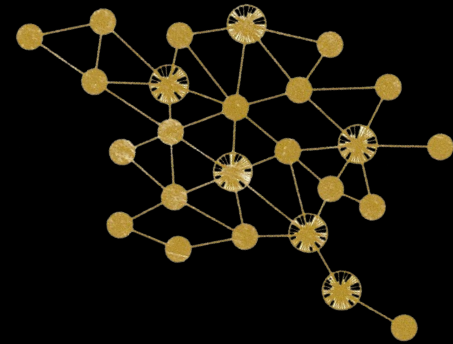


# The multiplexity of ecological communities

Sonia Kéfi



SANTA FE  
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Virginia Domínguez-García  
Vincent Miele

Sergio Navarrete  
Evie Wieters  
Eric Berlow

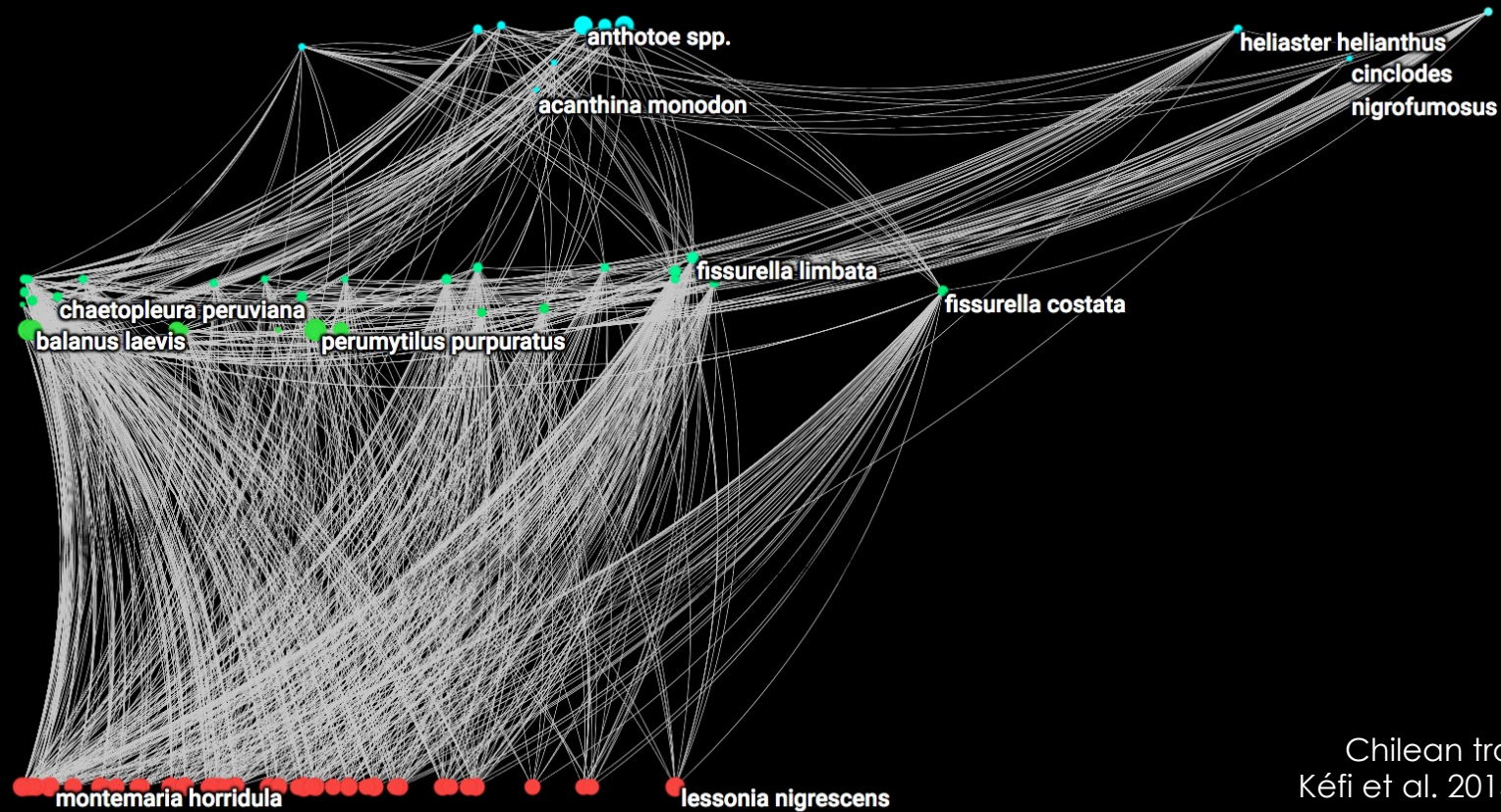
Shai Pilosof  
Mason Porter  
Mercedes Pascual

