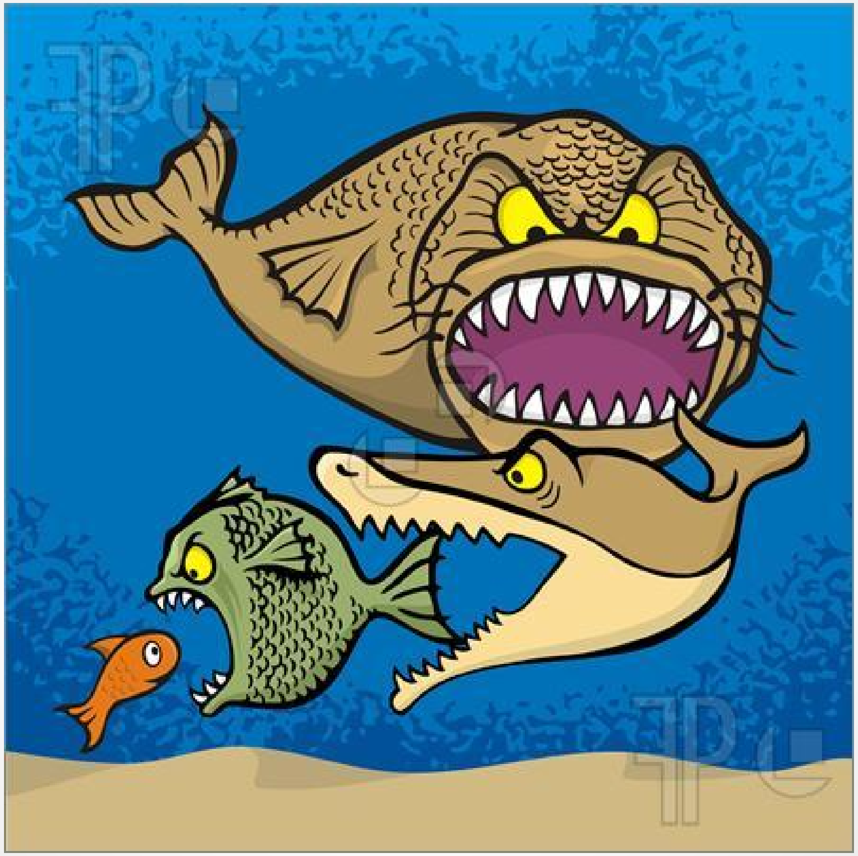
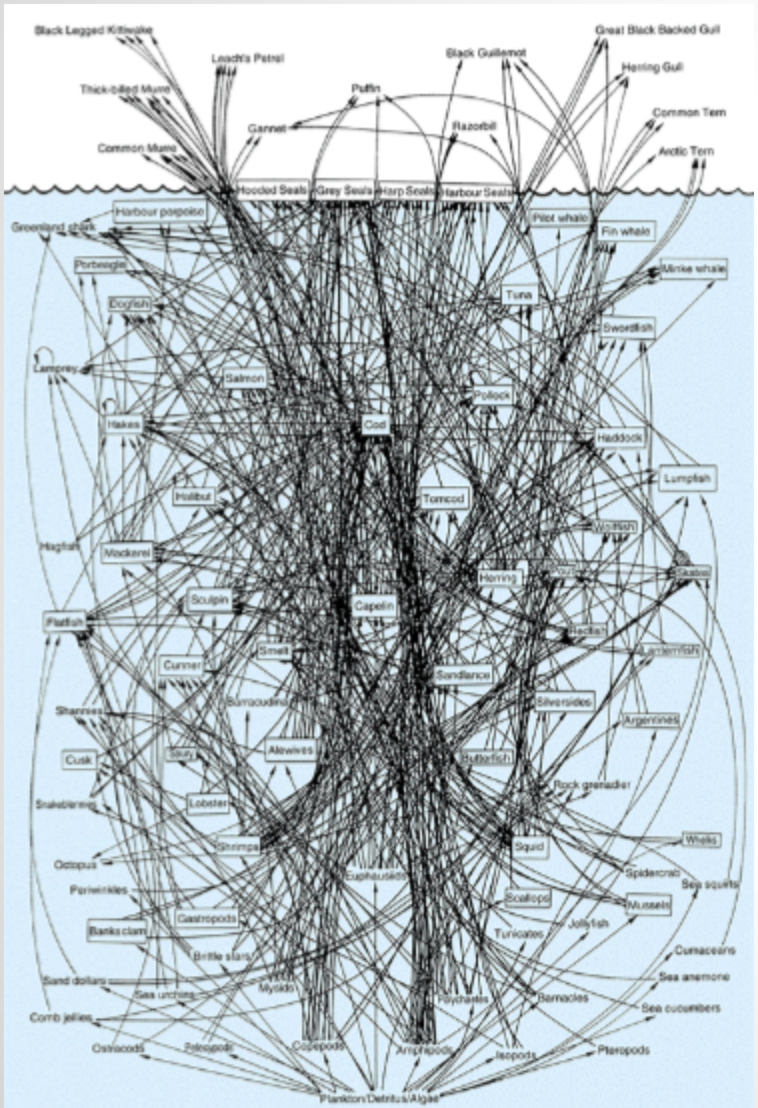
Coevolution in ecological networks: structure and stability



Nicolas Loeuille, nicolas.loeuille@upmc.fr
Institute of Ecology and Environmental Sciences

Are food webs complex?



A simplified food web for the Northwest Atlantic

-A large number of species

-A large number of links

-Many possible indirect effects (Yodzis 2000)

-Determined by demographic (eg, extinction), assembly and evolutionary processes, plus their interactions.

Reproducing food web structures

*Most basic ingredients: number of nodes (“species”) N and of edges (“interactions”) L. Connectance $C=L/(N(N-1))$

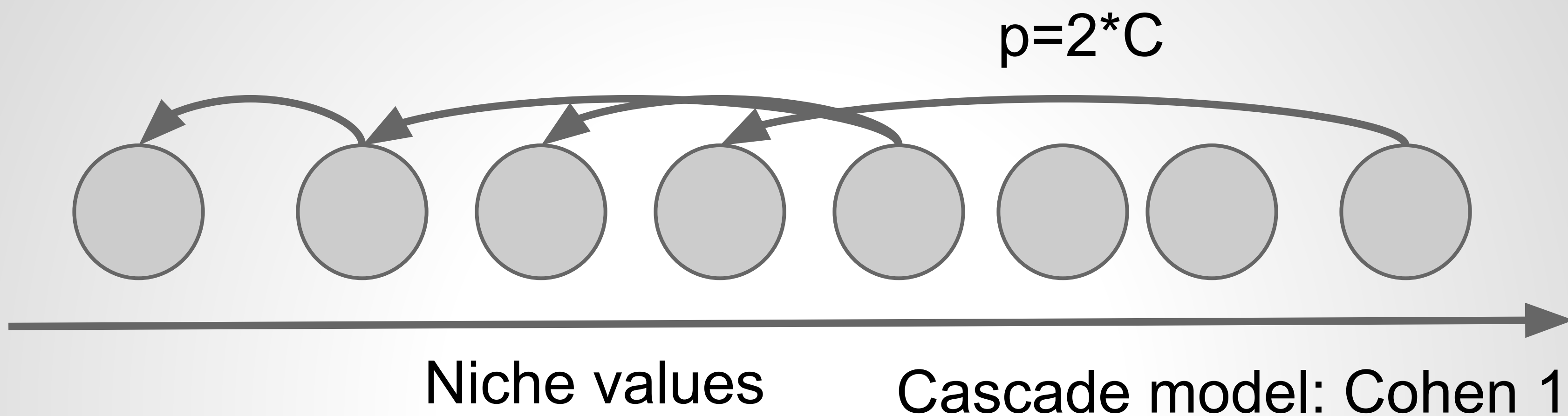
*Derived descriptors: food chain length, % of top or bottom species, vulnerability, generality, etc.

*N and L being fixed, food webs differ from random (eg, in degree distribution)

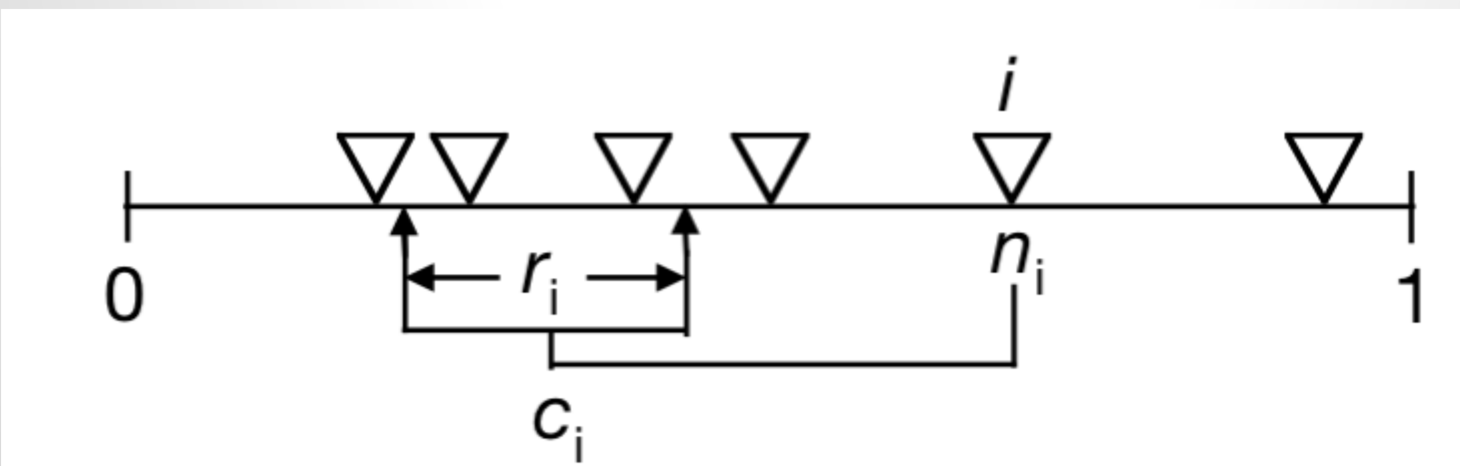
Complex structures , but they exhibit some regularities

- Food webs are small worlds (Montoya et al. 2006)
- Connectance is limited to a small interval (that can be explained by optimal foraging theory: Beckerman et al. 2006)
- Food chain length are quite small
- Usually four to five trophic levels

