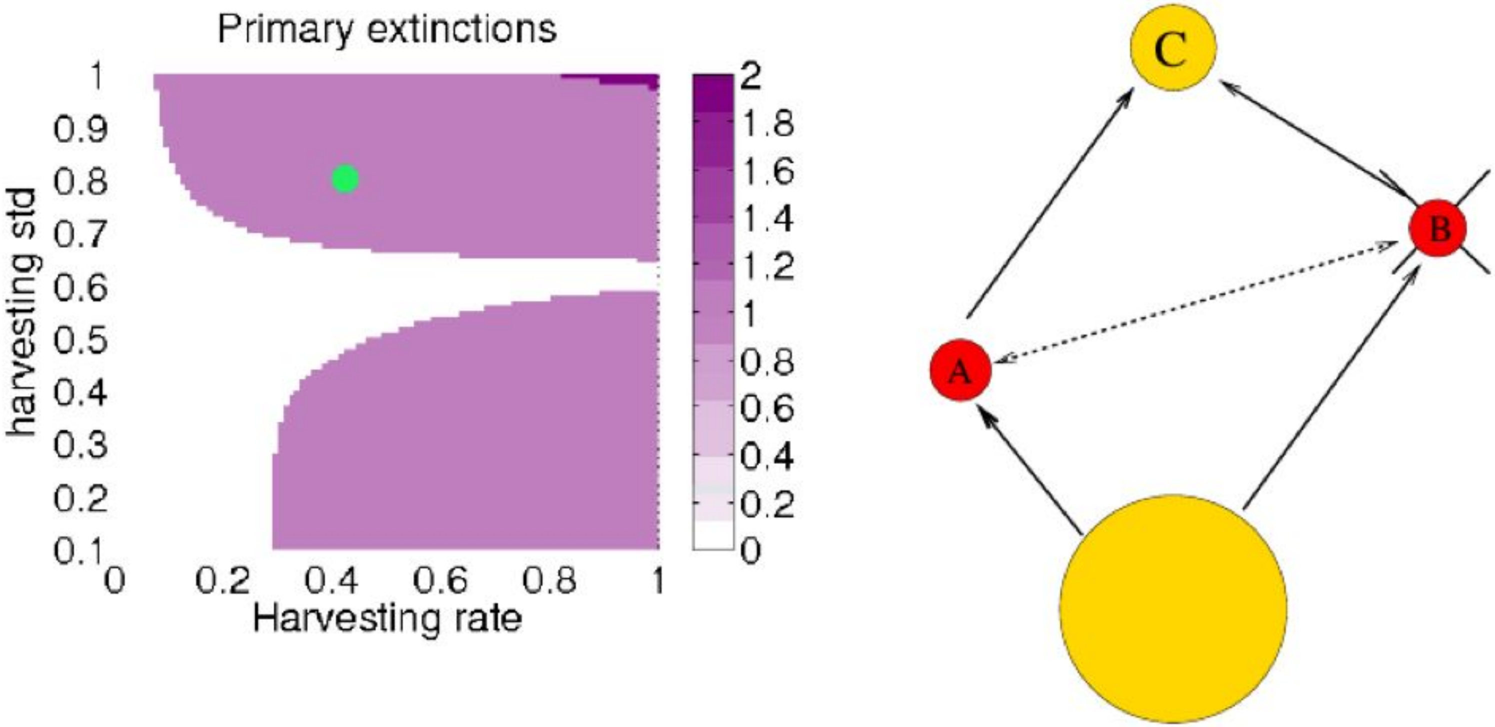

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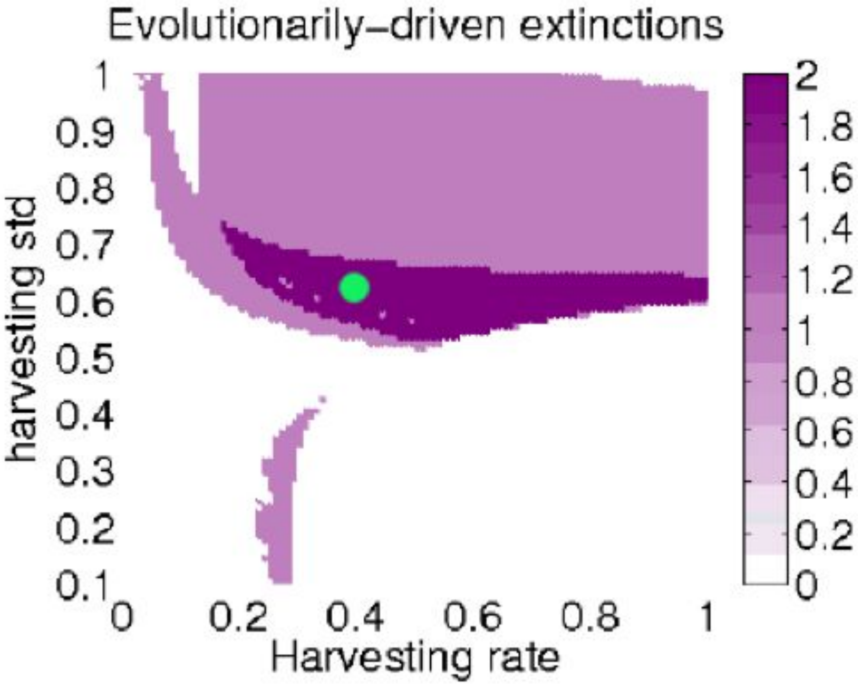
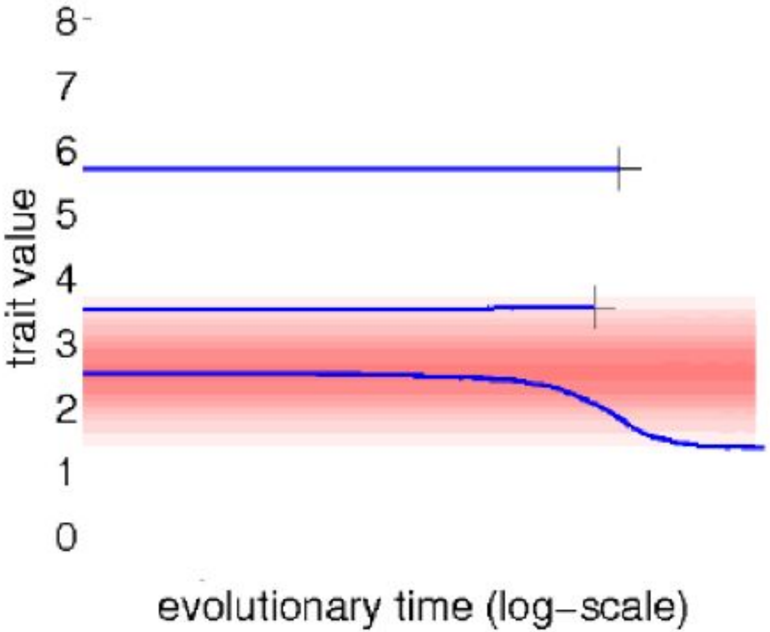
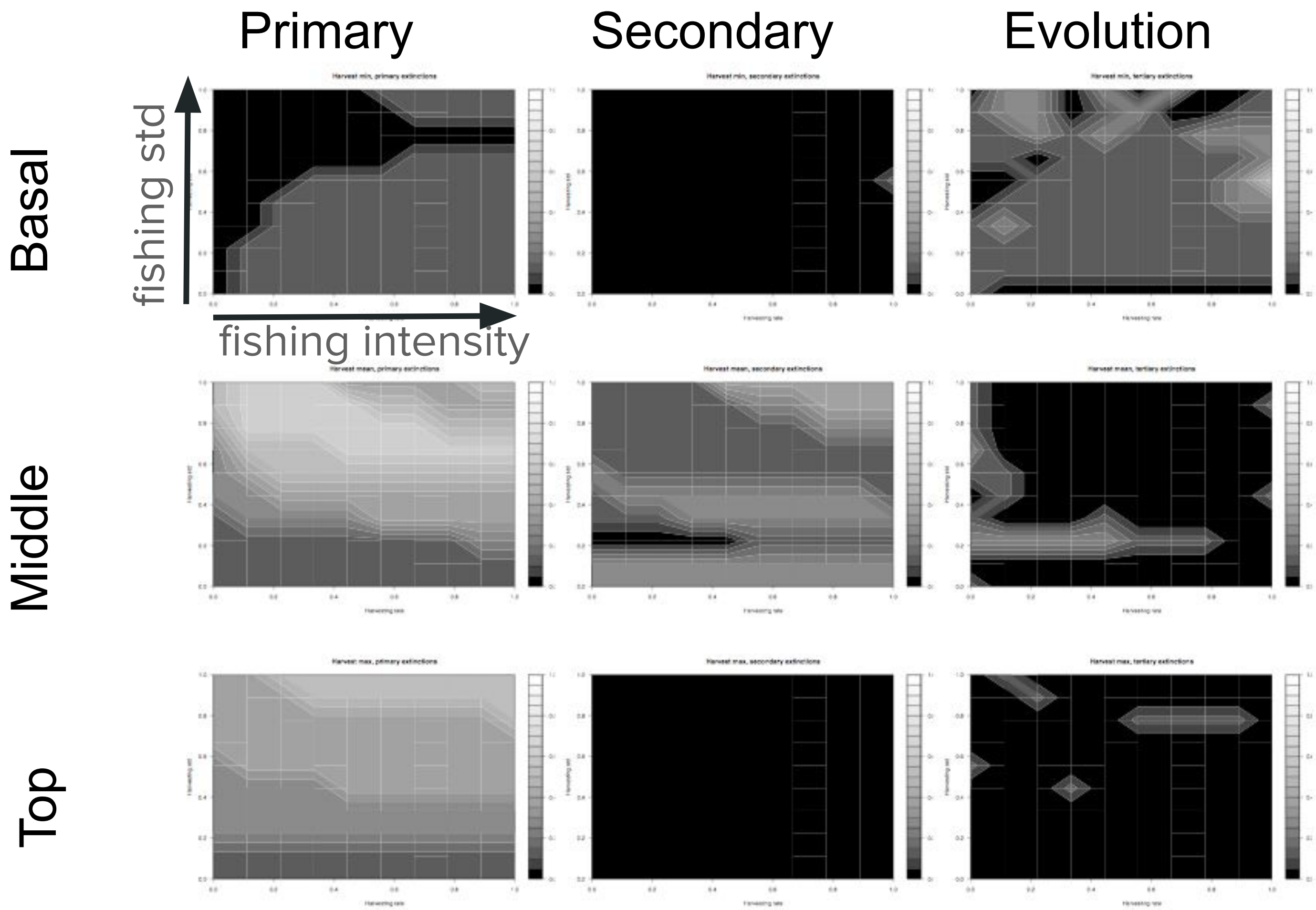




Evolutionary effects



Compiling this experiment on 20 webs

General conclusion

- Understanding the evolution of key traits may help us understand the emergence of structures and functional aspects within networks
- Some of these structures/functionings match various aspects of empirical datasets
- Fast evolution under global changes: how does it affect the robustness and resilience of natural communities?

Thanks

- My collaborators:

  Evolution of size & food webs: Michel Loreau

  Evolution of antagonistic vs mutualistic bipartite network: Odile Maliet, Hélène Morlon

  Evolution under climate change: Korinna Allhoff, François Massol, Avril Weinbach, Youssef Yacine

  Evolution in exploited systems: Ake Brannström, Ulf Dieckmann

- To you for listening!