Ian Donohue  
Alexandre Génin

Christian Guill  
Rodrigo Ramos-  
Jiliberto





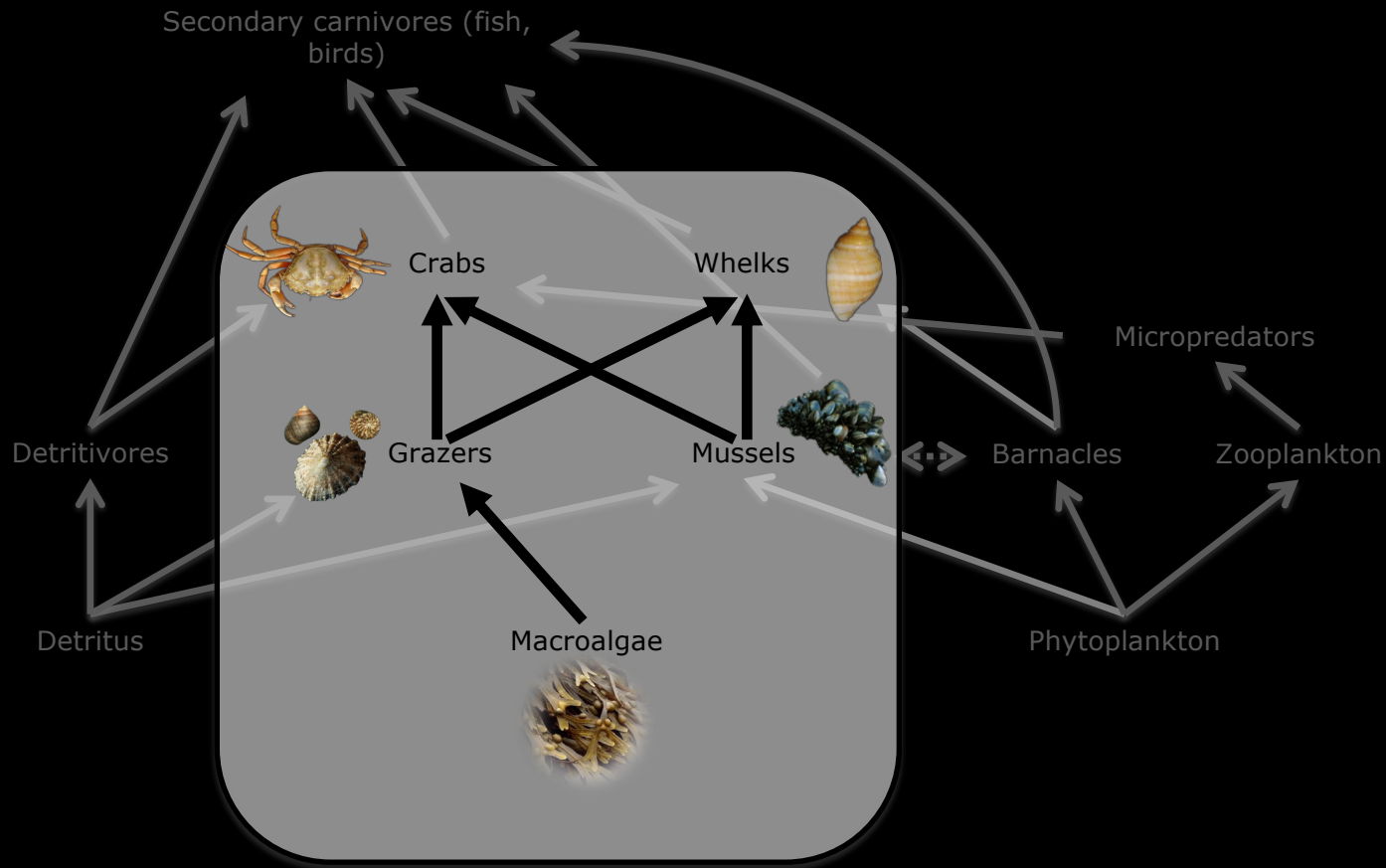


Chilean trophic web  
Kéfi et al. 2015, Ecology  
plotted with mappr

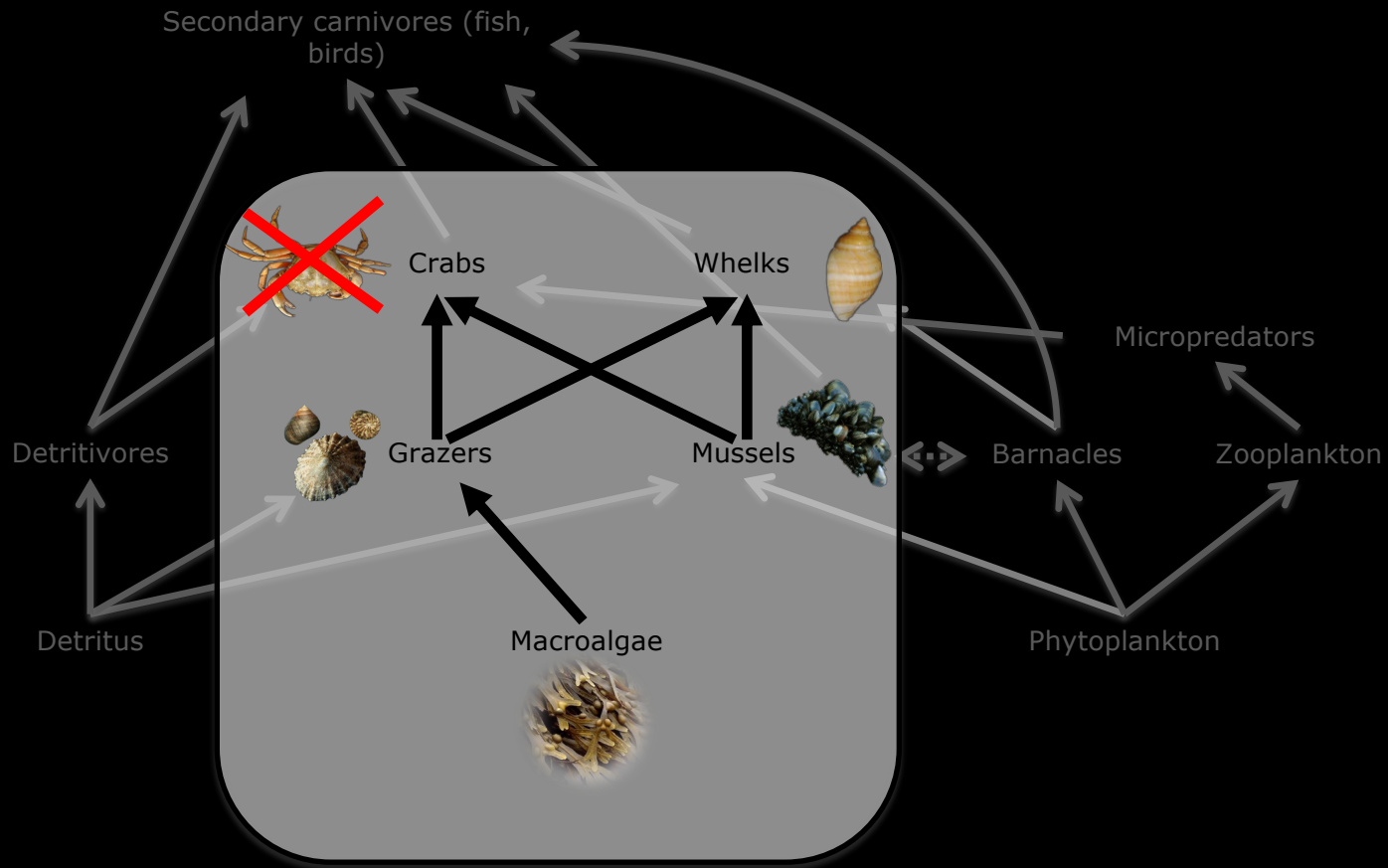


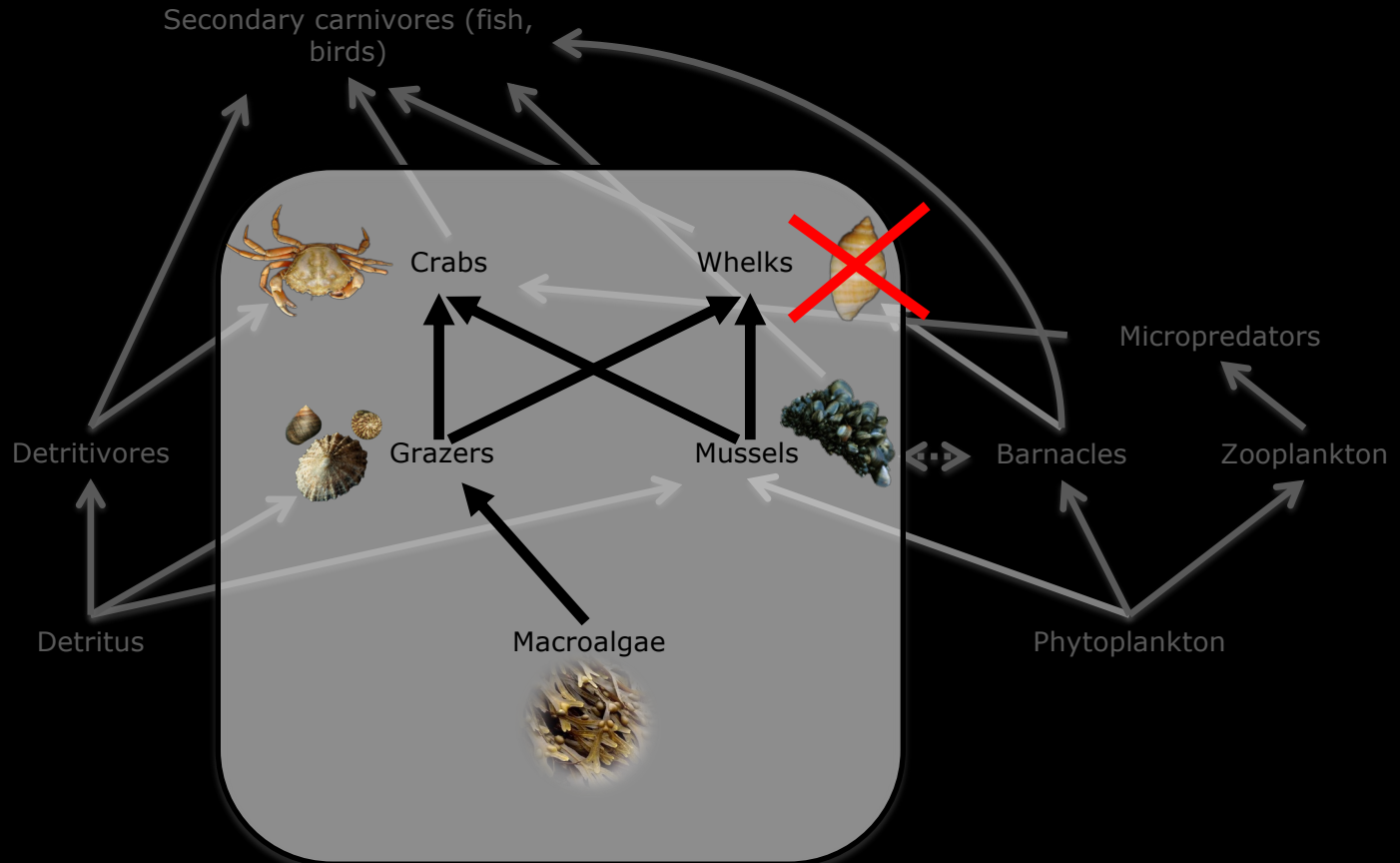


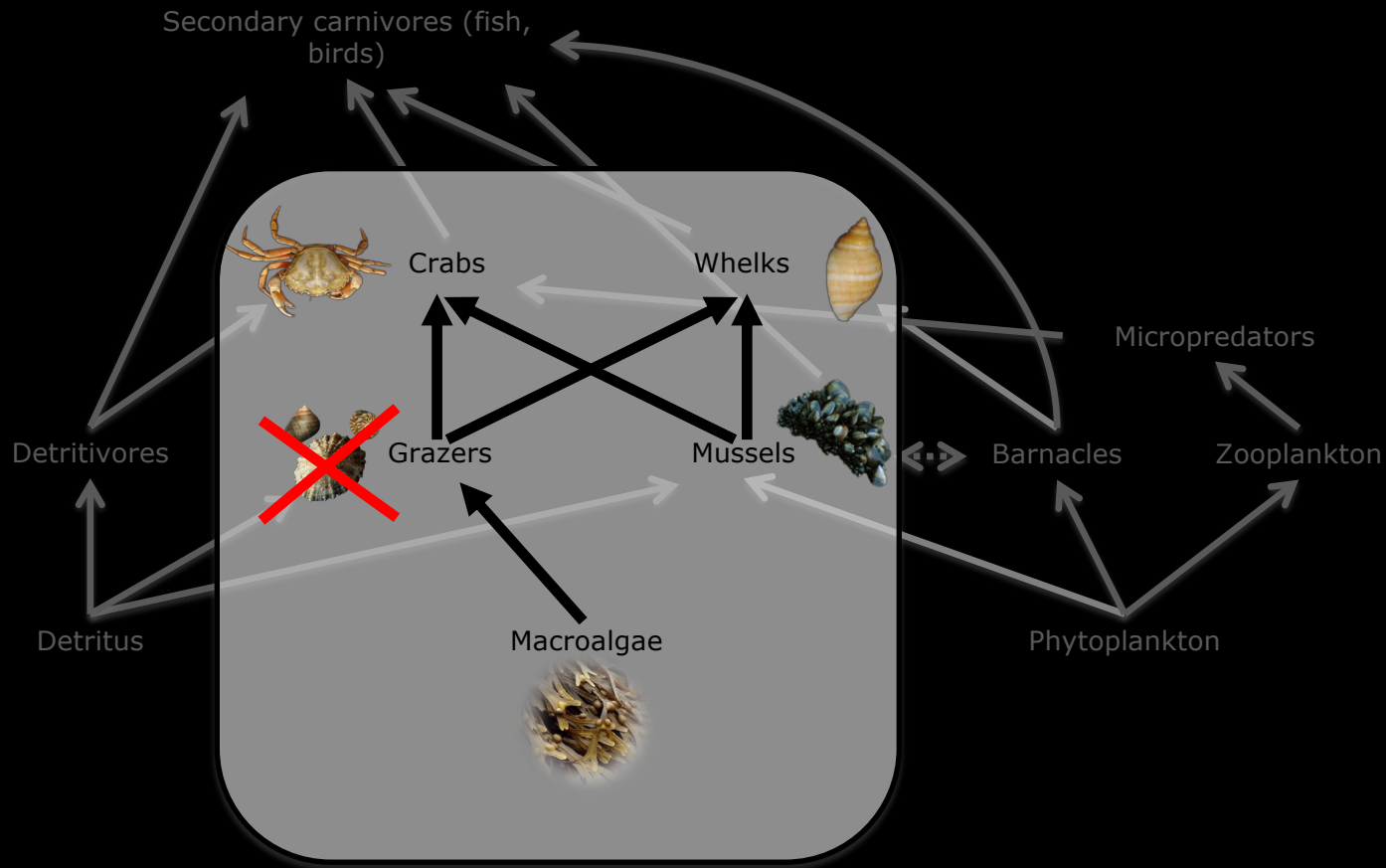
@ian Donohue