"Binary models" reproducing food web structures

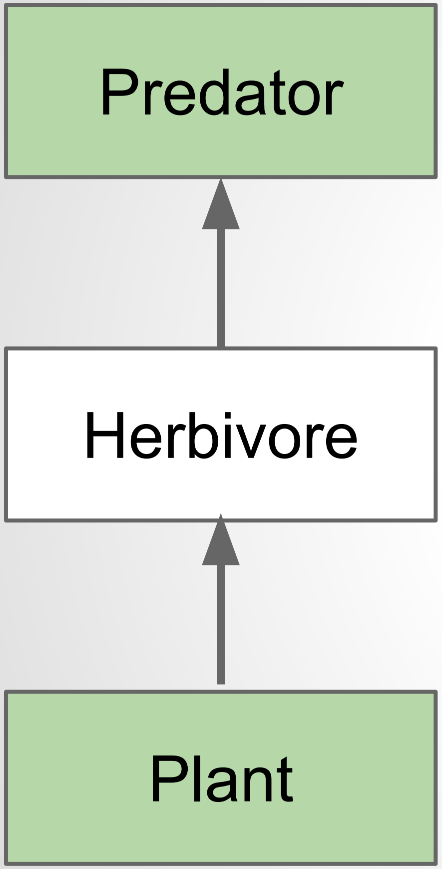


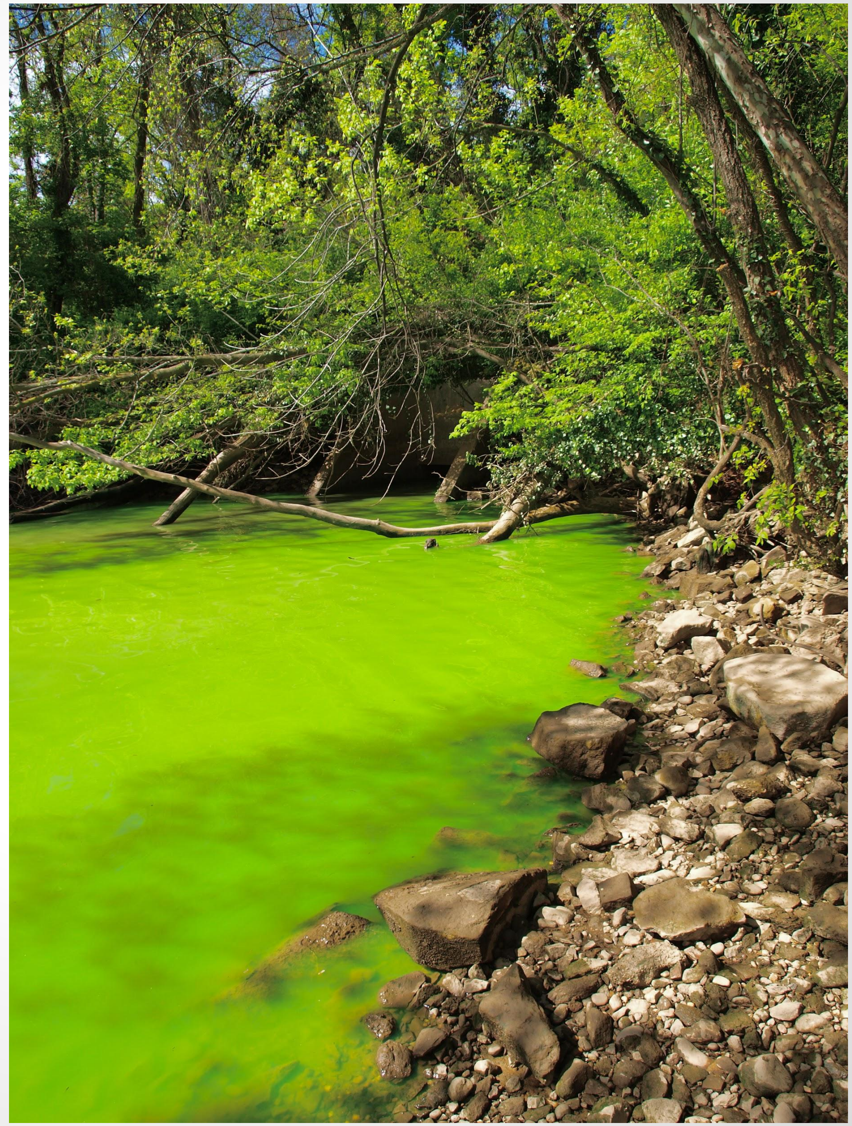
Cascade model: Cohen 1990



Niche model (Williams & Martinez 2000)

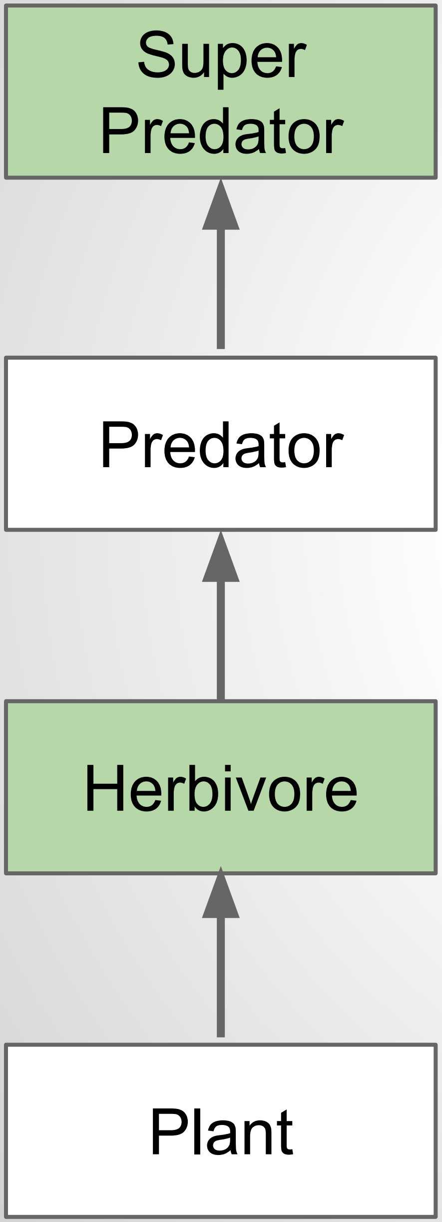
Linking structure and functioning





Hairston et al. 1960
Oksanen et al. 1981, 2000

Linking structure and functioning



Oksanen et al. 1981, 2000

Coevolution and the emergence of food web structure

- It allows a link between individual (fitness) and community structure or ecosystem functioning
- It allows a more integrative understanding of the effects of disturbances on food webs
- Statistical approach: use many traits (usually binary, not explicited): eg, webworld model (Caldarelli et al. 1998), matching model (Rossberg et al. 2006)
- One/two trait approach: body size as a good candidate

Possible questions for coevolution models applied to food webs

1) What kind of trophic structures emerge from the coevolution of species?
2) Interplay of evolutionary dynamics and ecological effects (eg, trophic cascades, bottom-up effects)
3) Linking evolutionary dynamics to stability (eg, resilience)

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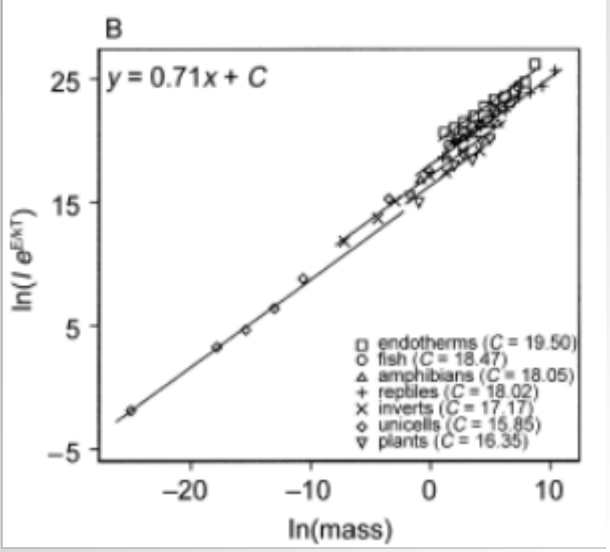
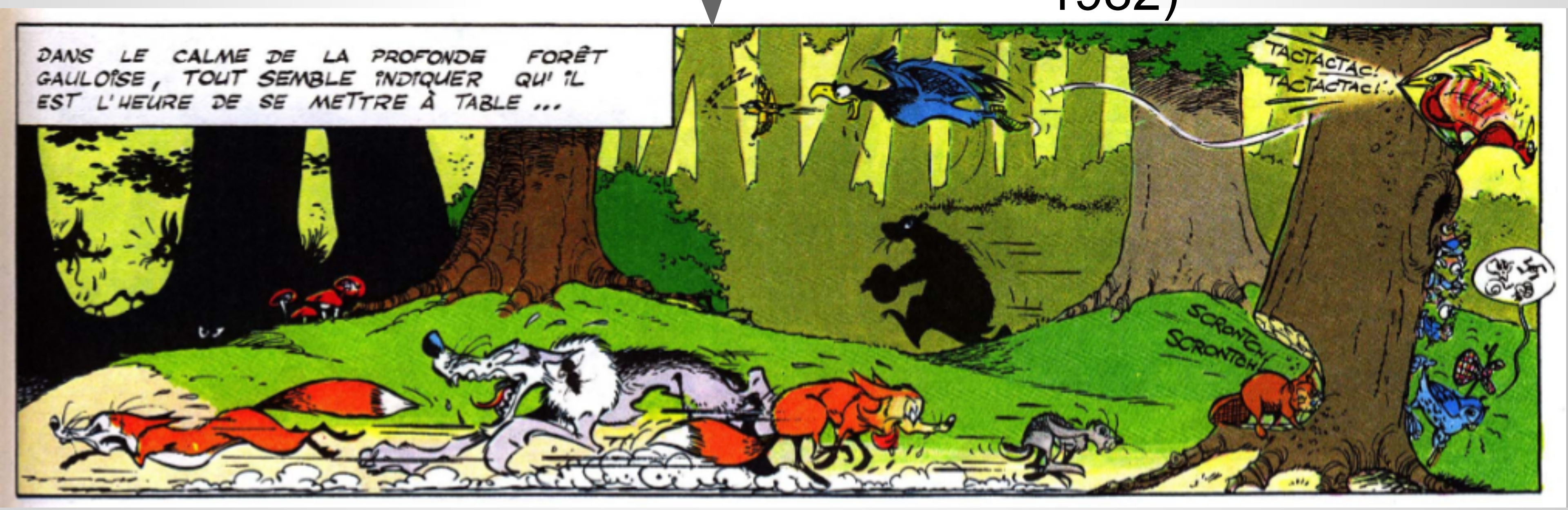


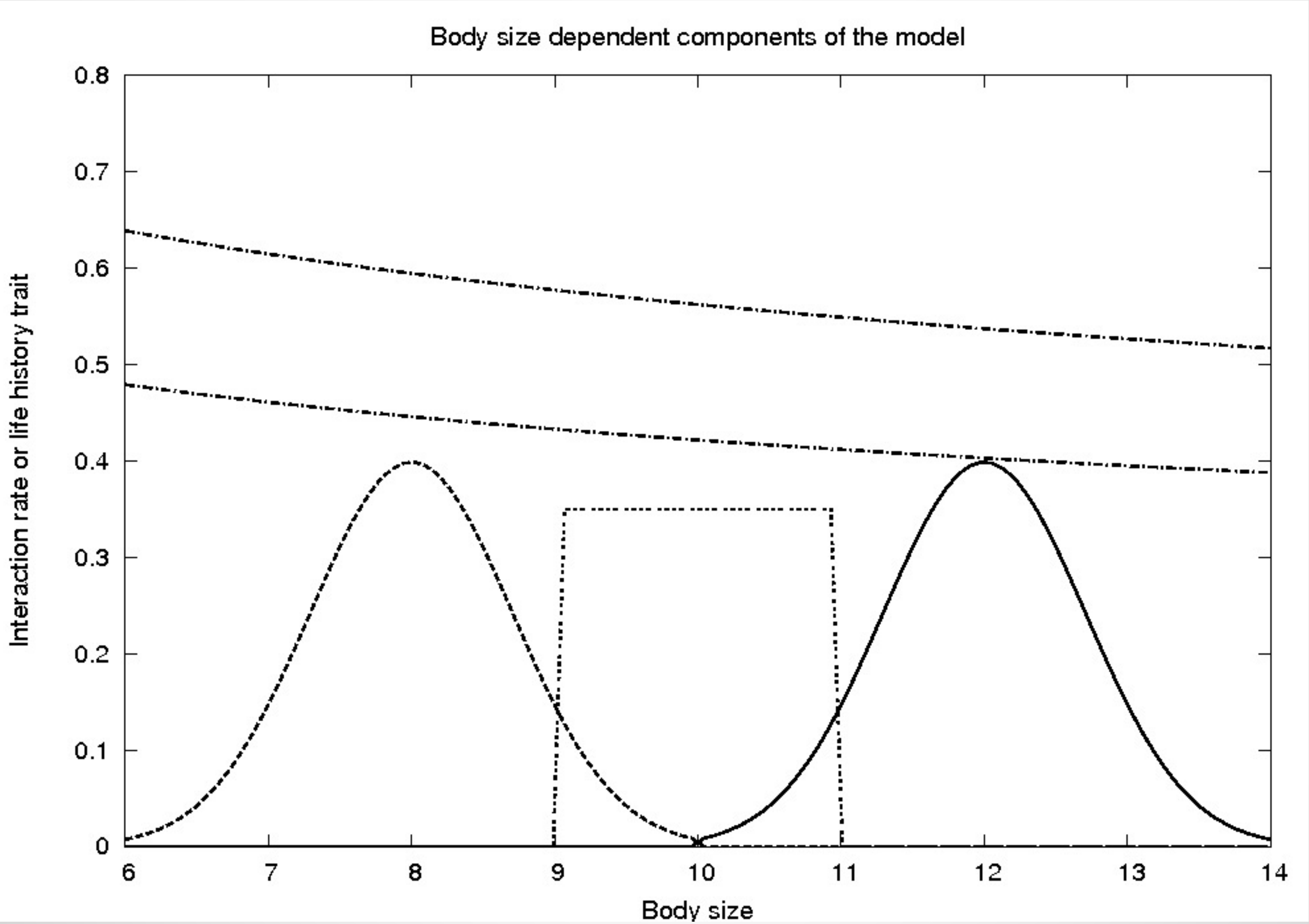
THV (eg, Brown et al. 2004)

Body size

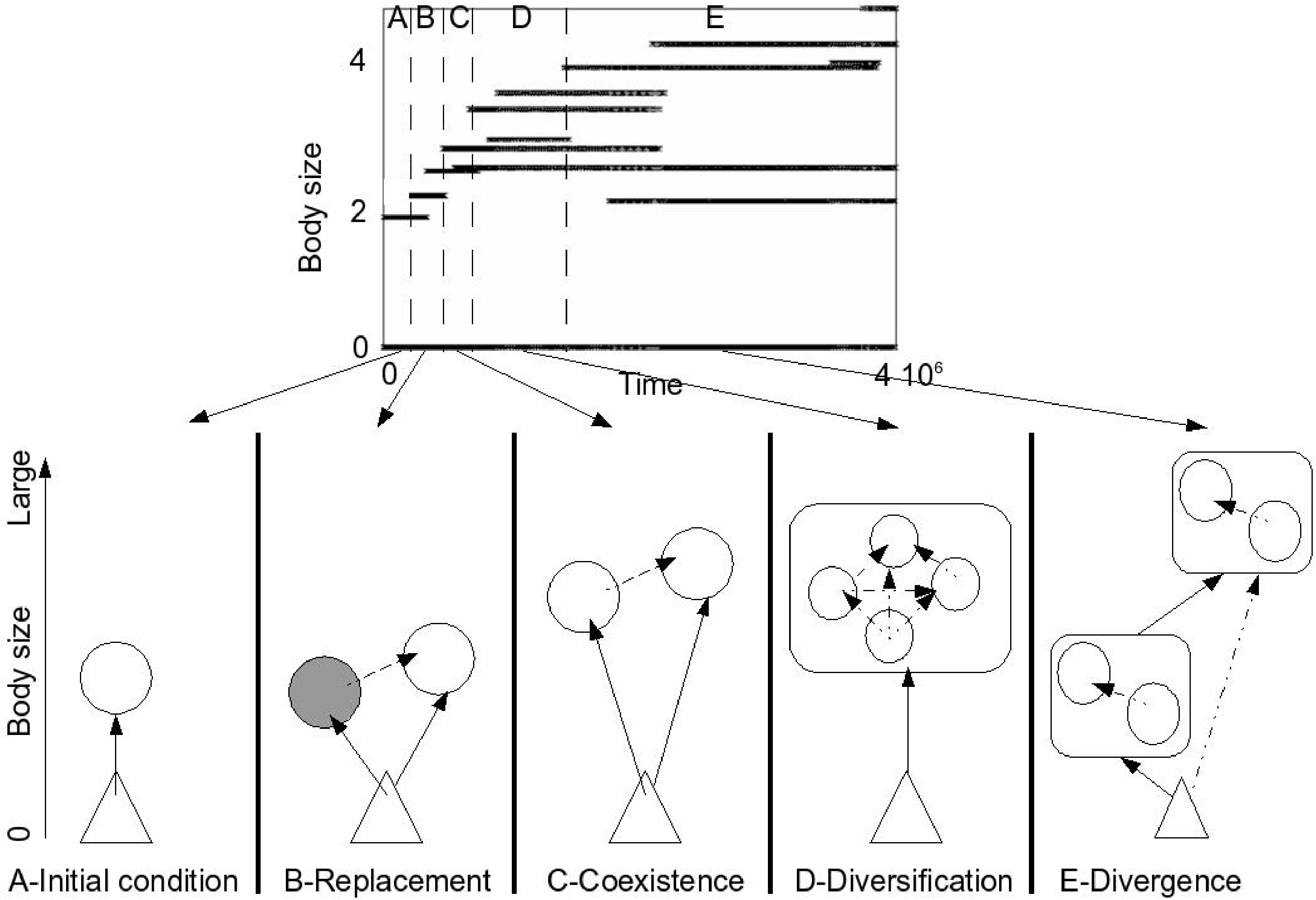
Competition (eg, Bowers & Brown 1982)



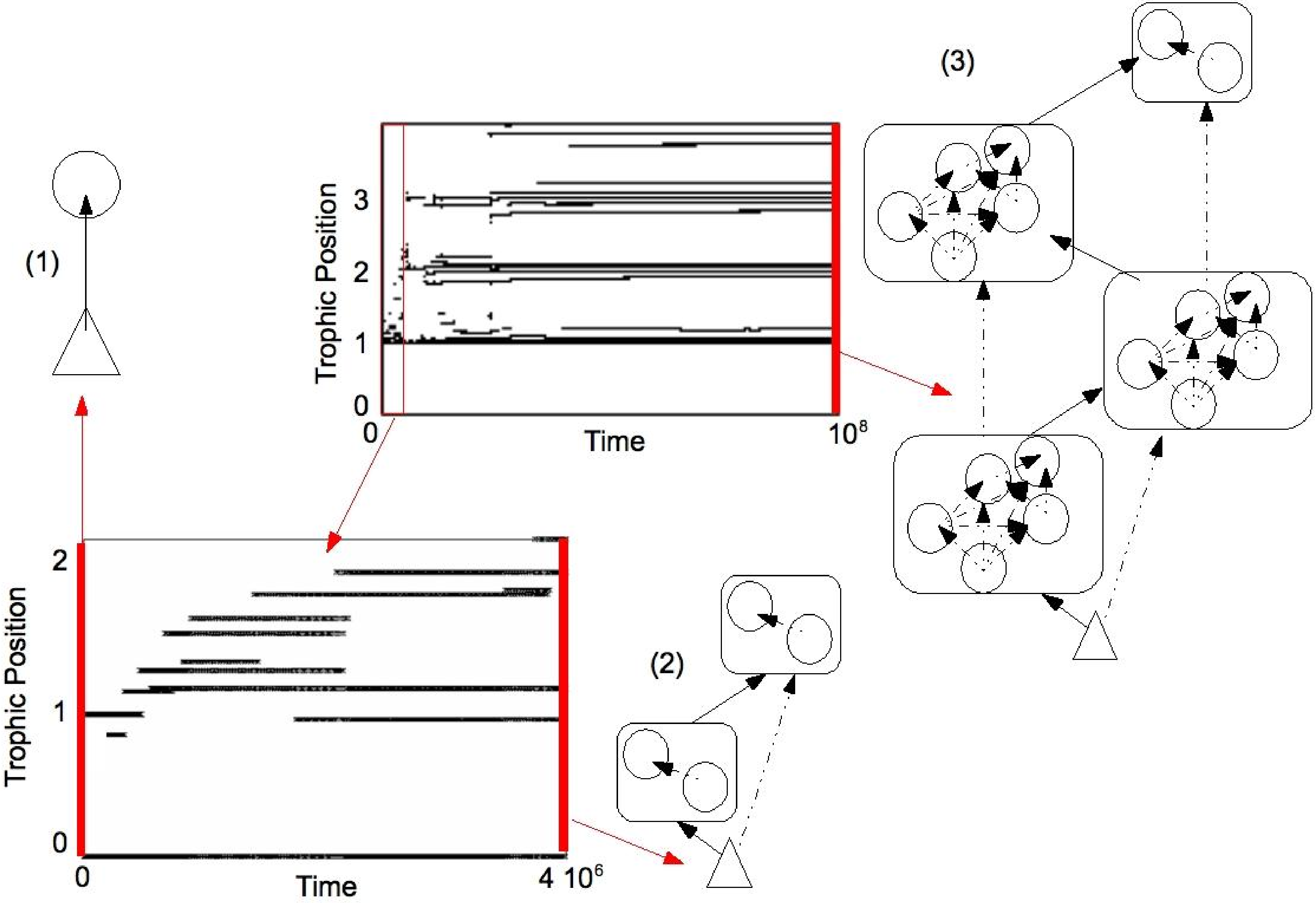
Trophic interactions (eg, Emmerson & Raffaelli 2004)



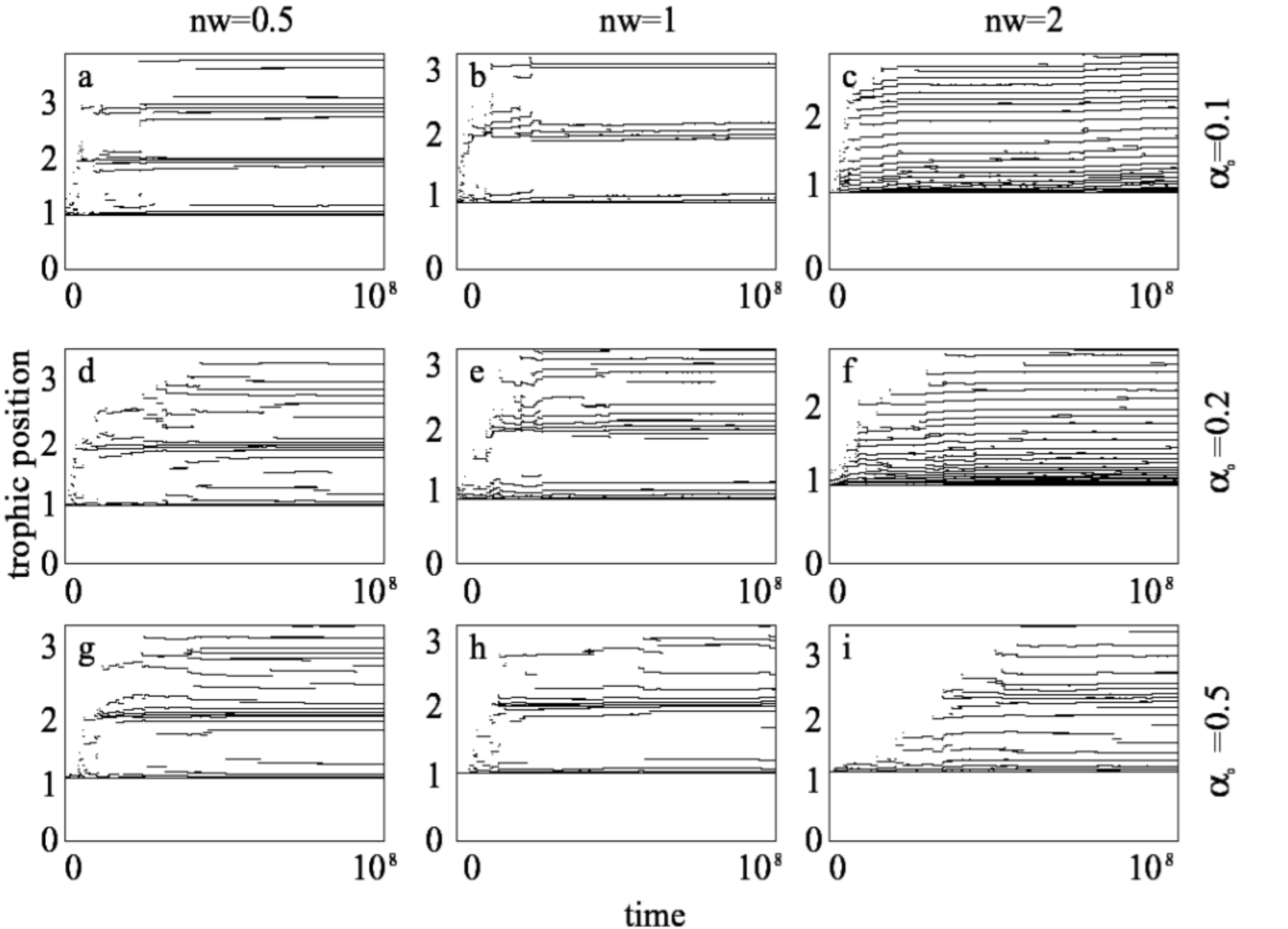
Body size in the model (Loeuille & Loreau 2005)