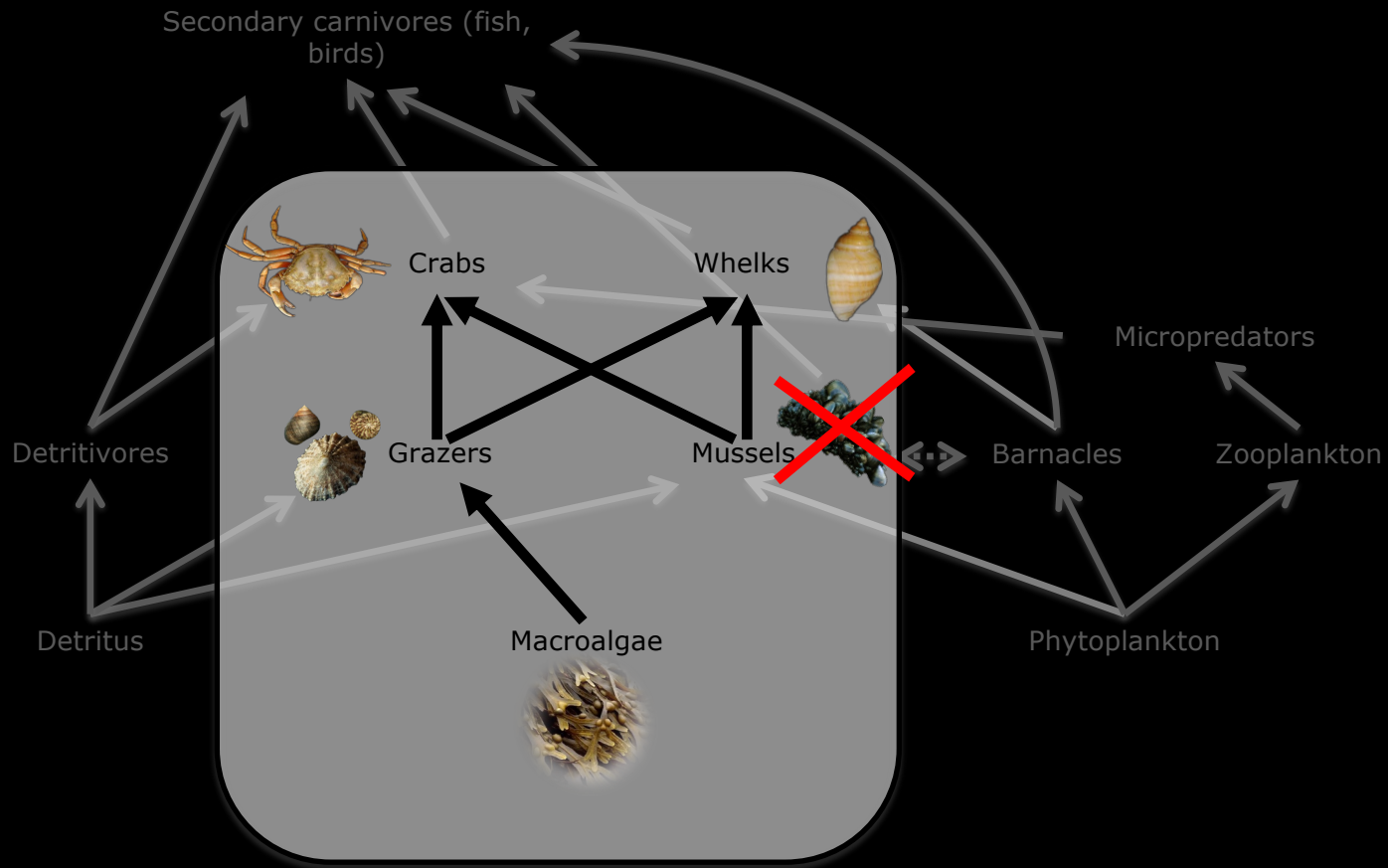


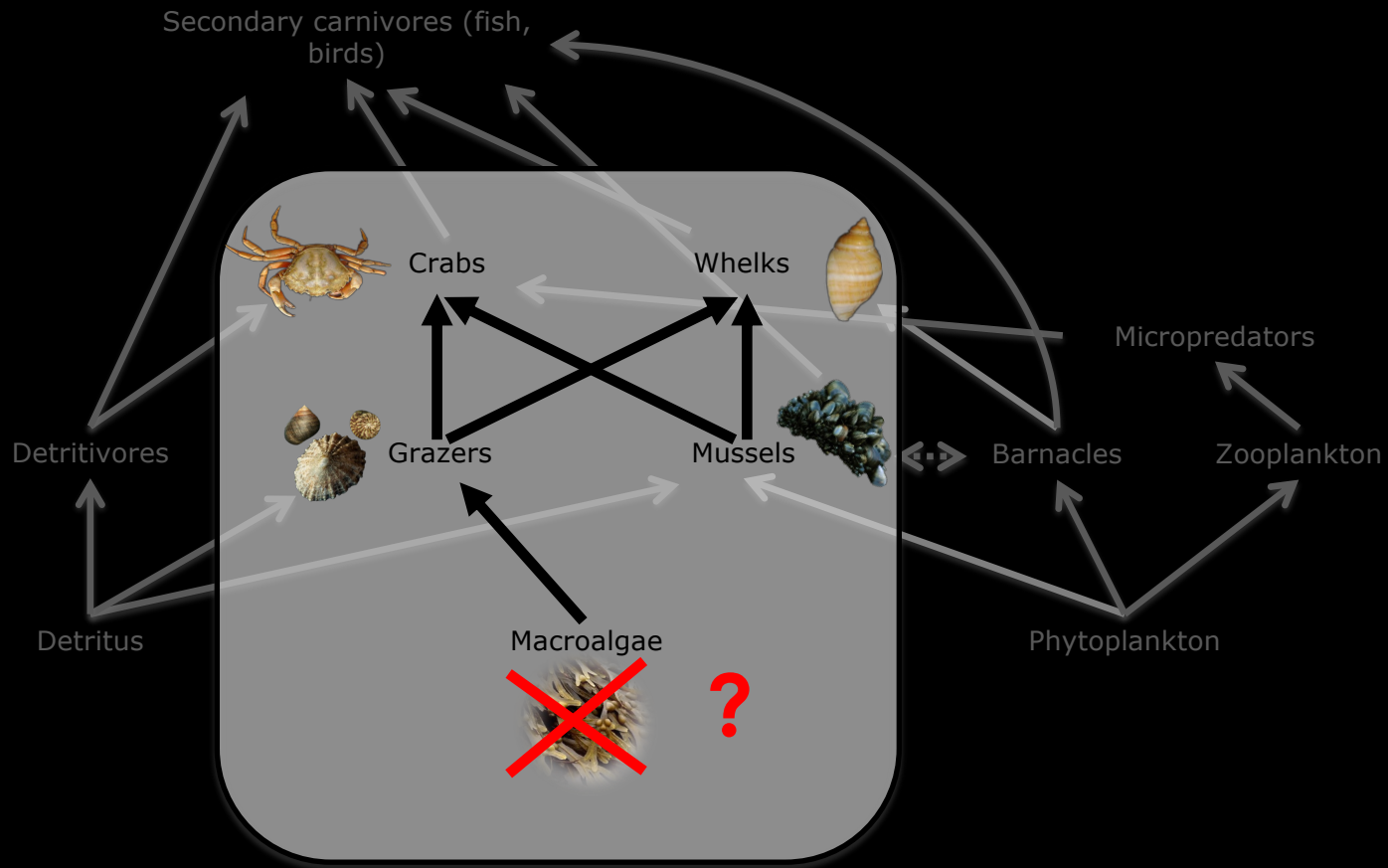


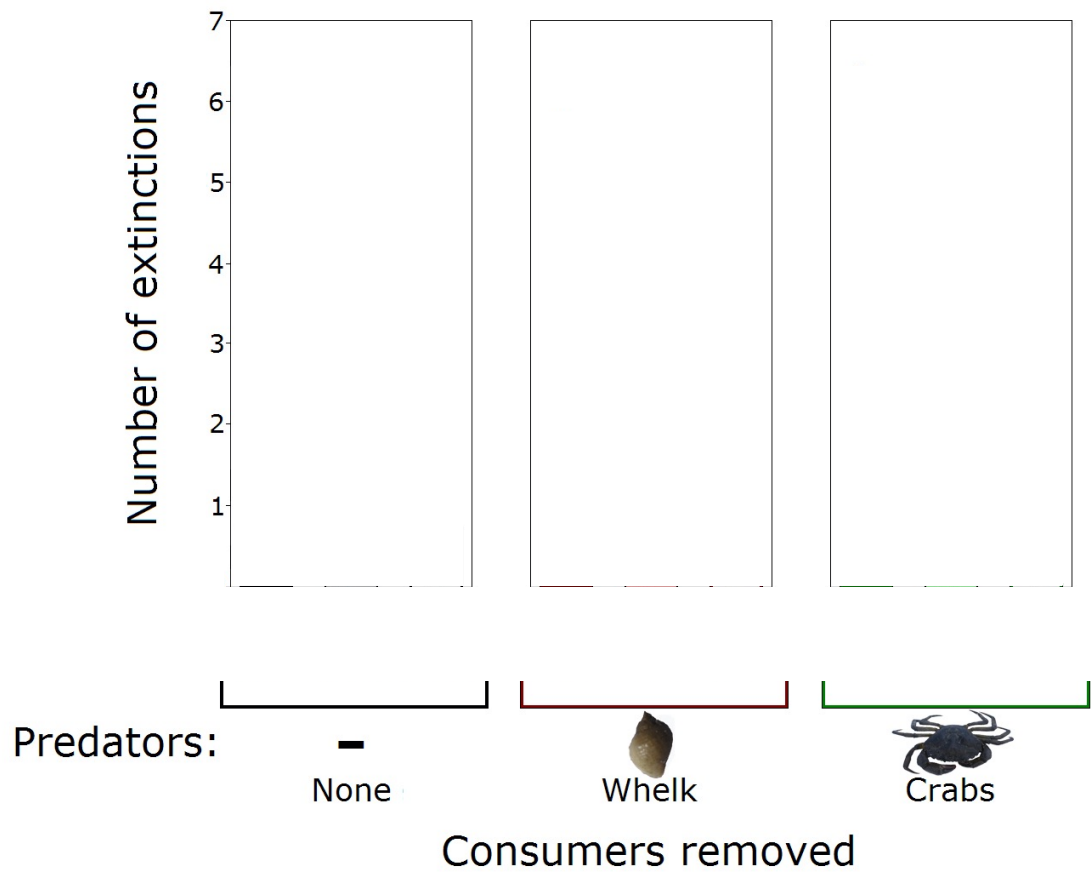


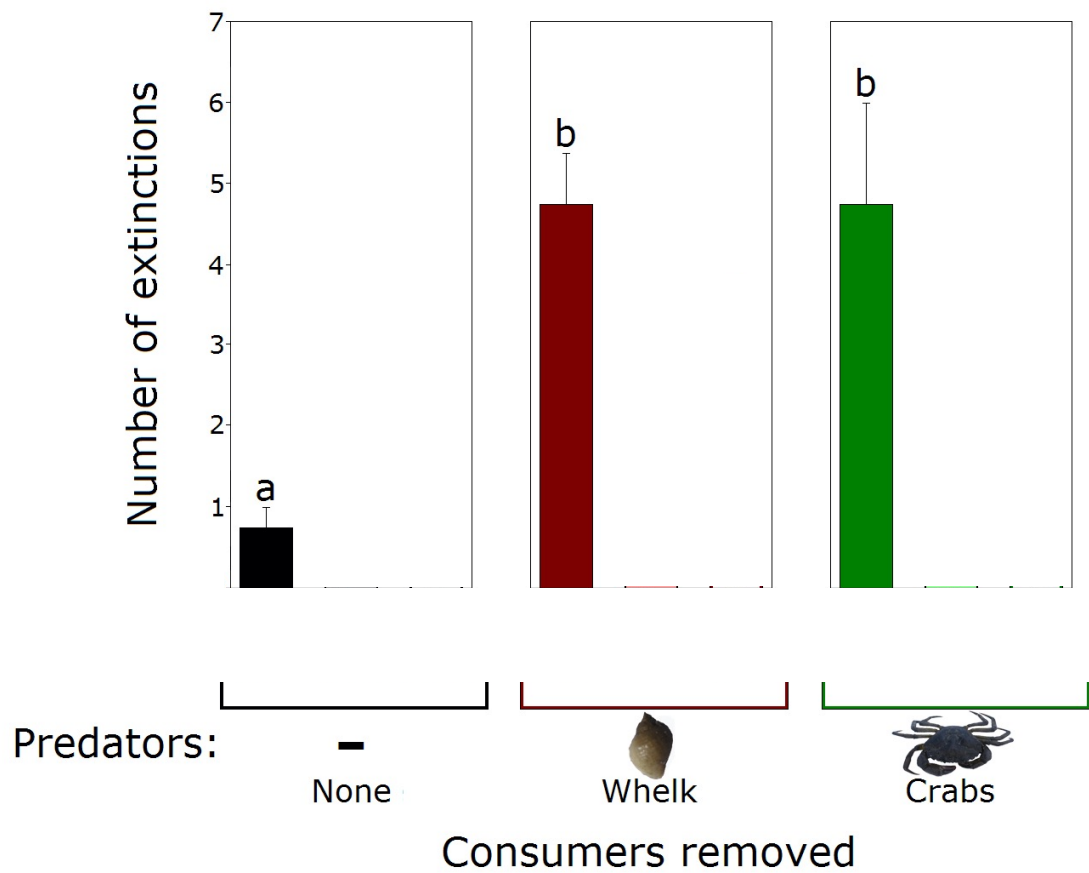


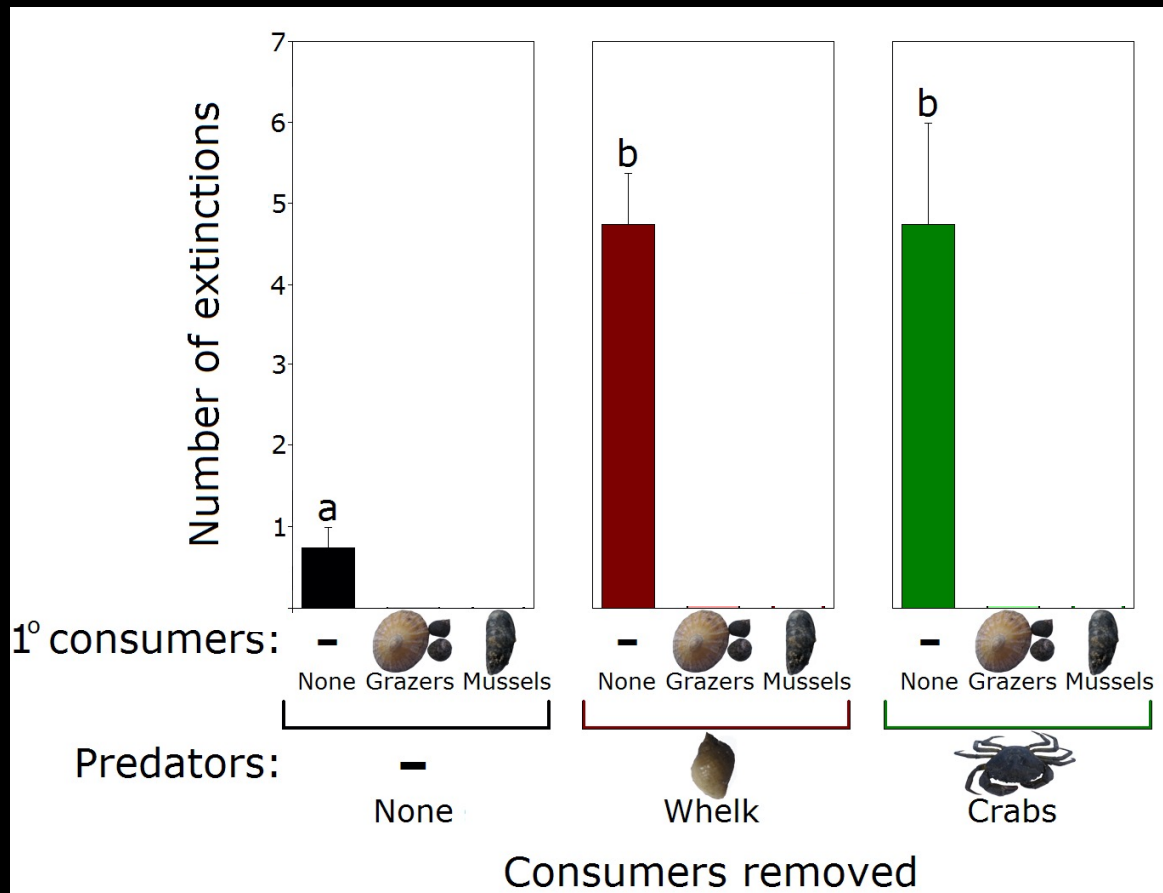












1° consumers:

- None Grazers Mussels

- None Grazers Mussels

- None Grazers Mussels

Predators:

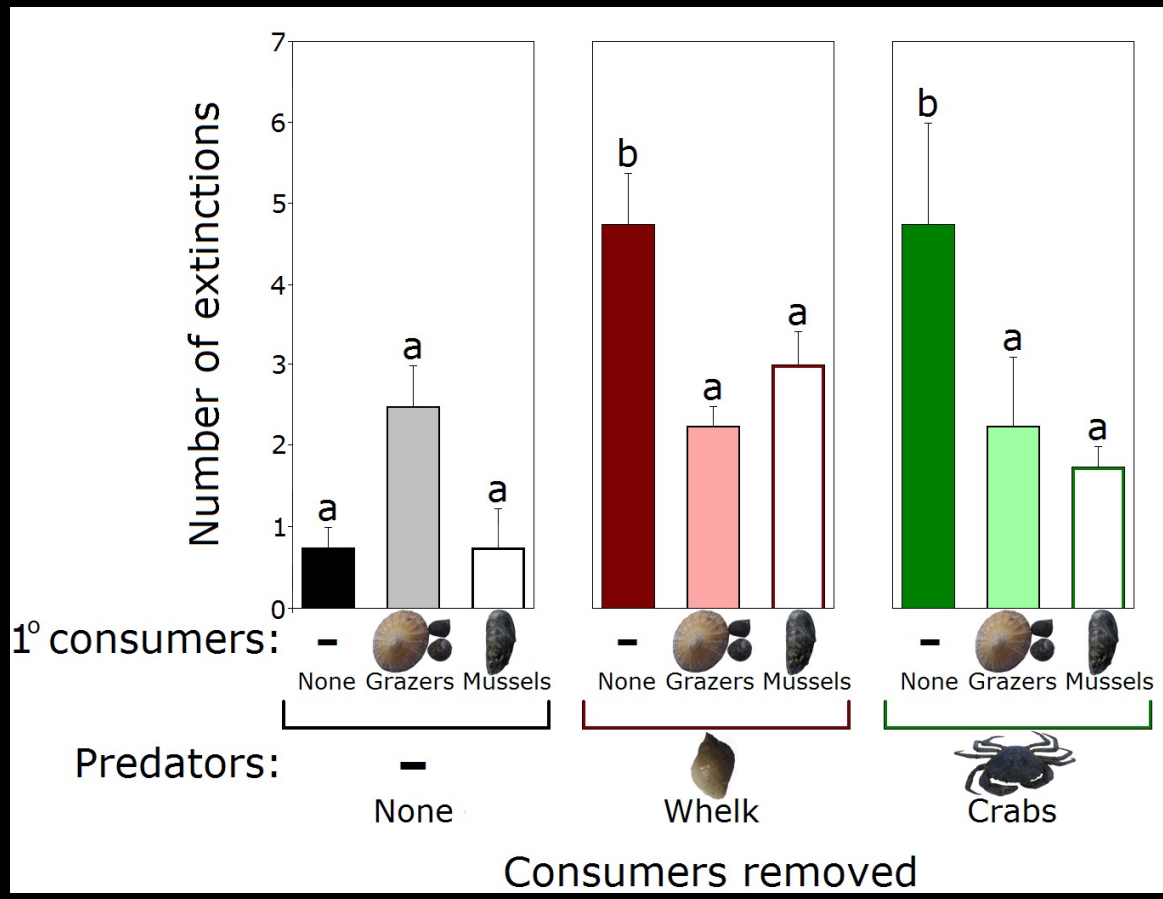
None