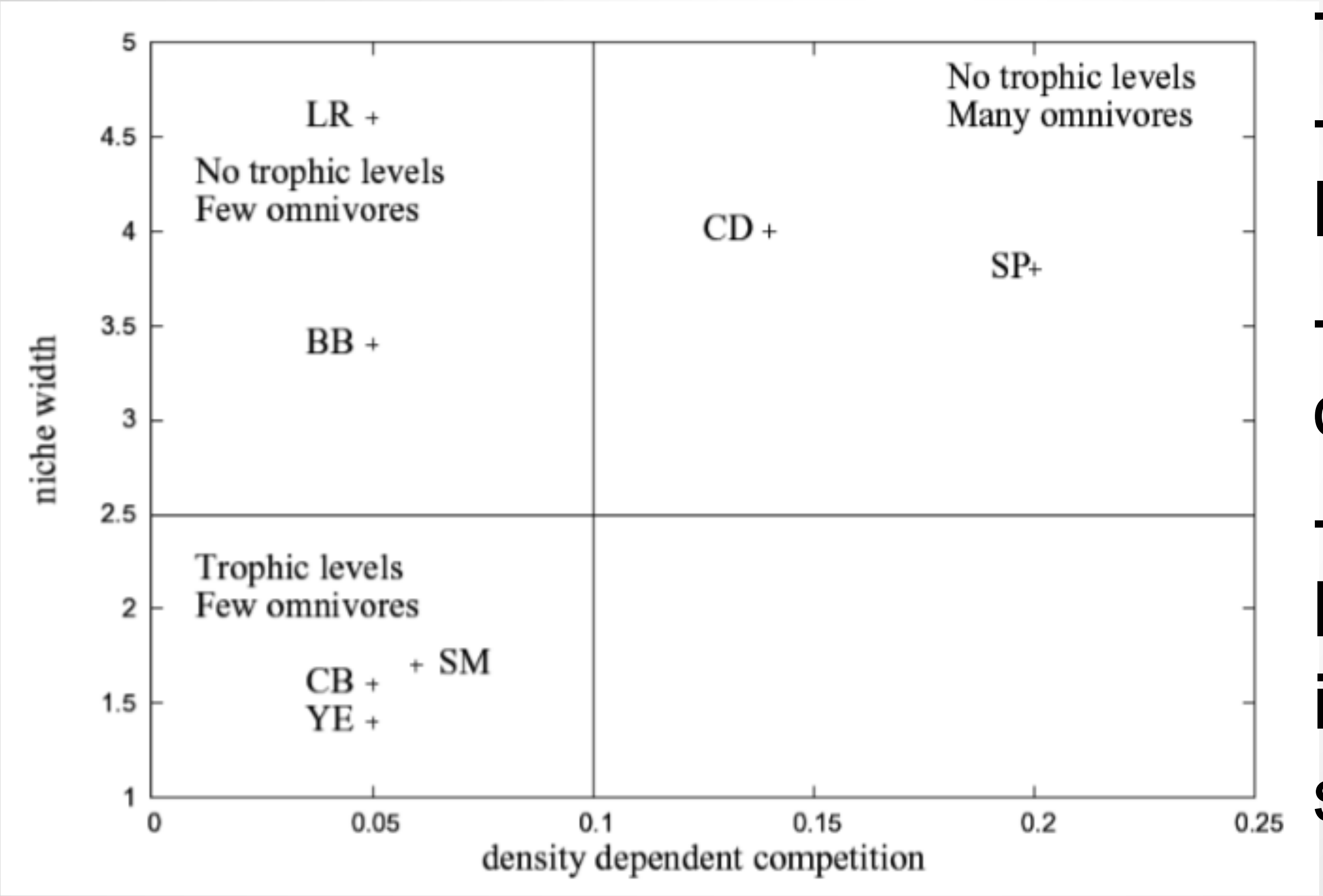
Food web evolutionary assembly



Food web evolutionary assembly (II)


nw=0.5
nw=1
nw=2
a
b
c
d
e
f
g
h
i
trophic position
time
0
10^8
α_o=0.1
α_o=0.2
α_o=0.5

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 species harvesting

Possible questions for coevolution models applied to food webs

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Eco-evolutionary dynamics in exploited webs

Demographic and evolutionary effects

-At population scale

*population decreases

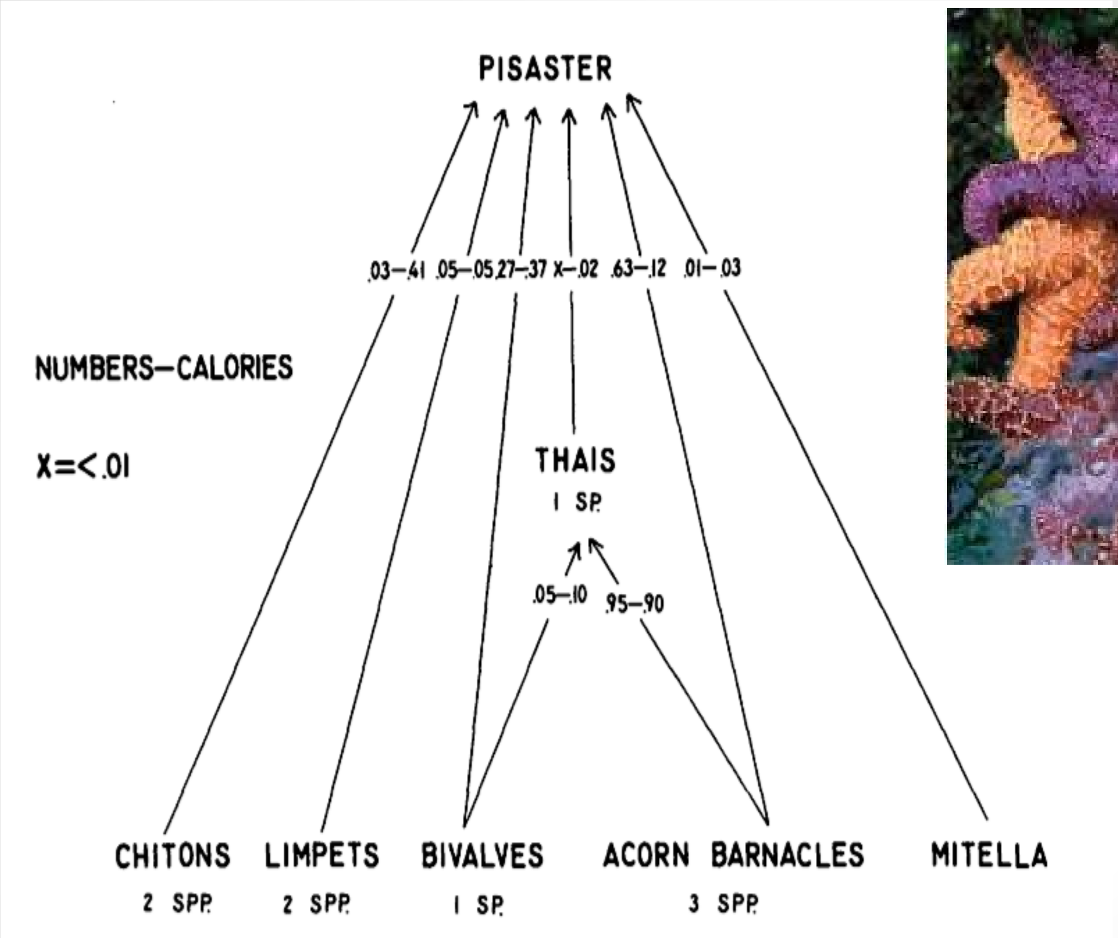
*possibly, extinction of the exploited population (primary extinction)

-At community scale:

*Variation of connected populations, propagation of indirect effects

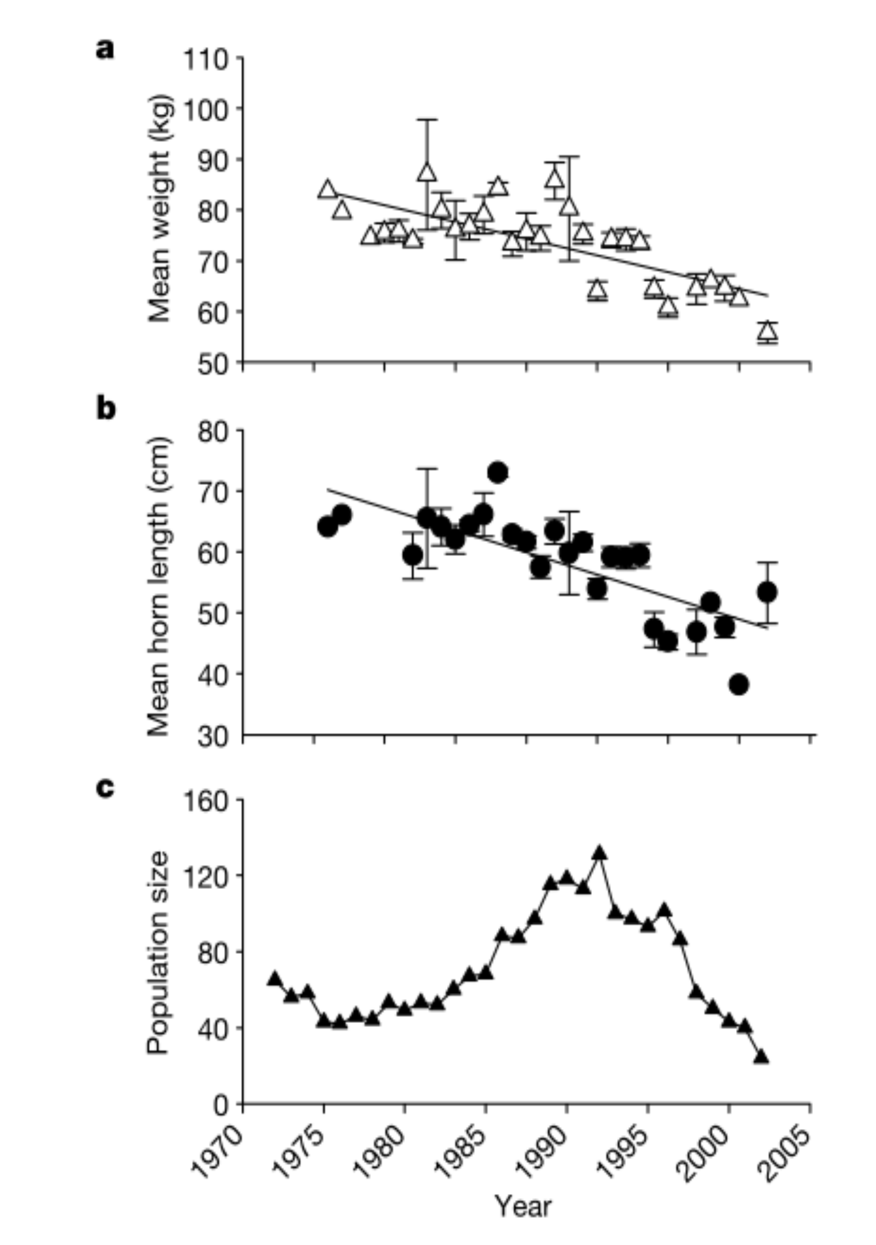
*may lead to secondary extinctions

-Evolutionary effects: variations in phenotypic traits. Especially in the case of “targeted exploitation”

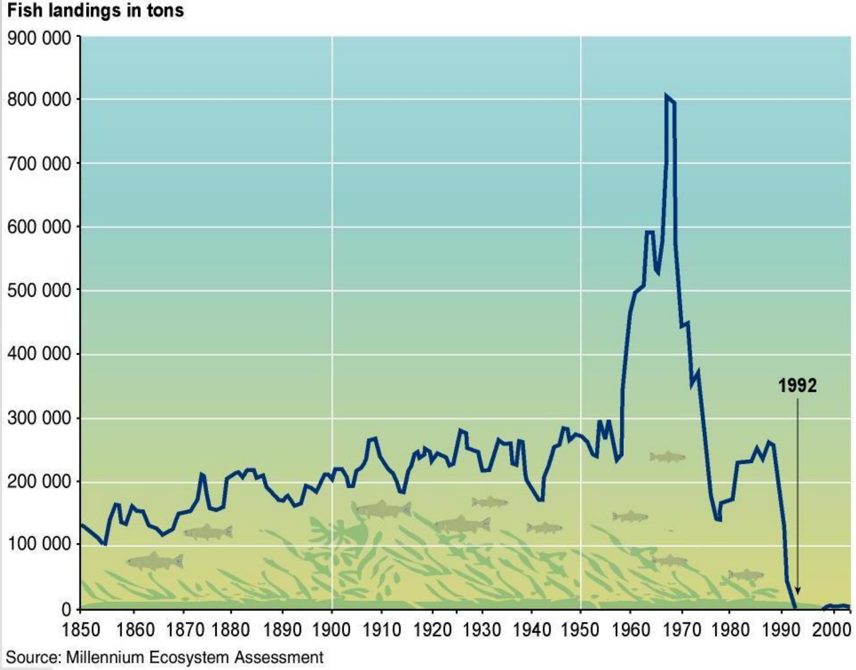


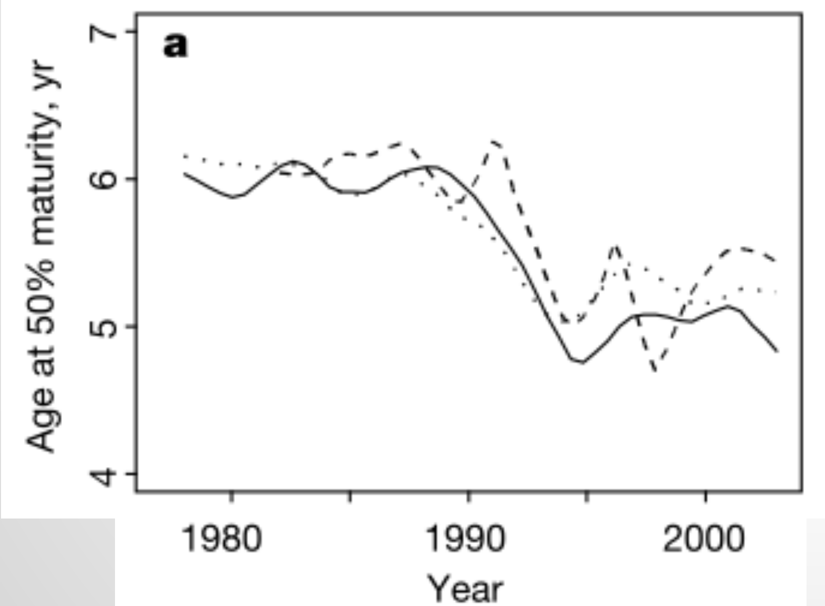
Paine, 1966

Indirect demographic effects (Paine 1966)

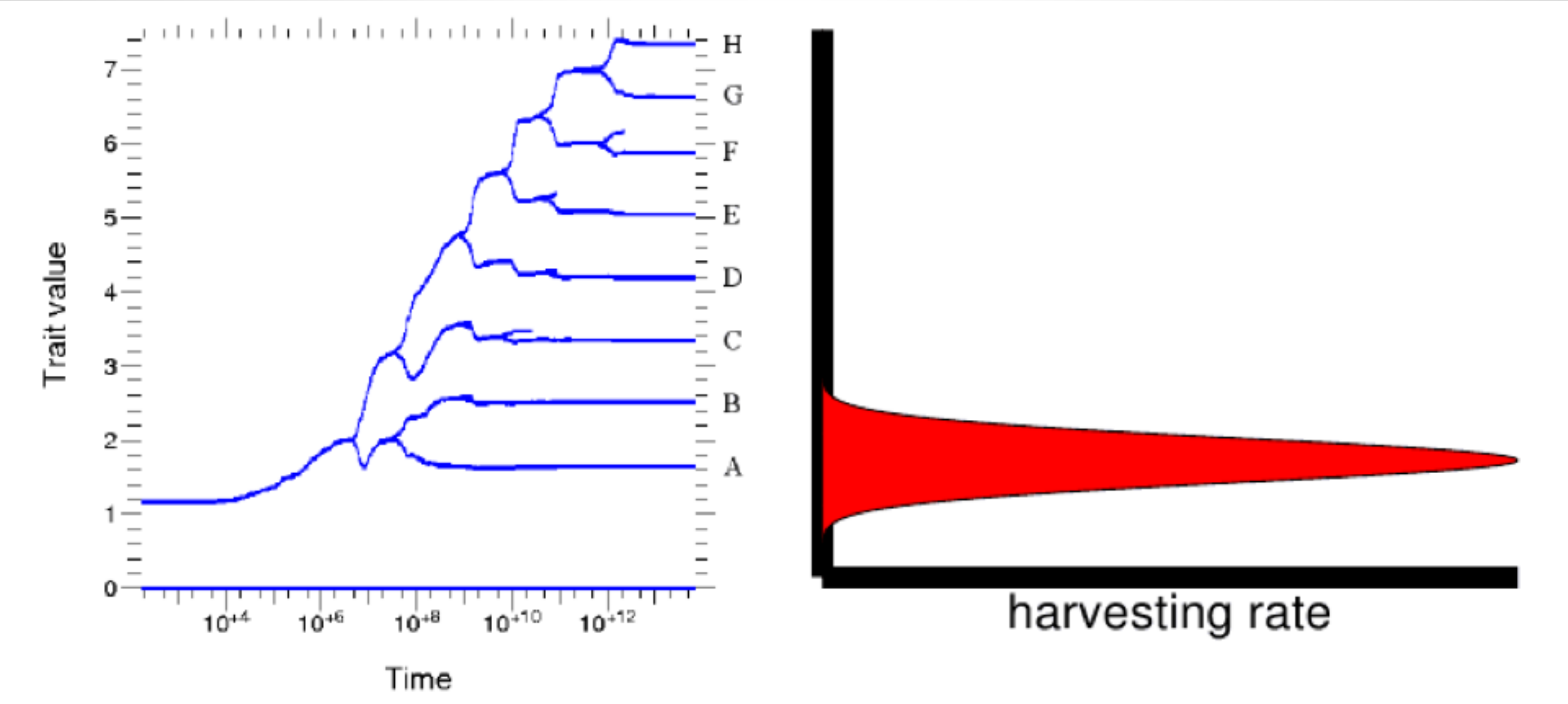


Direct evolutionary effects: Coltman et al 2003

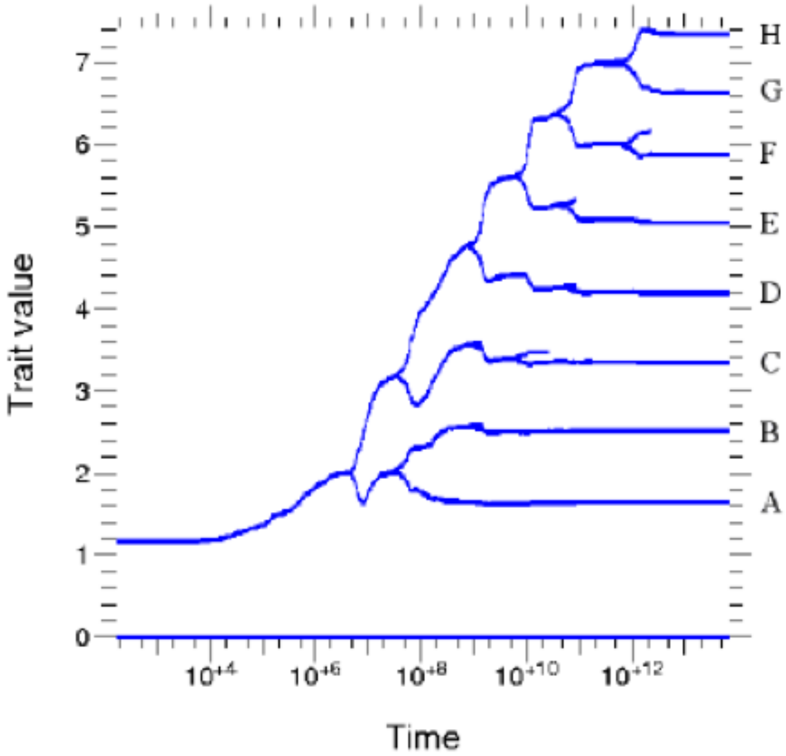


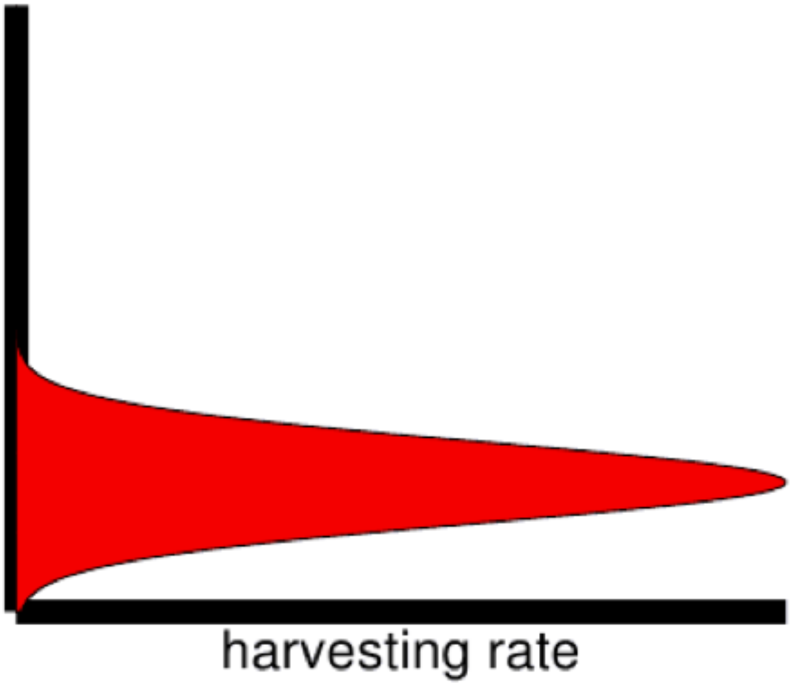


Direct evolutionary effects: Olsen et al. 2004

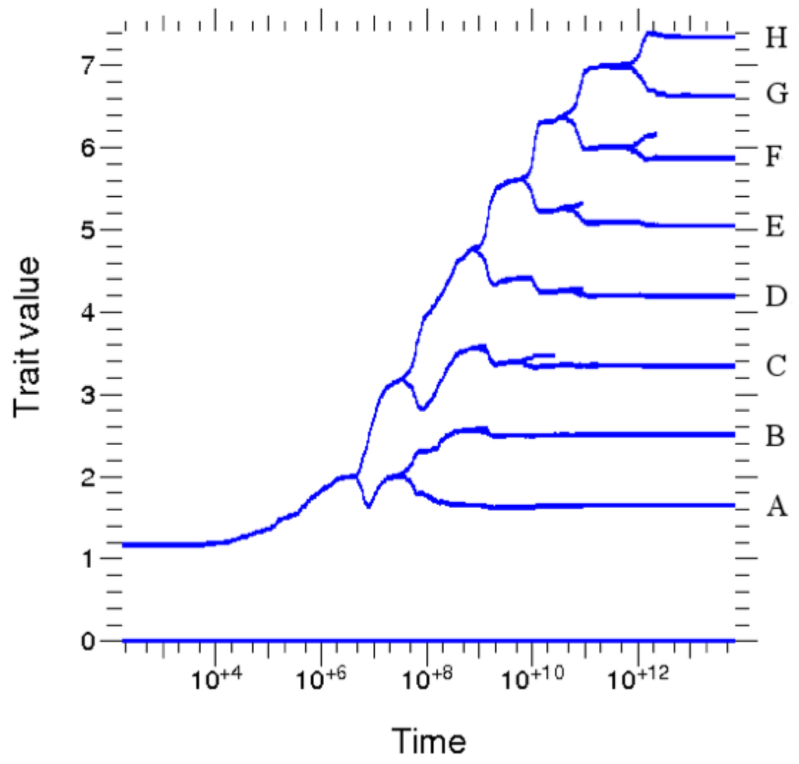


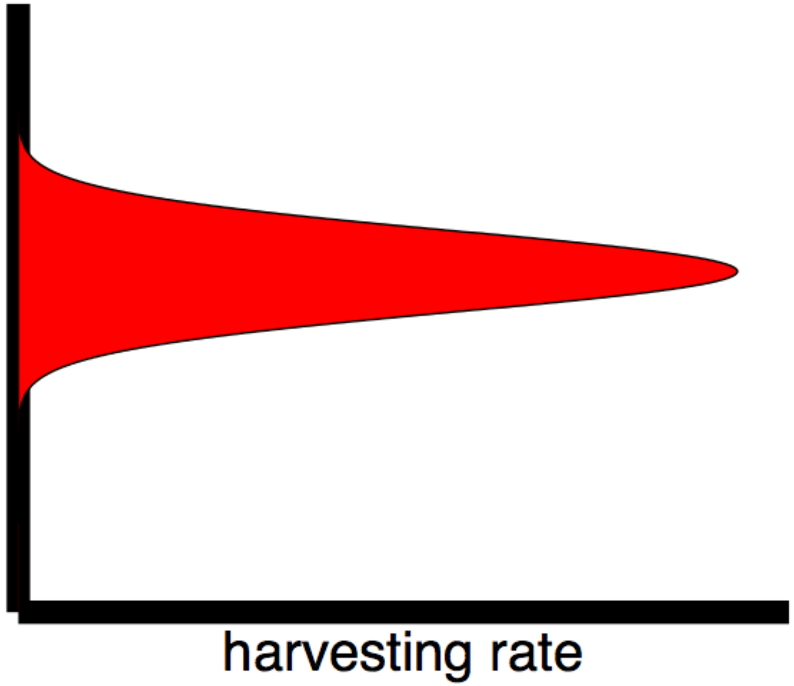
Targeting a given size range within the food web