Whelk

Crabs

Consumers removed





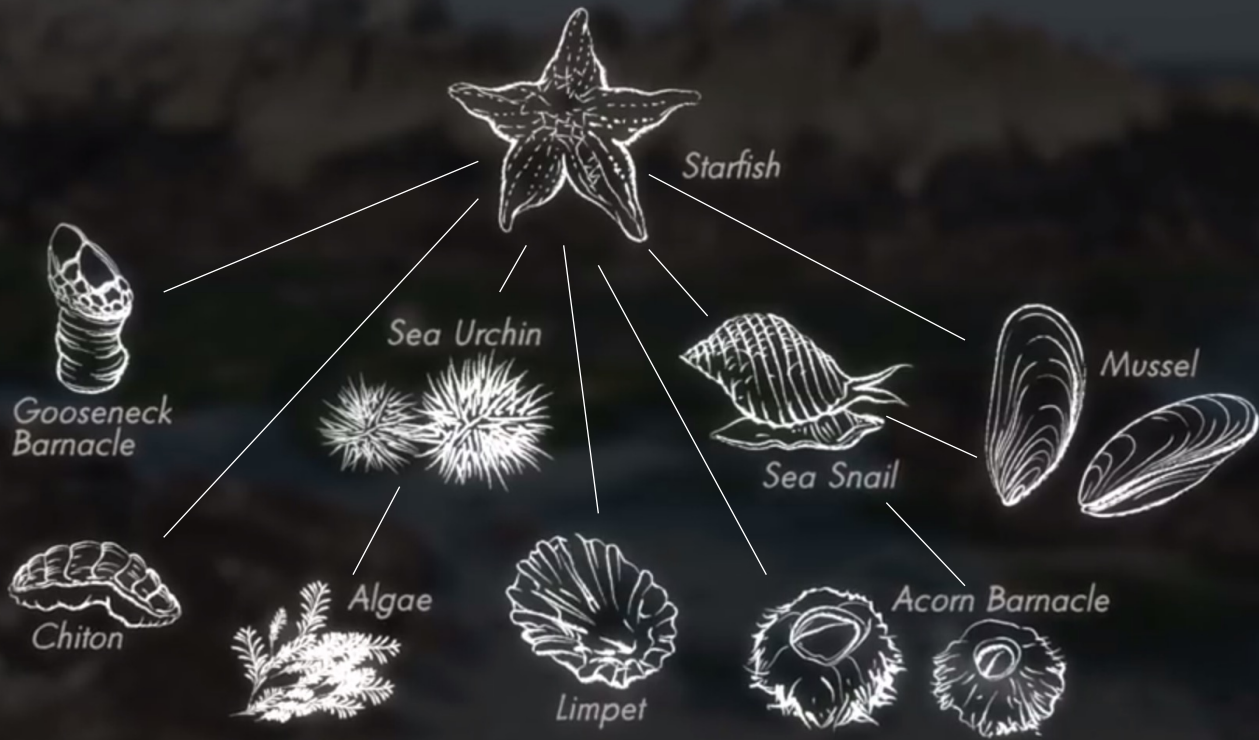
1/3 of the macroalgal taxa lost following the removal of either predator species

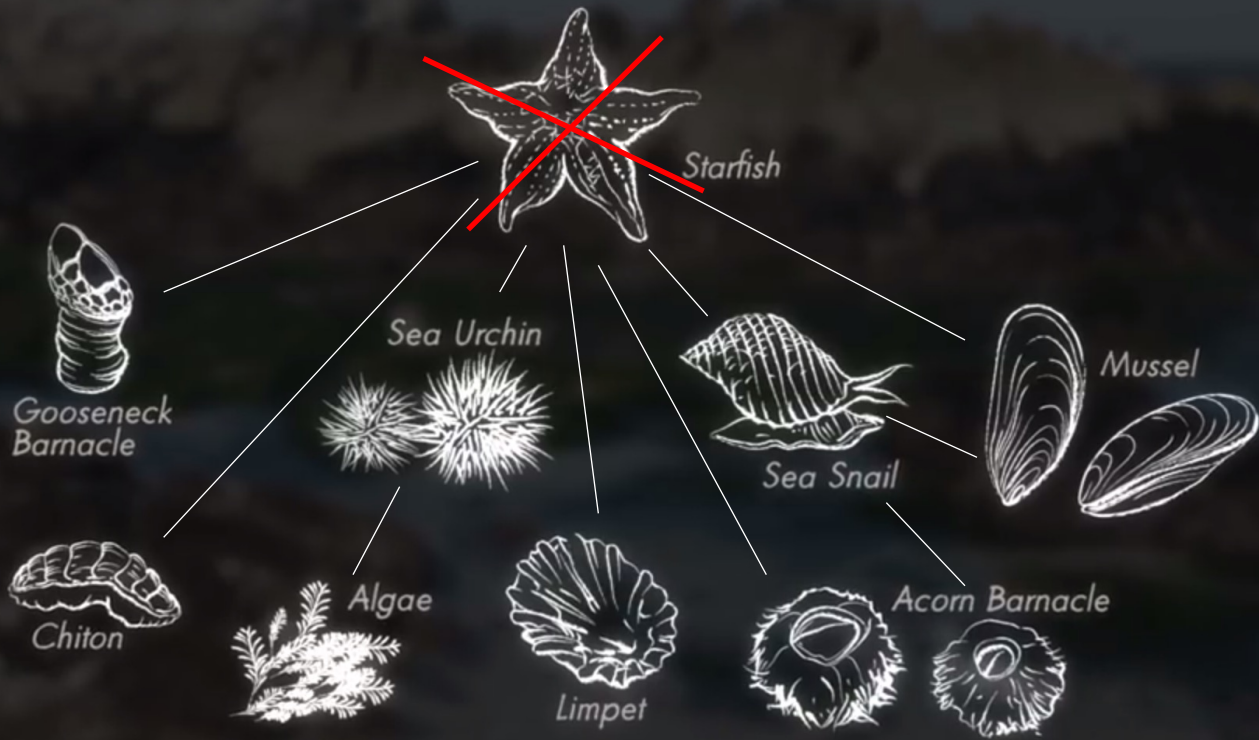
an order of magnitude greater than in models

e.g. Ebenman *et al.* 2006  
Eklöf and Ebenman 2006  
Quince *et al.* 2005  
Petchey *et al.* 2008