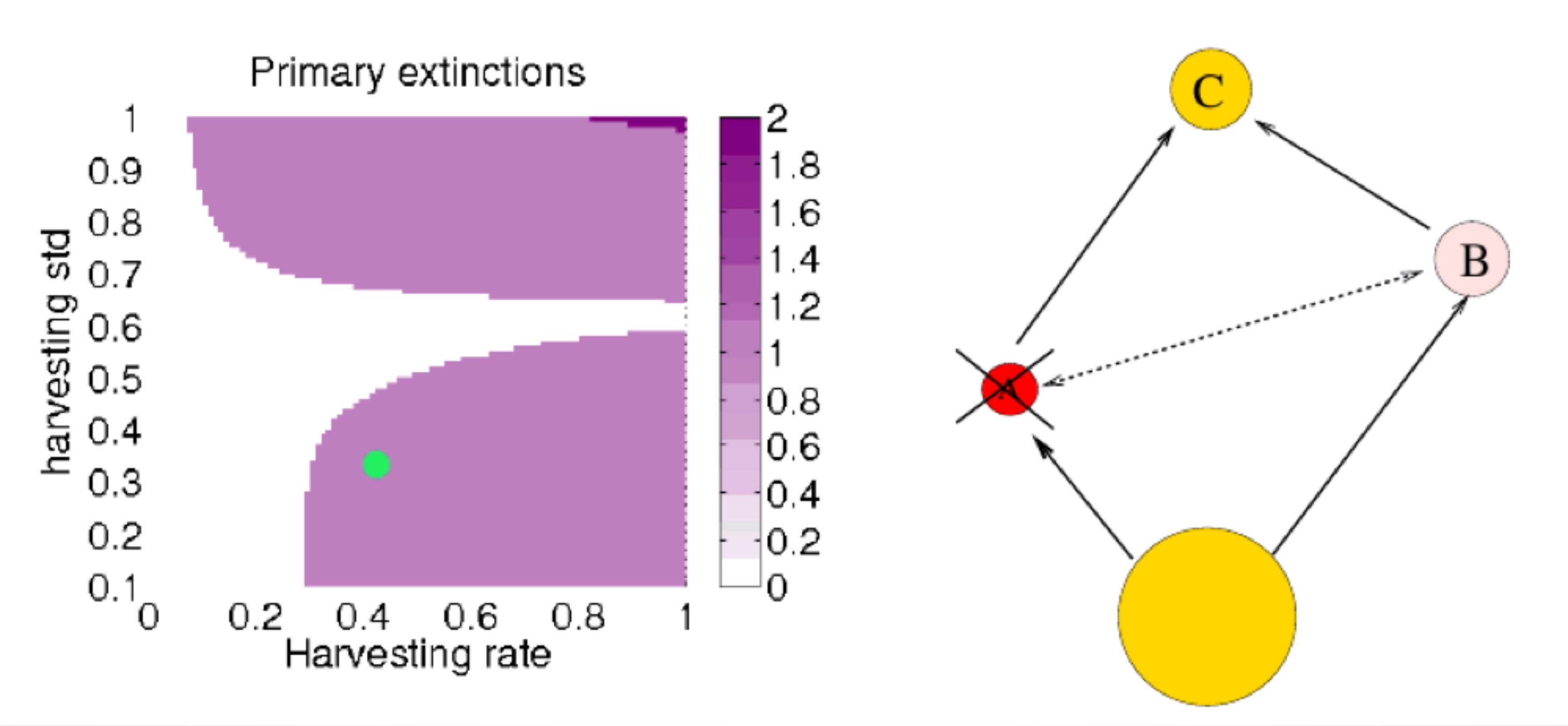


Exploiting a larger size range

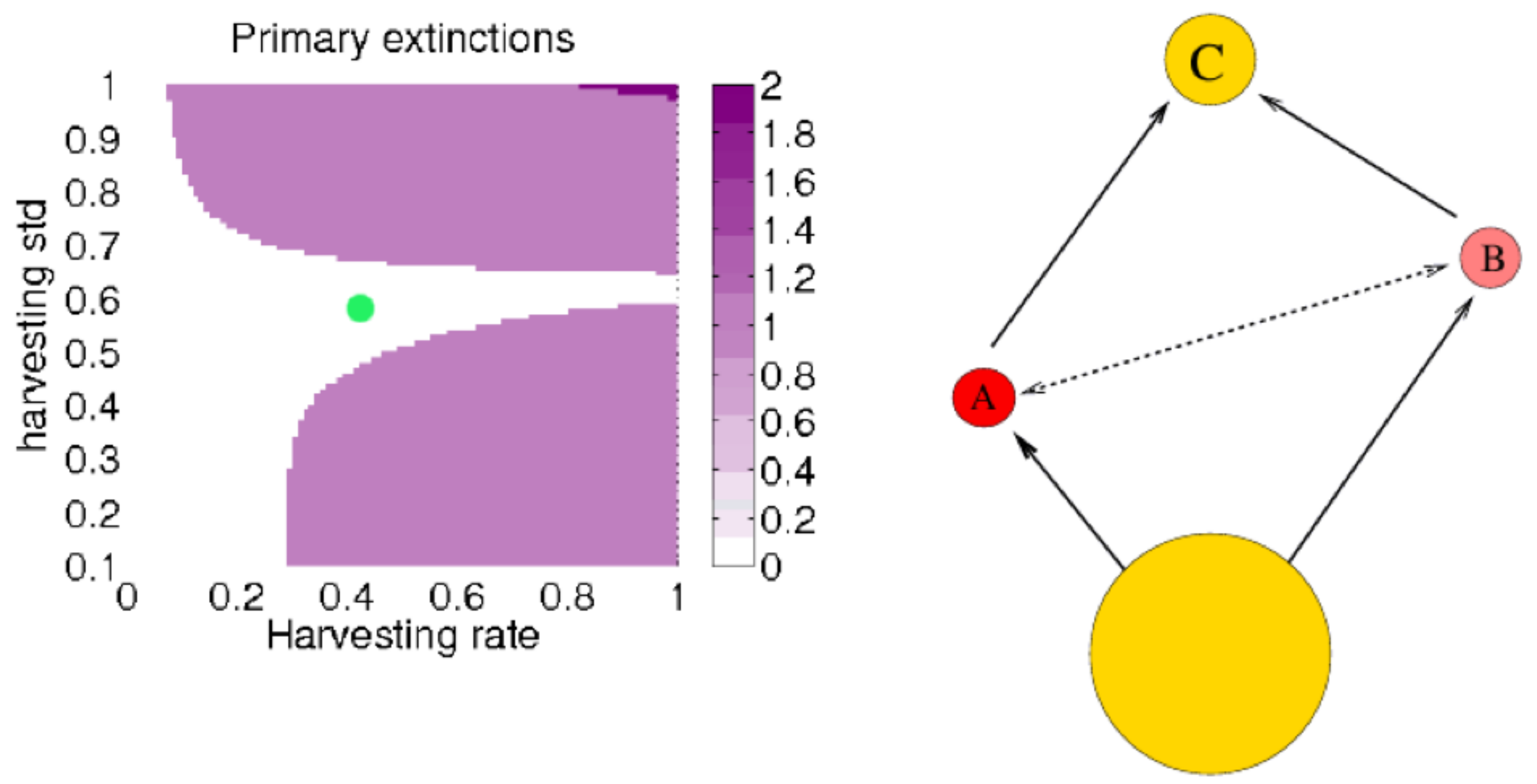




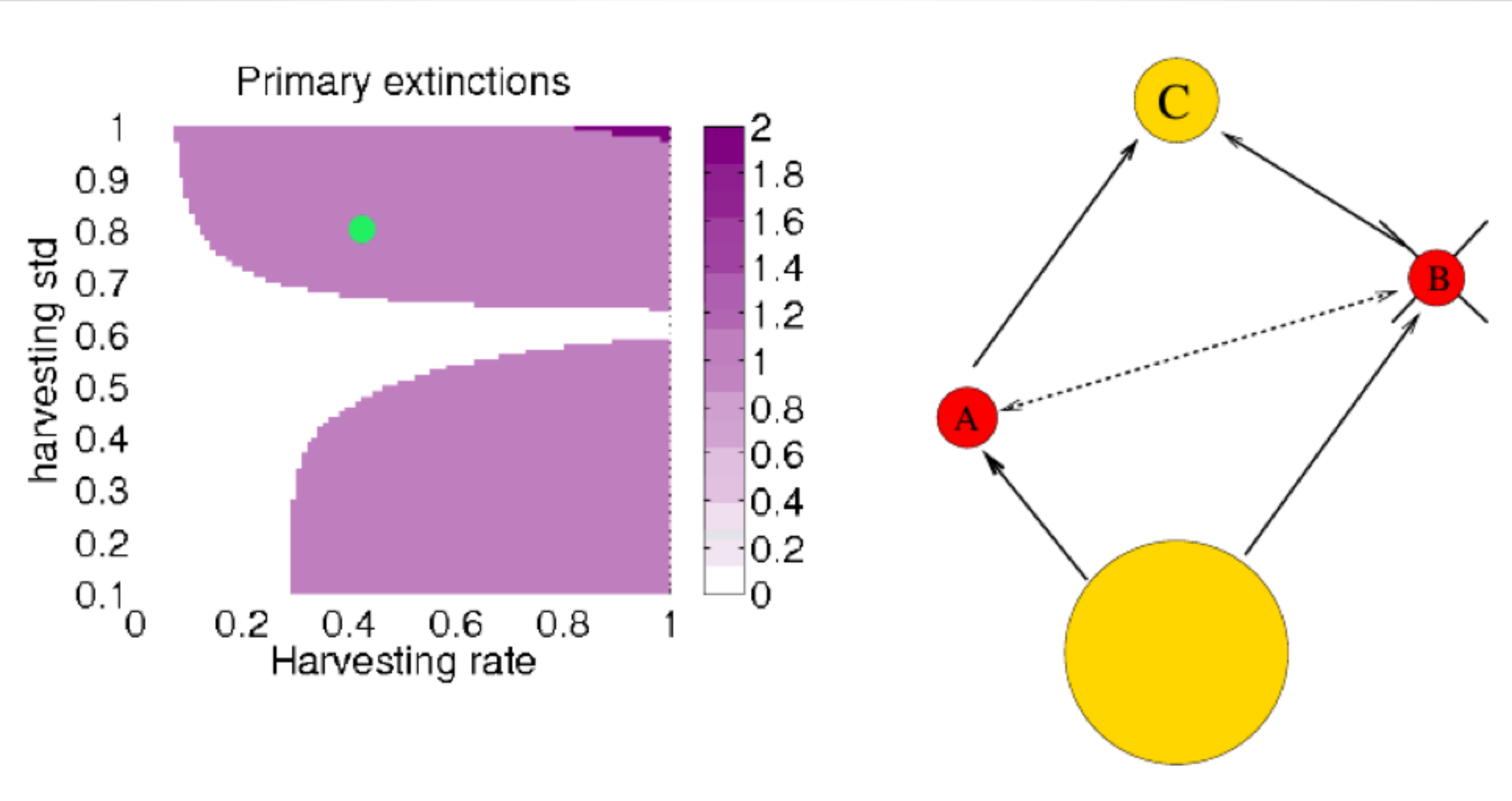
Targeting different parts of the web



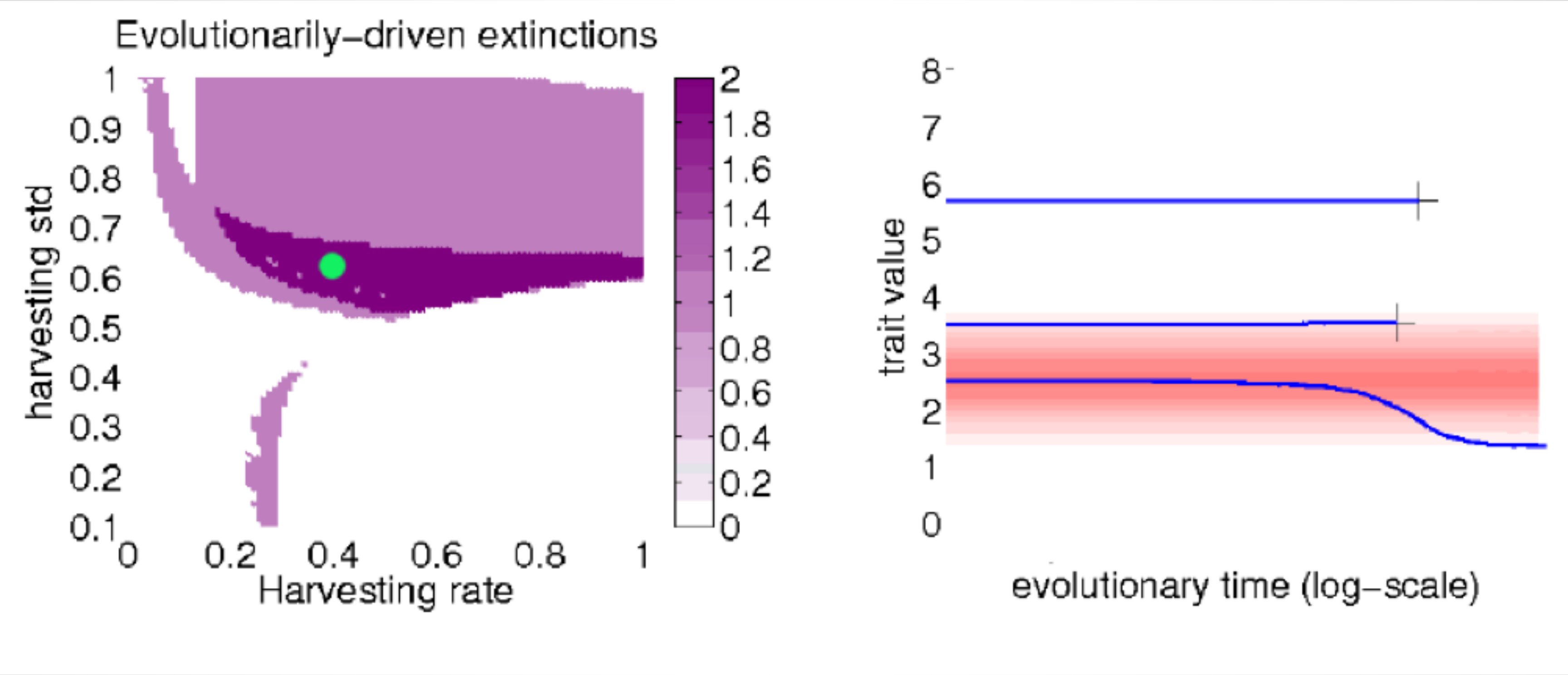
Exploiting the basal species



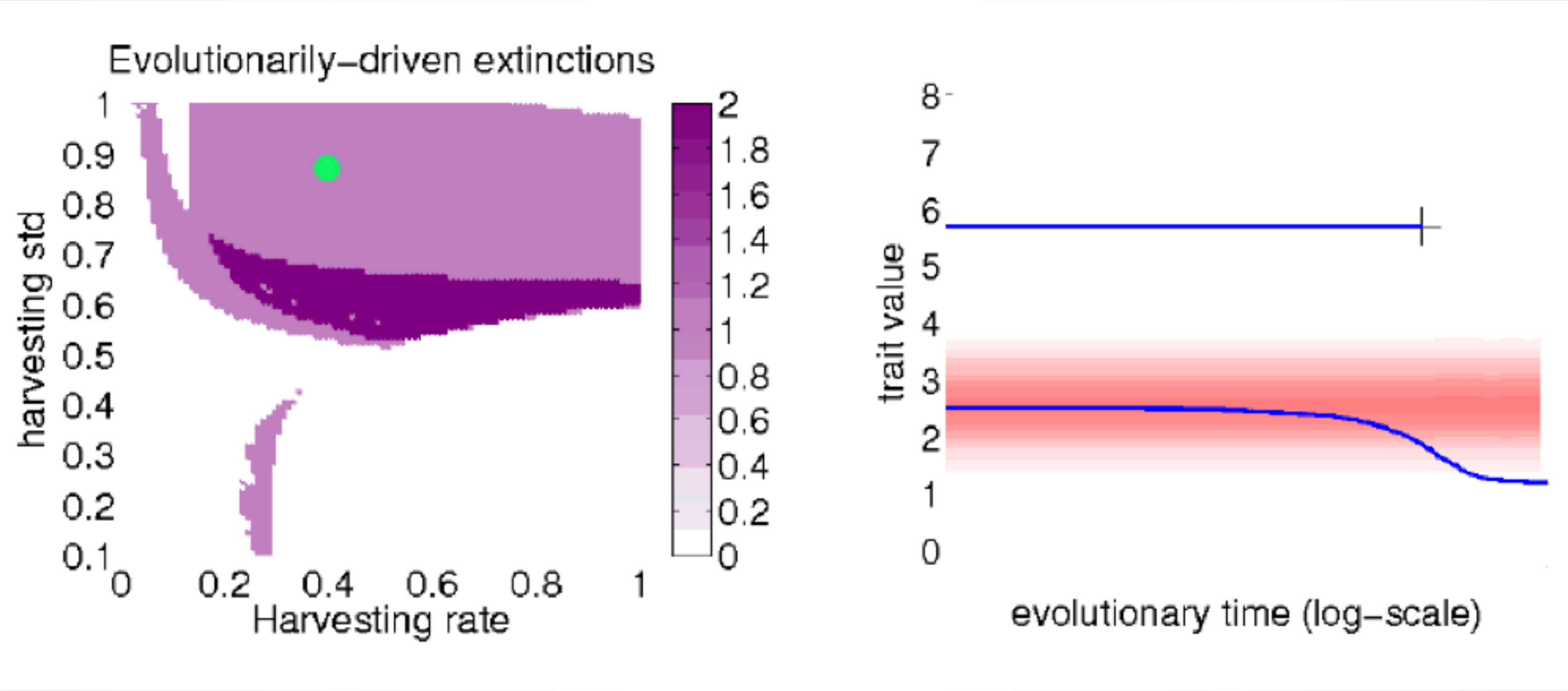
Exploiting the basal species



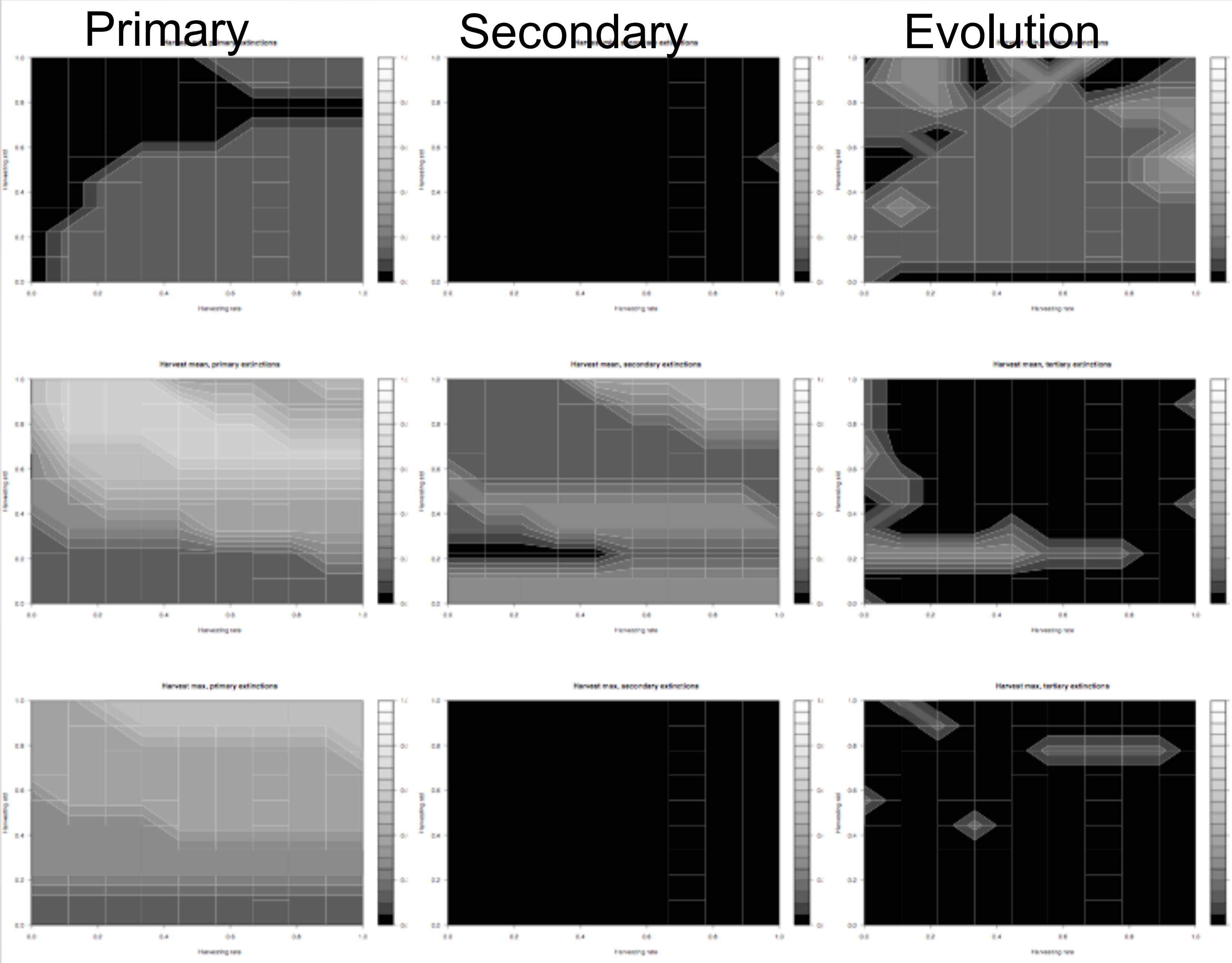
Exploiting the basal species



Evolutionary effects



Evolutionary effects



Compiling this experiment on several webs

Extinctions and evolution in food webs

-Primary extinctions are the most numerous

-Range of targeted body sizes is more important than intensity of exploitation

-Secondary extinctions happen when the middle part of the web is exploited

-Evolutionary extinctions are more prevalent when the bottom of the web is exploited

-Few indirect effects when exploiting the top of the web

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How does evolution affect the stability of complex webs?

Loeuille 2010, Ecol Let

Stable if and only if:
$s\sqrt{(nC)}<1$

Stability decreases diversity (May 1973)

Hypotheses and shortcomings

-hyp of May: all types of interactions, interaction strengths drawn at random, with mean *s*

-adding food web constraints (conversion efficiency, self-regulation of higher trophic levels, donor control) increases stability (De Angelis 1975)

-Interaction strengths are not random because they depend on the assembly process

-Interaction strengths are not random because of species evolution/coevolution

Goals

Determine how the effect of evolution on stability depends on:

1) Interaction type

2) Cost associated with phenotypic trait

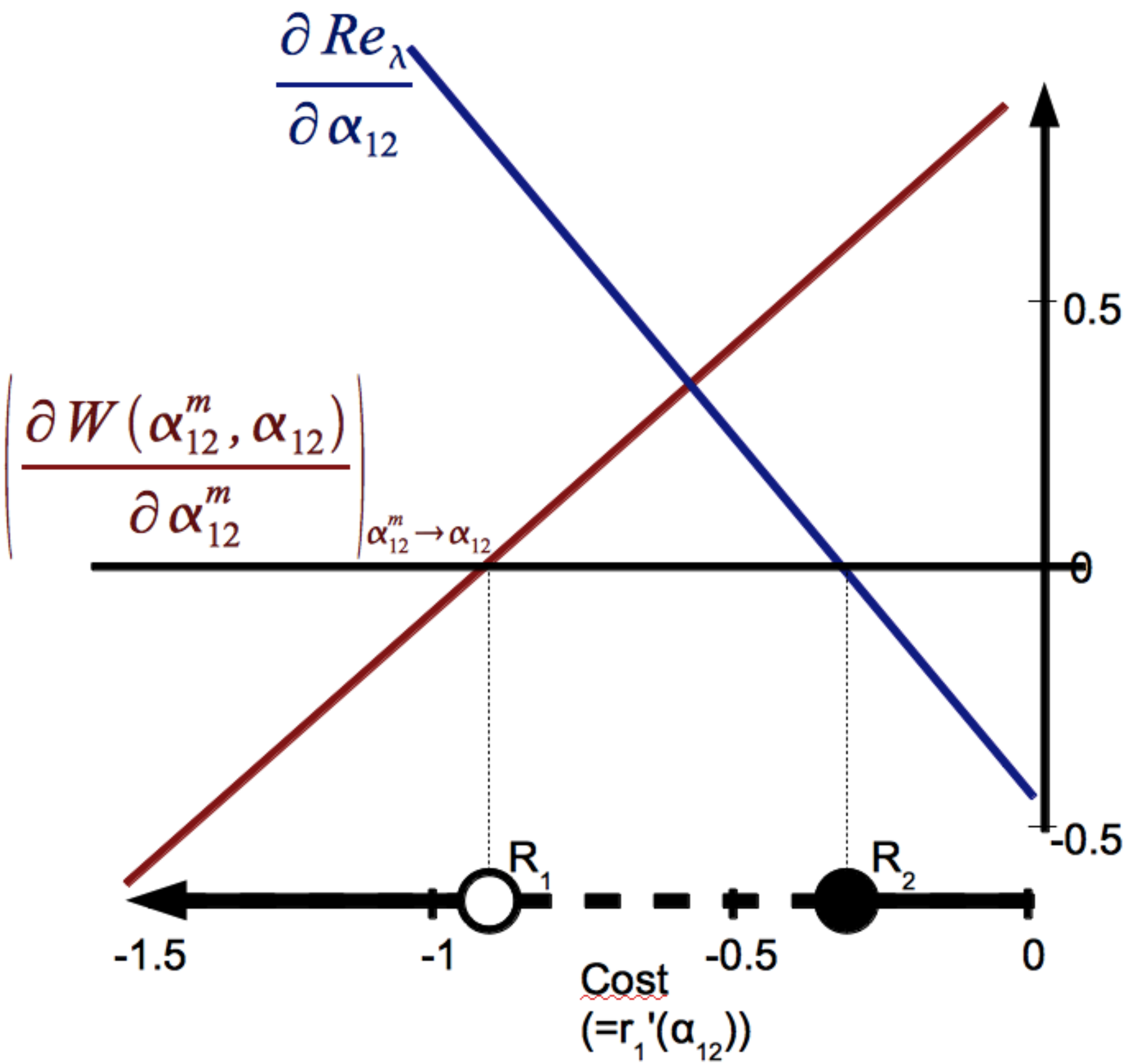
3) Diversity of the community

$$\begin{cases} \frac{dN_1}{dt} = N_1(r_1 + \alpha_{11}N_1 + \alpha_{12}N_2) \\ \frac{dN_2}{dt} = N_2(r_2 + \alpha_{21}N_1 + \alpha_{22}N_2) \end{cases}$$

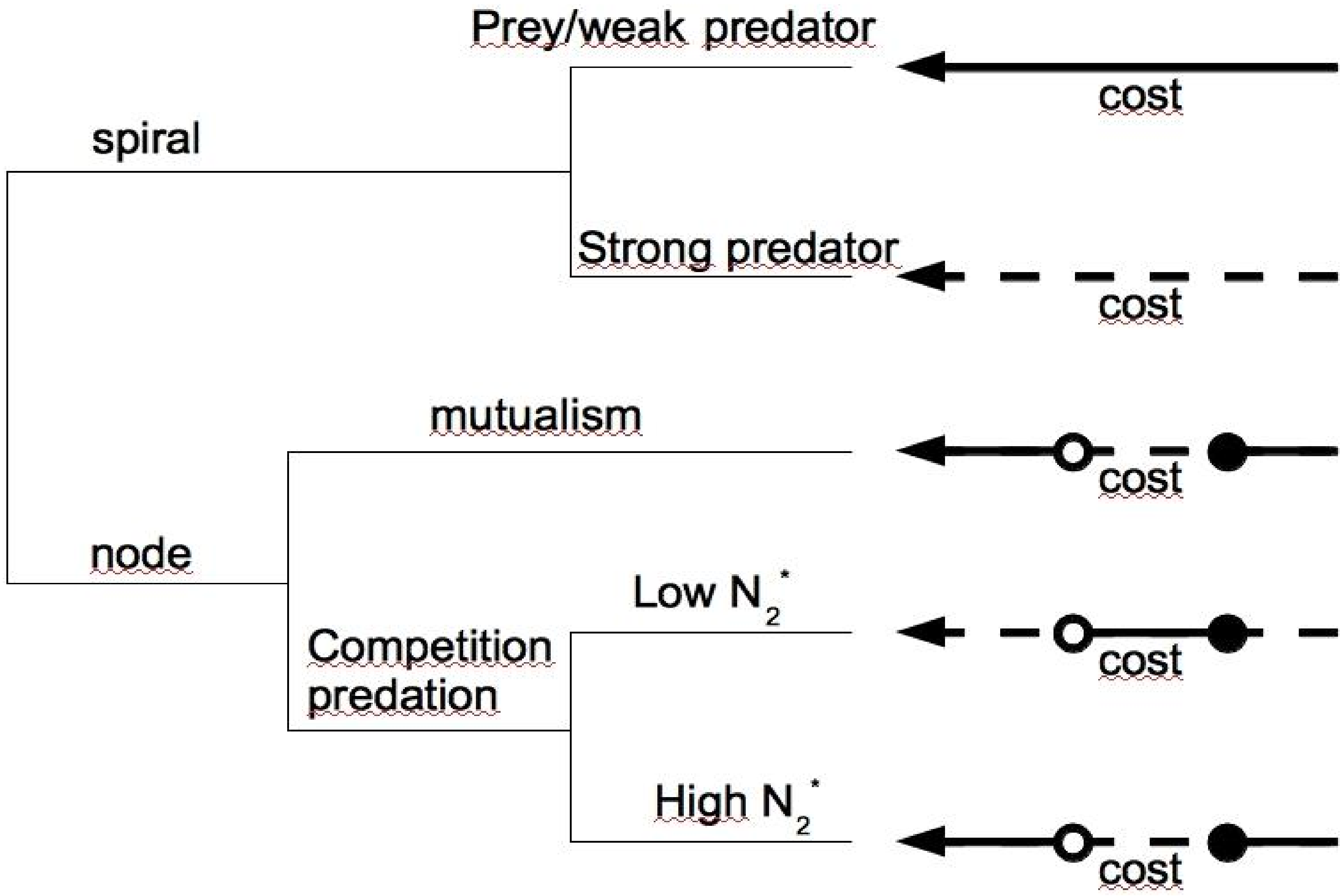
$$\lambda_{1,2} = \frac{Tr(J^*) \pm \sqrt{Tr(J^*)^2 - 4Det\,(J^*)}}{2}$$

$$\frac{dRe_\lambda(x(t))}{dt} = \frac{\partial Re_\lambda}{\partial x}\frac{dx}{dt} \propto \frac{\partial Re_\lambda}{\partial x}\left(\frac{\partial W(x_m, x)}{\partial x_m}\right)_{x_m \longrightarrow x}$$

A simple model



Mutualistic interaction, allocation trade-off



Summary of results, allocation costs

A few general results

-For trophic interactions, spiral cases with allocation costs lead to all or nothing results: always stabilization if prey or "weak" predator, destabilization else.

Consequence: overall more probability of stabilization when trophic interaction.

-Extreme cost scenarios more often lead to stabilization.

-Results are qualitatively similar for the two cost types.

On the effects of diversity

-Communities are made using May's recipe.

C=0.1

s=0.2

n varies between 5 and 100

-Check that equilibrium is stable and positive; record resilience.

-Use fitness gradient to determine next successful mutant; record new resilience.

-allocation costs: 140000 communities

ecological costs: 880000 communities

In total over 20 millions of mutations.

How does evolution affect May's results?

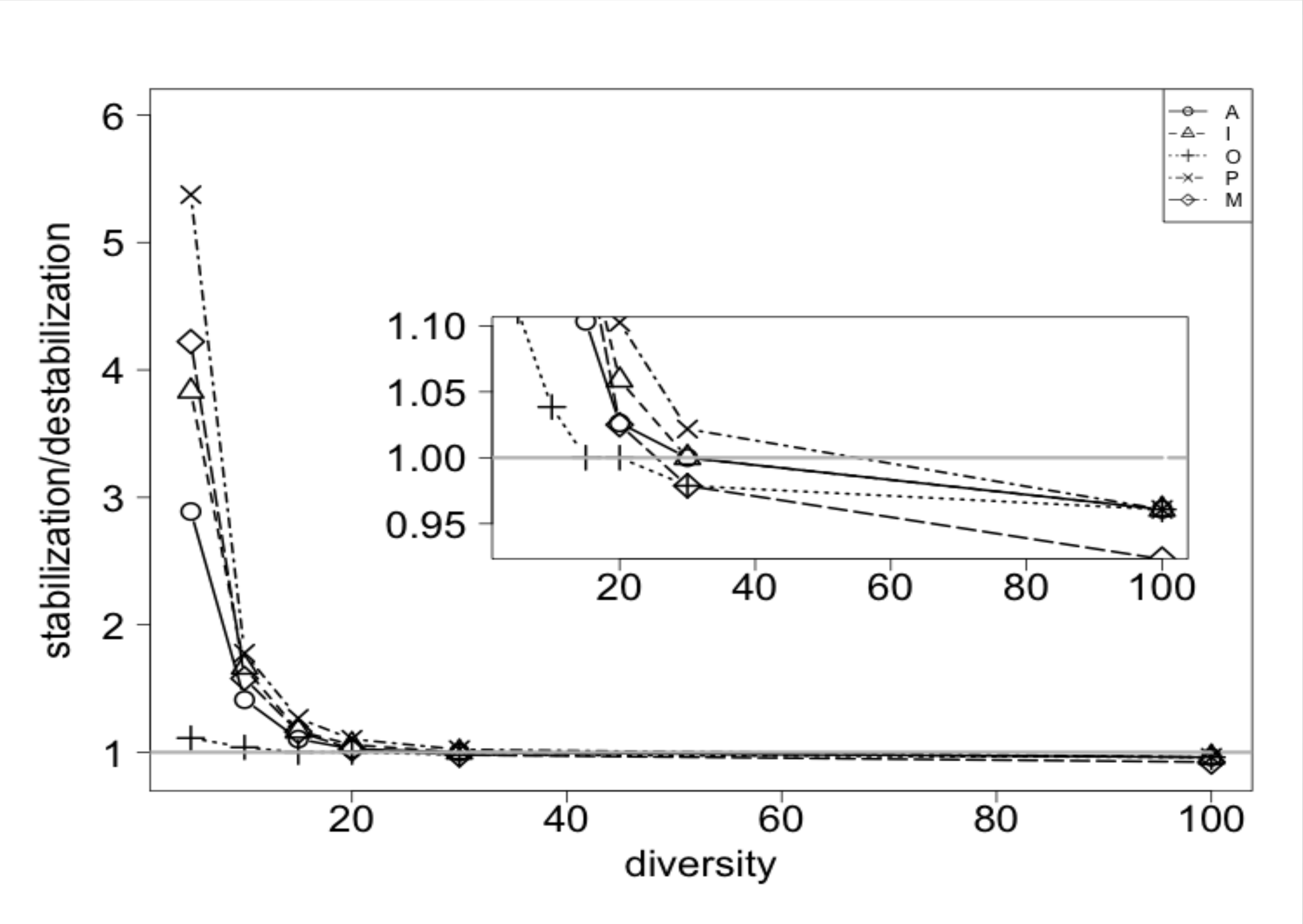
-Recall: May: More diversity begets less stability when communities are randomly assembled.

-Evolution can counteract this effect if:

*It overall leads to more stability regardless of diversity

or

*Its effect on stability is positive for high diversity communities.



Overall effects (allocation costs)

General conclusions

-Little qualitative effects of the cost types.

-Evolution most often stabilizes communities.

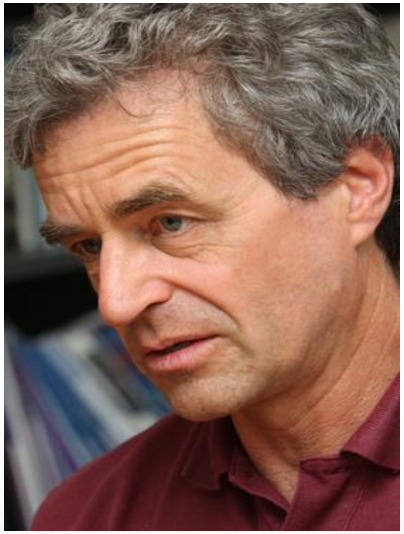
-Evolution is destabilizing at high diversity, therefore may not counteract the destabilizing effect of diversity observed by May.

-Evolution of trophic interaction is more often stabilizing compared to other interactions.

-Even more so when they are weak, which reinforce the results of McCann et al. (1998).

Ake Brännström

Ulf Dieckmann



Michel Loreau

Thanks to collaborators on this