Robert Paine  
Credit: Alamy. Telegraph obituary





15 species initially



7 species after 1,5 year





1 species after 7 years



→ puzzling discrepancy between observations and the prediction of most theoretical models





feeding interactions



@Evie Wieters

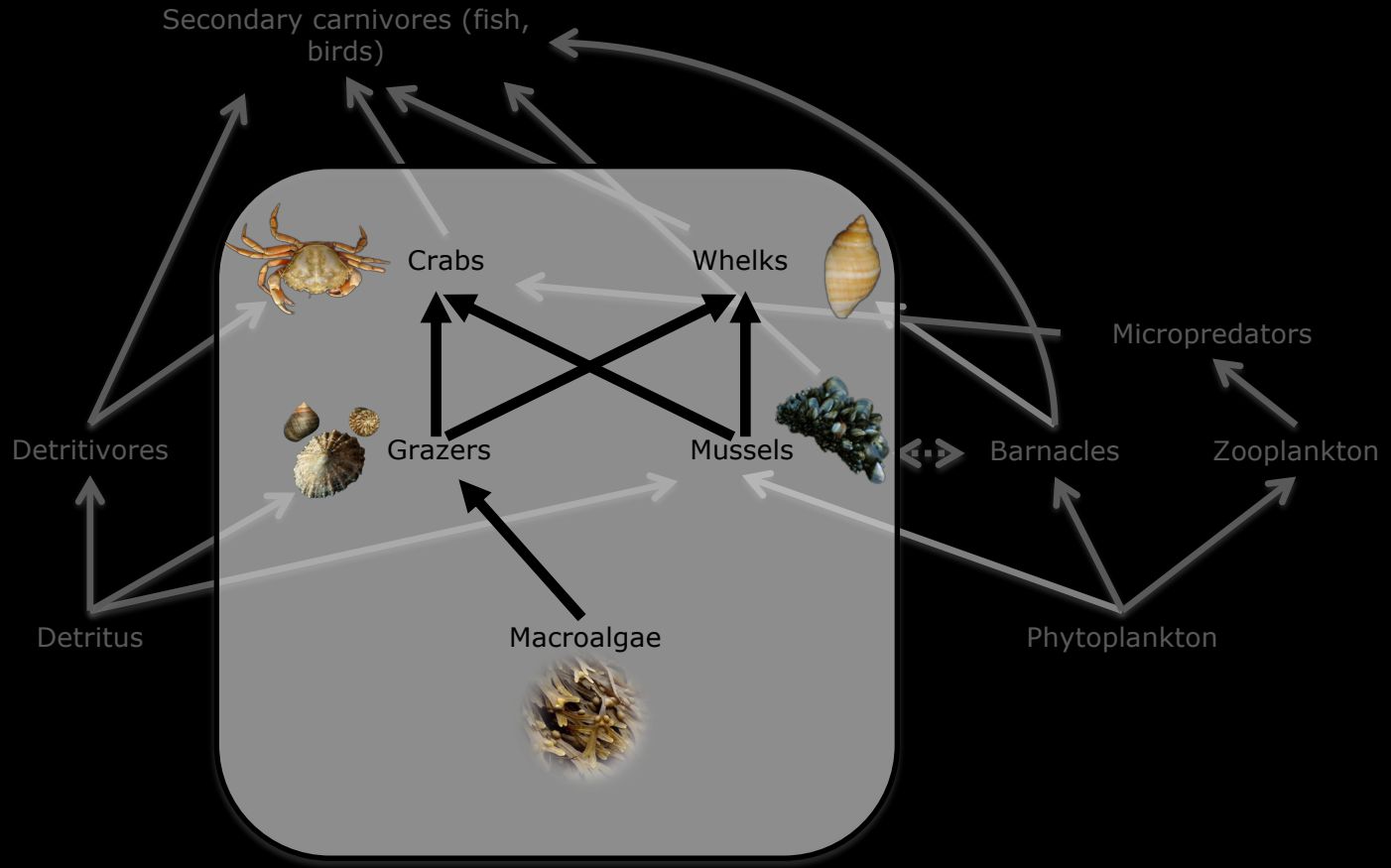


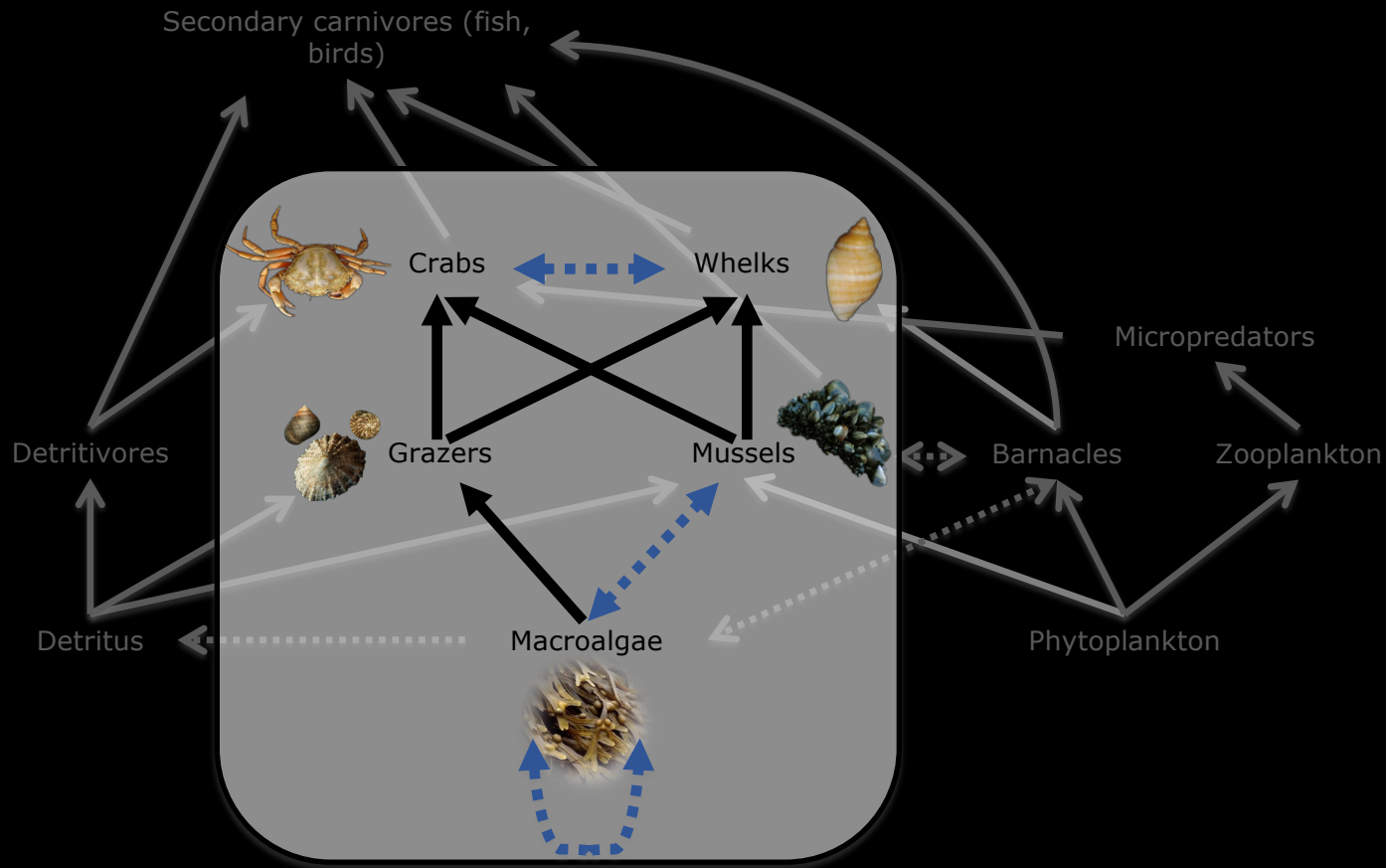












dynamical model  
[bioenergetic consumer-resource model]

$$\frac{dB_i}{dt} = r_i \left(1 - \frac{B_i}{K_i}\right) B_i + eB_i \sum_j F_{ij} - \sum_k F_{ki} B_k - x_i B_i$$

Yodzis and Innes 1992  
Brose et al. 2005, 2006  
Stouffer et al. 2011

$$\frac{dB_i}{dt} = \underbrace{r_i \left(1 - \frac{B_i}{K_i}\right) B_i}_{\text{growth}} + \underbrace{e B_i \sum_j F_{ij}}_{\text{consumption (eats)}} - \underbrace{\sum_k F_{ki} B_k}_{\text{consumption (is eaten)}} - \underbrace{x_i B_i}_{\text{metabolism}}$$

primary producers
non-primary producers

Yodzis and Innes 1992  
 Brose et al. 2005, 2006  
 Stouffer et al. 2011

$$\frac{dB_i}{dt} = \underbrace{r_i \left(1 - \frac{B_i}{K_i}\right) B_i}_{\text{growth}} + \underbrace{e B_i \sum_j F_{ij}}_{\text{consumption (eats)}} - \underbrace{\sum_k F_{ki} B_k}_{\text{consumption (is eaten)}} - \underbrace{x_i B_i}_{\text{metabolism}}$$

$$F_{ij} = \frac{w_i b_{ij} B_j^{1+q}}{1 + w_i h_i \sum_k b_{ik} B_k^{1+q}}$$

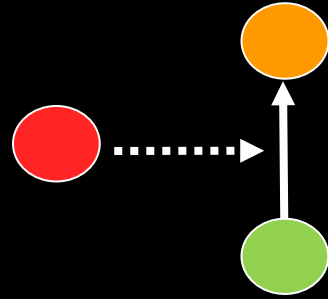
Yodzis and Innes 1992  
 Brose *et al.* 2005, 2006  
 Stouffer *et al.* 2011

+ non-trophic interactions



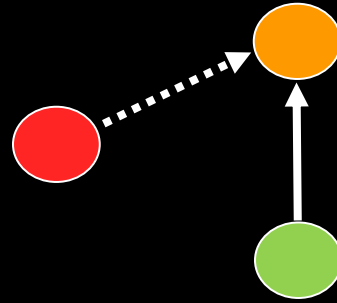


How to integrate the great diversity of non-trophic interactions in current food web models?



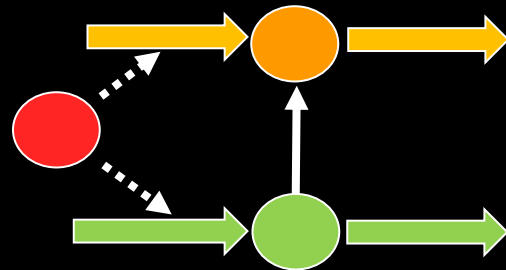
Modification of  
trophic interactions

Handling time  
Capture efficiency



## Modification of node attributes

Mortality  
Establishment  
Growth rate  
Reproduction



Input/output of matter  
(open systems)

Immigration/Emigration  
Incoming/outcoming flow of a  
resource

Kéfi *et al.* 2012 *Eco. Lett.*

The relevant model parameters become  
functions of the source species

# Example: competition for space



$$\frac{dB_i}{dt} = \underbrace{g_i \left[ r_i \left( 1 - \frac{B_i}{K_i} \right) B_i \right]}_{\text{grows}} + \underbrace{e B_i \sum_j F_{ij}}_{\text{eats}} - \underbrace{x_i B_i}_{\text{dies}} - \underbrace{\sum_k F_{ki} B_k}_{\text{is eaten}}$$

# Example: competition for space



$$g_i = 1 - \sum_k c_{ik} B_k$$

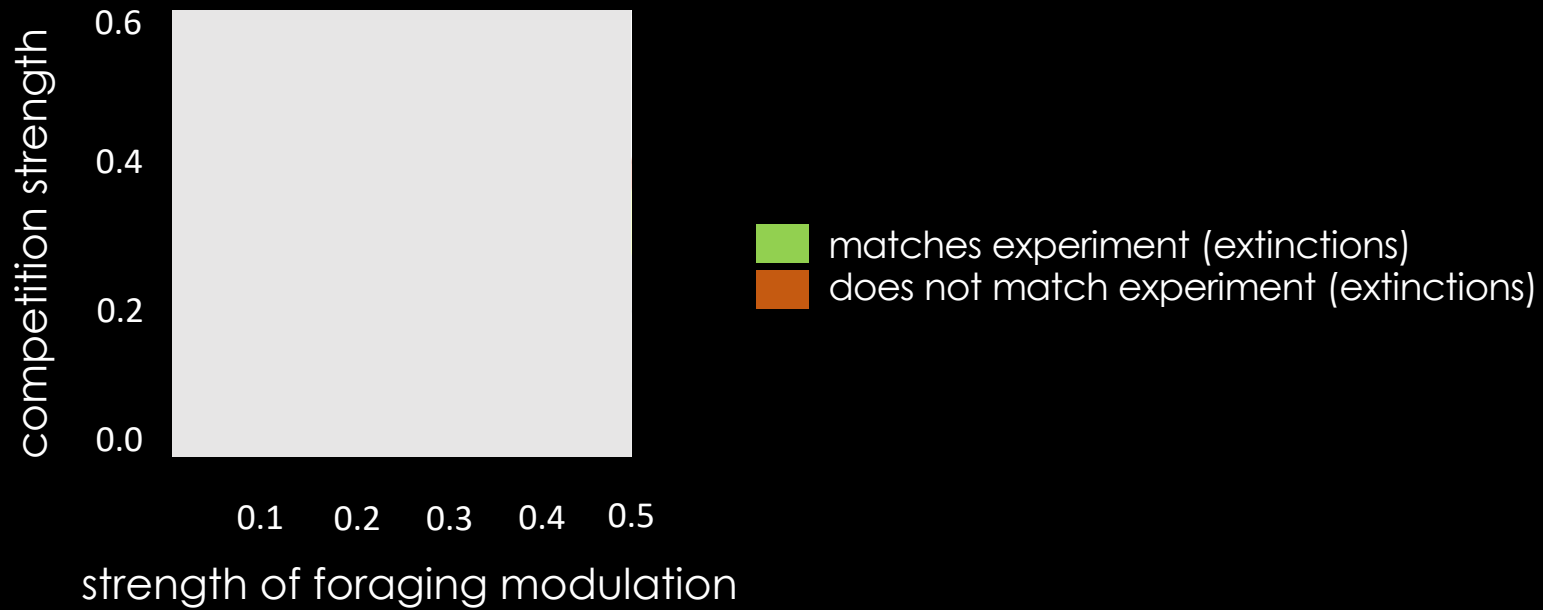


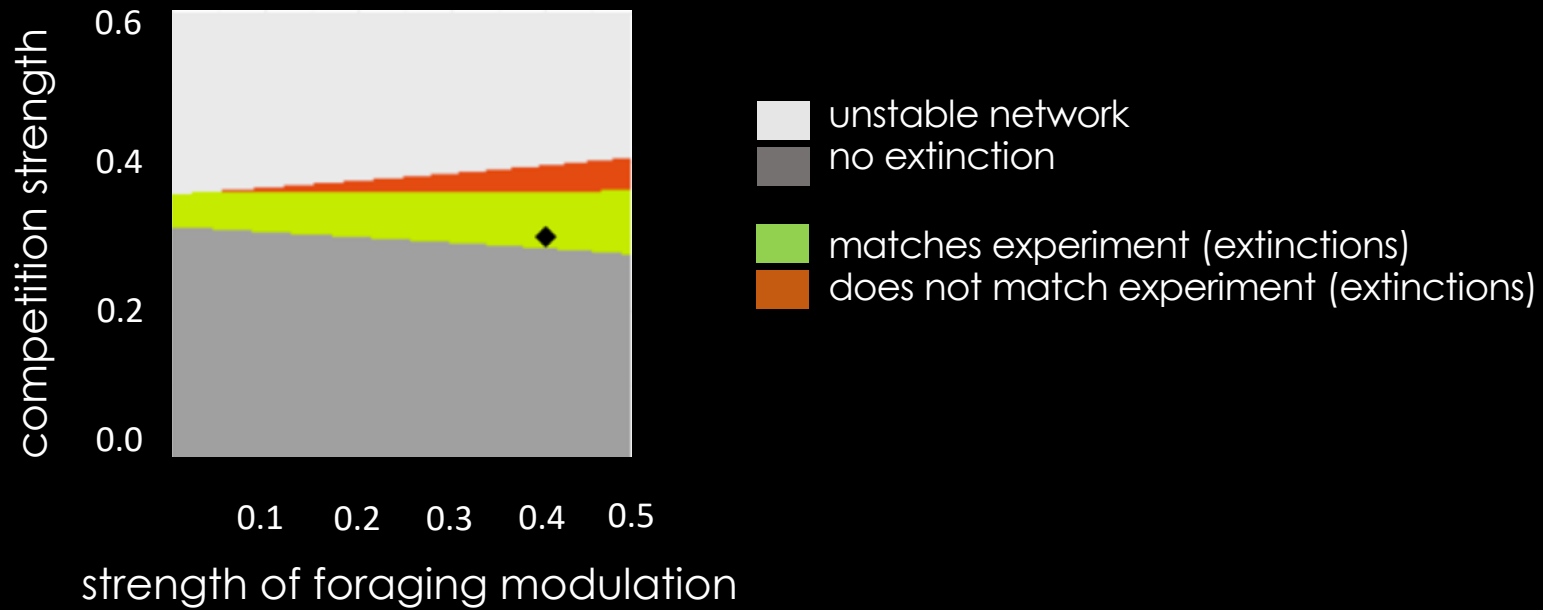
$$\frac{dB_i}{dt} = \underbrace{g_i \left[ r_i \left( 1 - \frac{B_i}{K_i} \right) B_i \right]}_{\text{grows}} + \underbrace{e B_i \sum_j F_{ij}}_{\text{eats}} - \underbrace{x_i B_i}_{\text{dies}} - \underbrace{\sum_k F_{ki} B_k}_{\text{is eaten}}$$

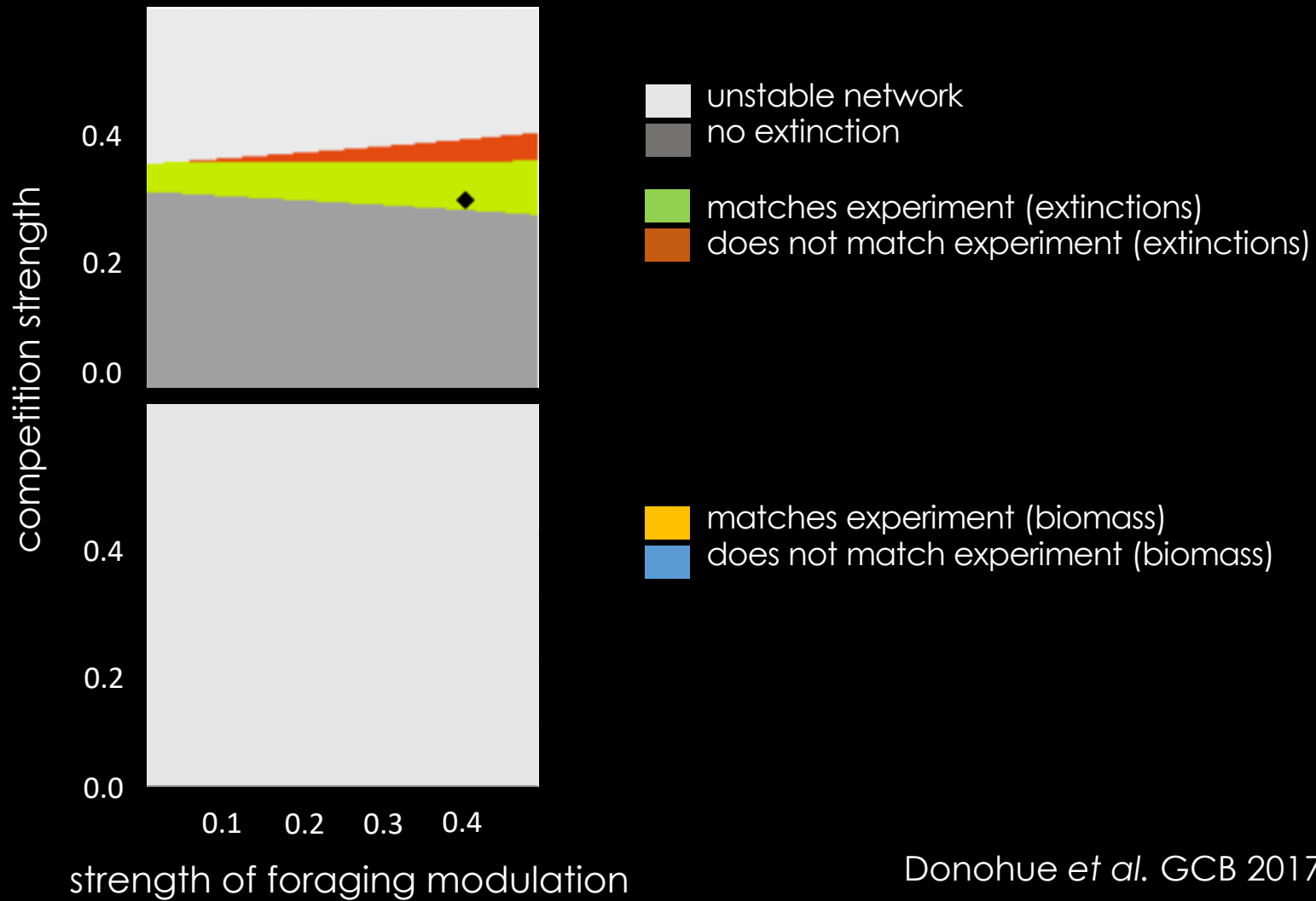
dynamical model  
[bioenergetic consumer-resource model]

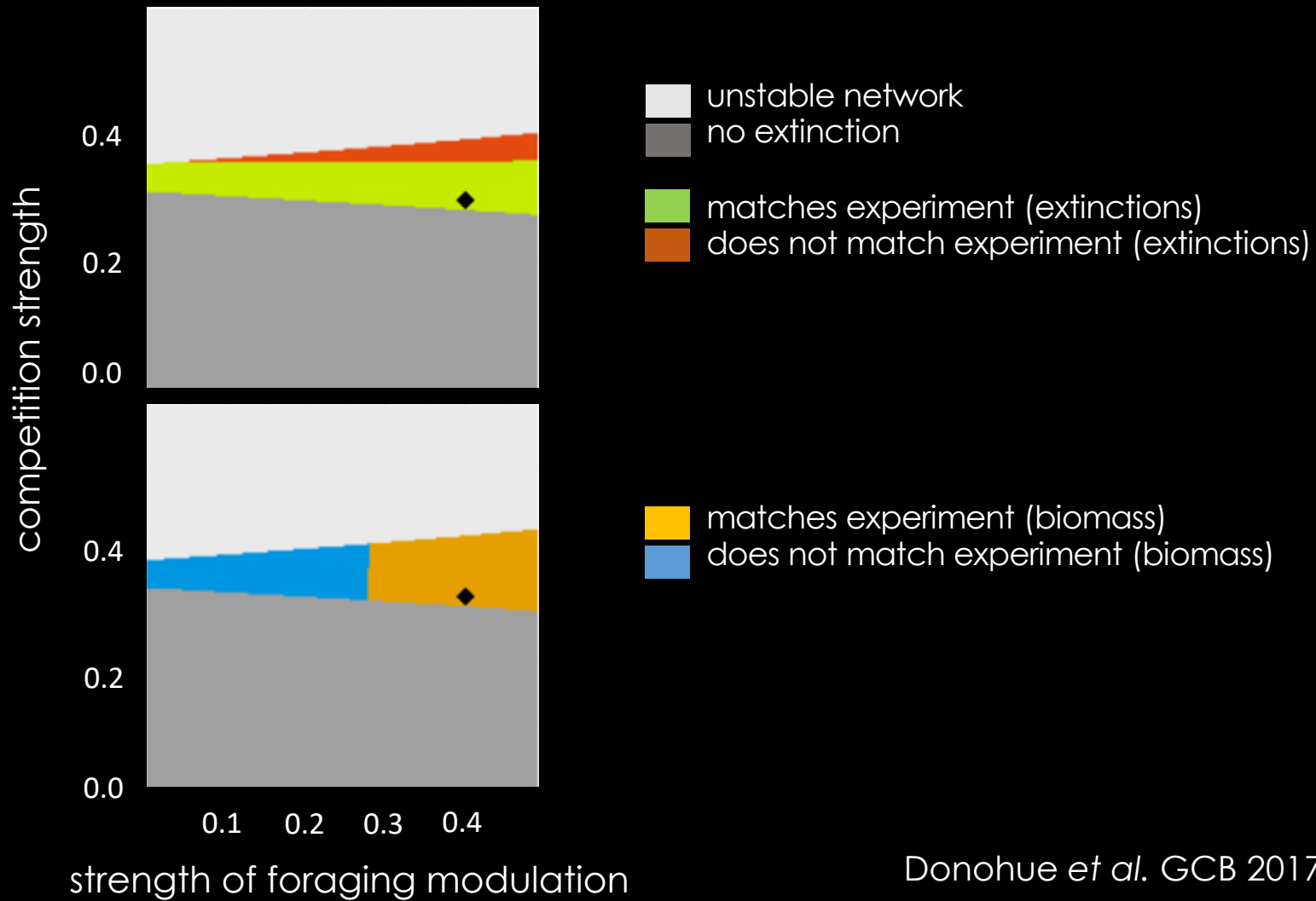
+ non-trophic interactions  
competition for space  
foraging modulation











The diversity of interaction types is needed to reproduce the results of the experiments



How does the diversity of interaction types affect functioning?

dynamical model  
[bioenergetic consumer-resource model]



dynamical model  
[bioenergetic consumer-resource model]

+ non-trophic interactions

Competition for space

Predator interference

Recruitment facilitation

Refuge provisioning

Positive and negative effects on survival

# Simulations

Niche model for food web skeleton, 100 species incl. 20 plants

# Simulations

Niche model for food web skeleton, 100 species incl. 20 plants  
Plug NTI 'links randomly'

# Simulations

Niche model for food web skeleton, 100 species incl. 20 plants  
Plug NTI 'links randomly'  
Run dynamics **with and without NTI**

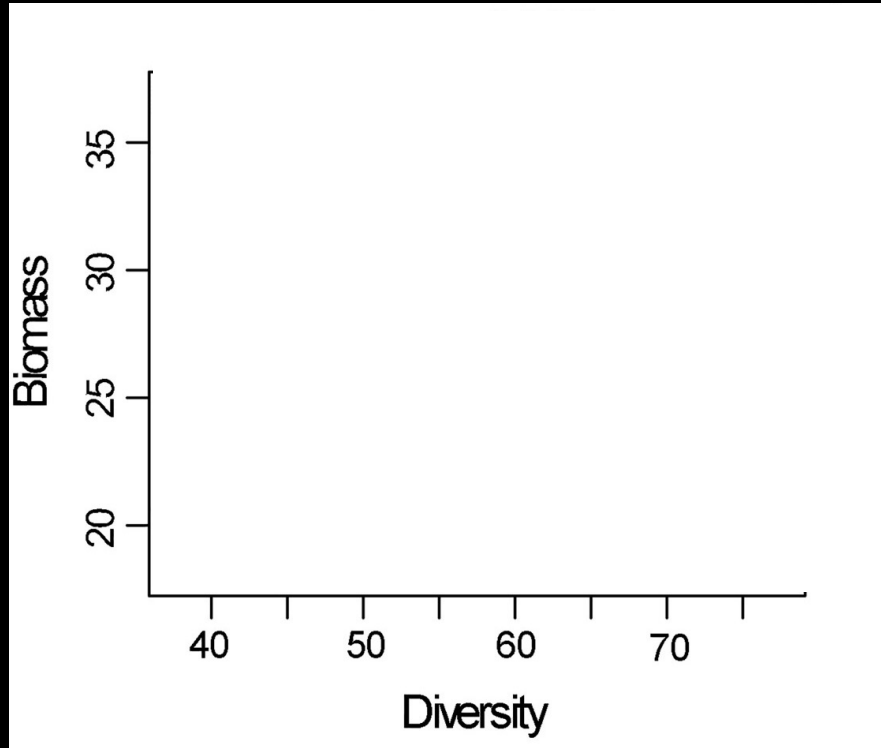
# Simulations

Niche model for food web skeleton, 100 species incl. 20 plants  
Plug NTI 'links randomly'  
Run dynamics with and without NTI

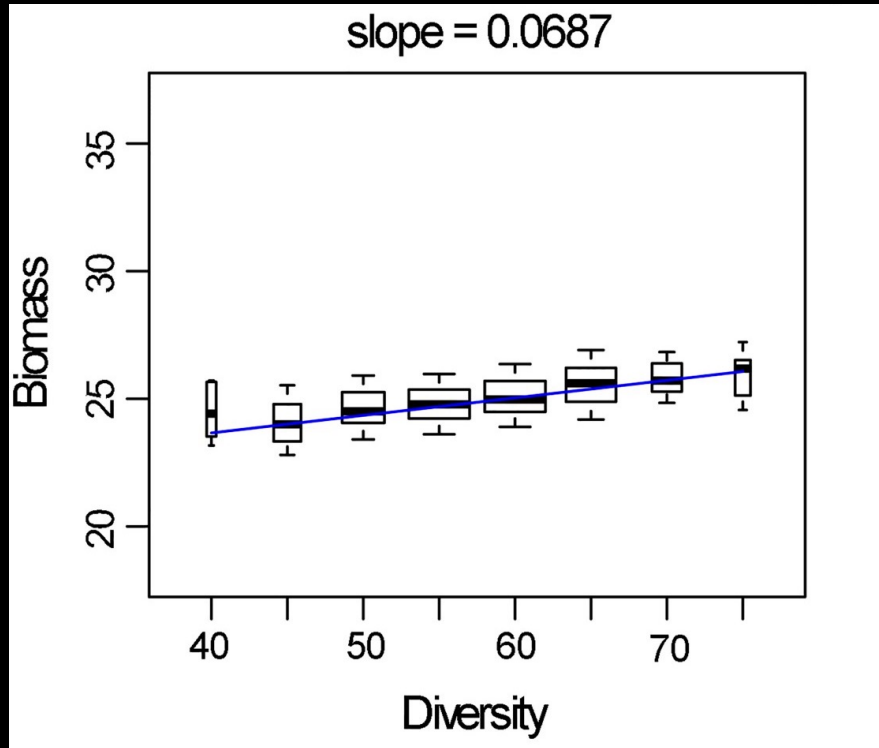


Calculate species diversity and total biomass

# One interaction type (trophic)

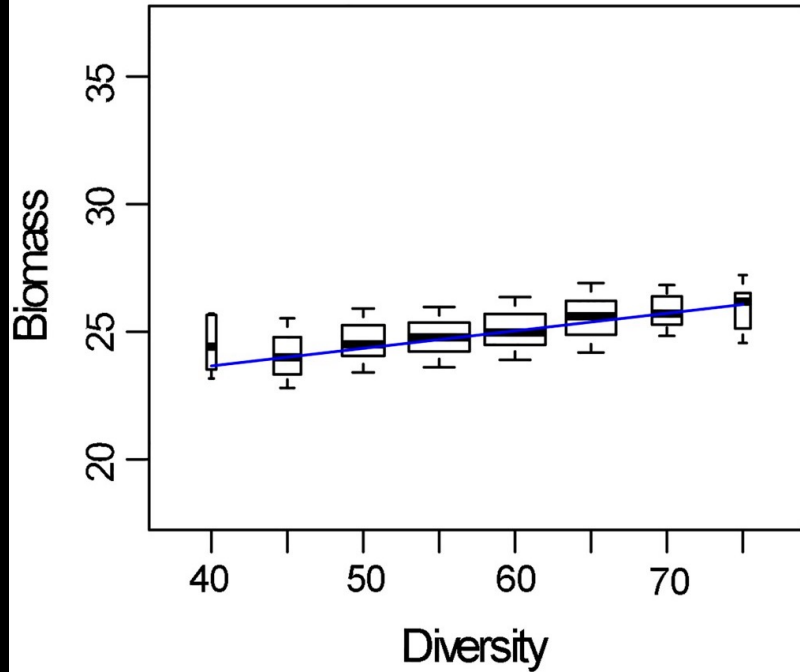


# One interaction type (trophic)



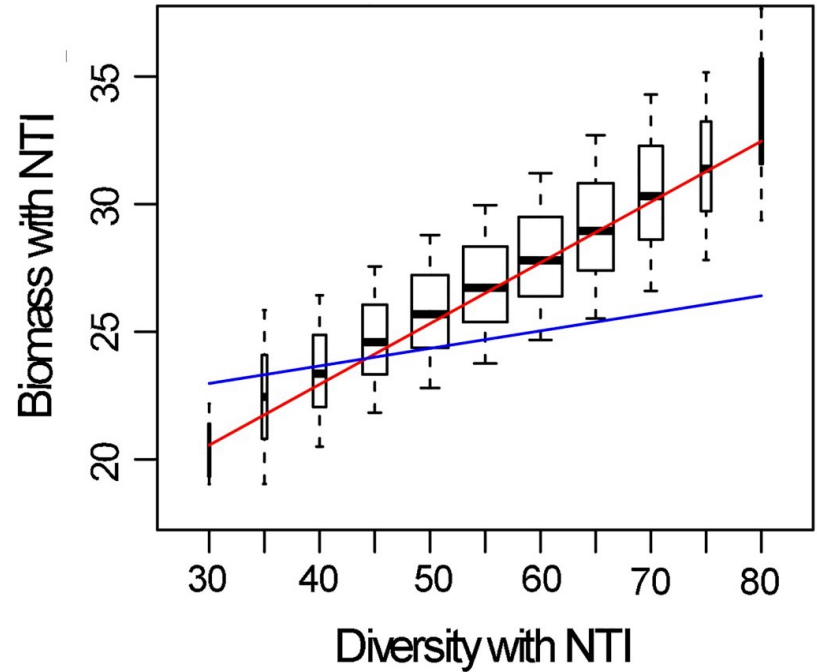
## One interaction type (trophic)

slope = 0.0687



## Diverse interactions types (multiplex)

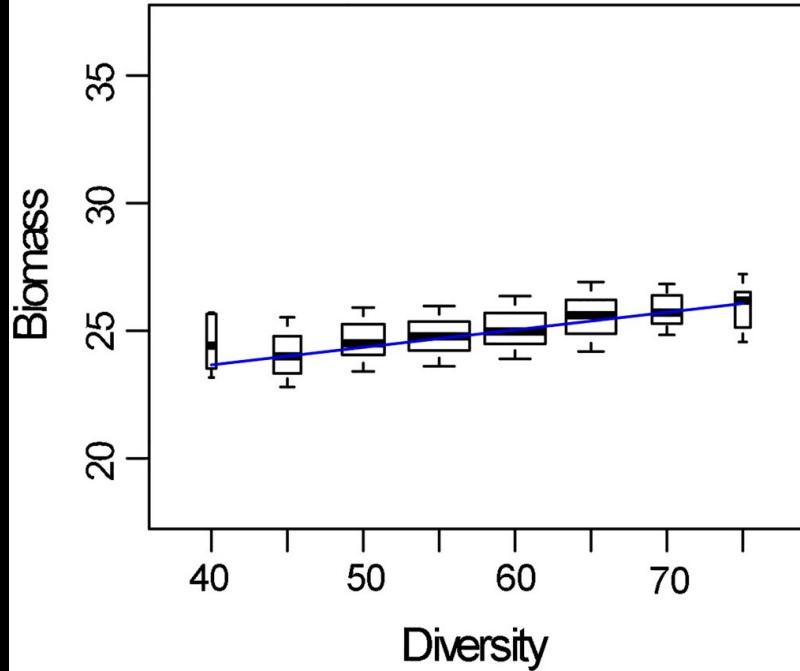
slope = 0.238





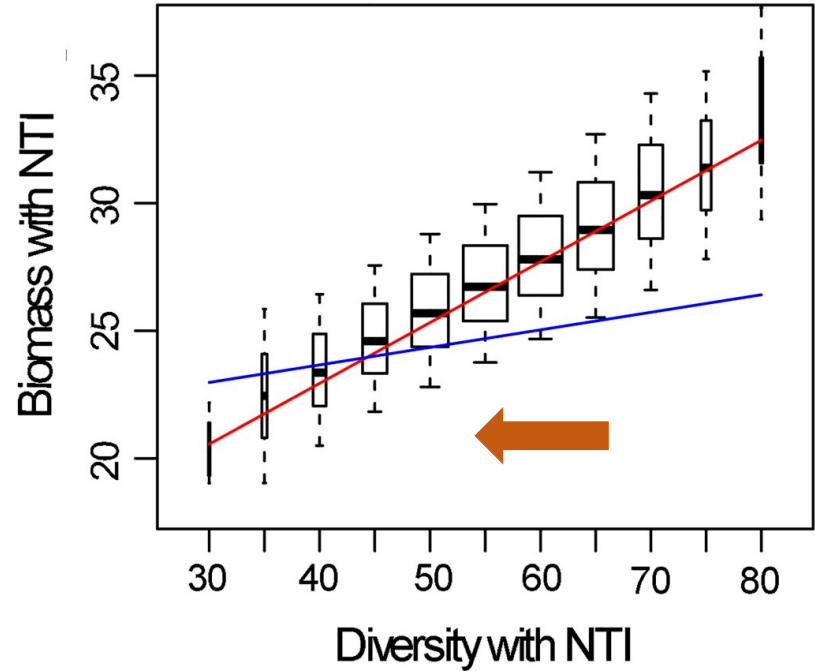
## One interaction type (trophic)

slope = 0.0687



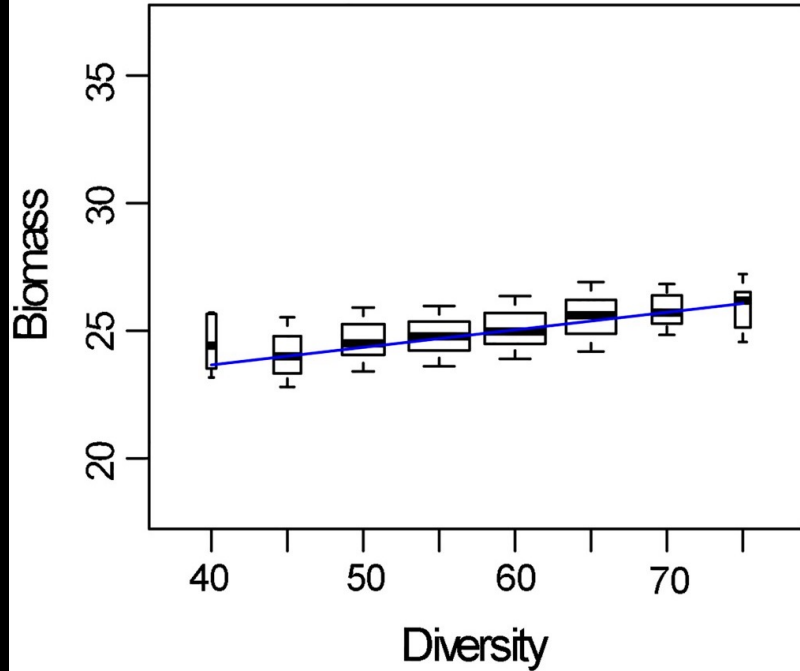
## Diverse interactions types (multiplex)

slope = 0.238



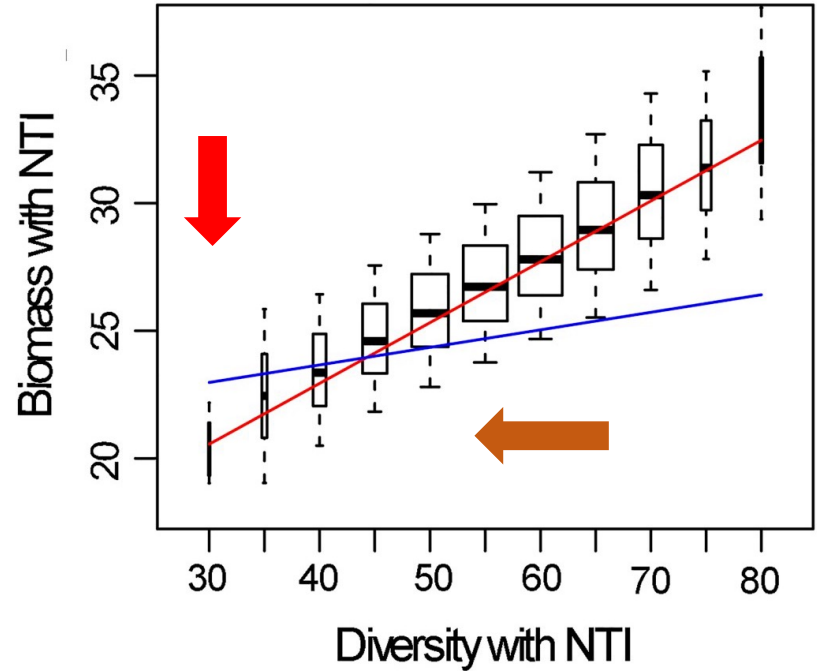
## One interaction type (trophic)

slope = 0.0687



## Diverse interactions types (multiplex)

slope = 0.238



NTIs affect species diversity, community  
functioning and their relationship



How do different interaction types map  
onto each other?



multiplex ecological network



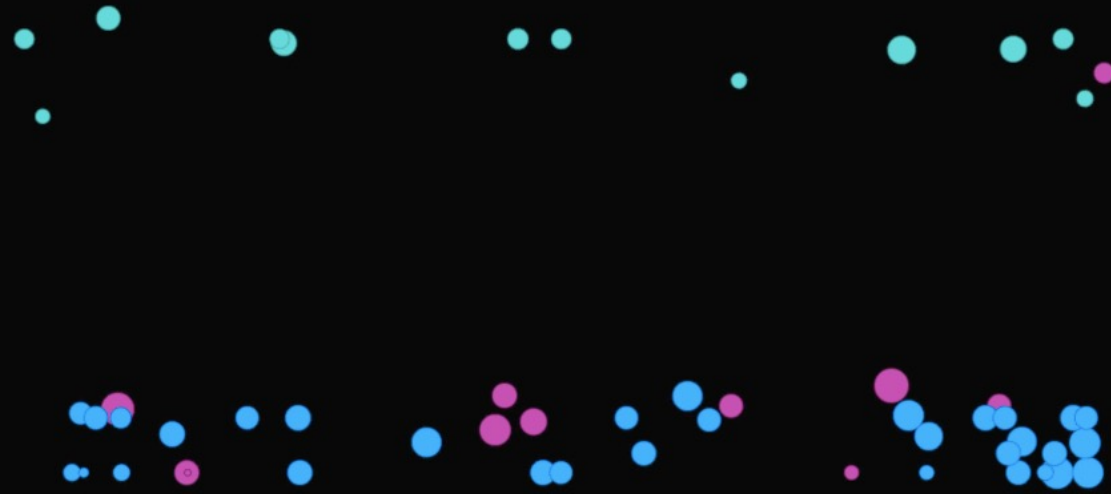
Sergio Navarrete,  
Evie Wieters

*Kéfi et al. 2015*









# CHILEAN MARINE ECOLOGICAL NETWORK



## NODES 104

	46	Basal
	32	Intermediate
	12	Top
	14	zHarvested

## EDGES 1611

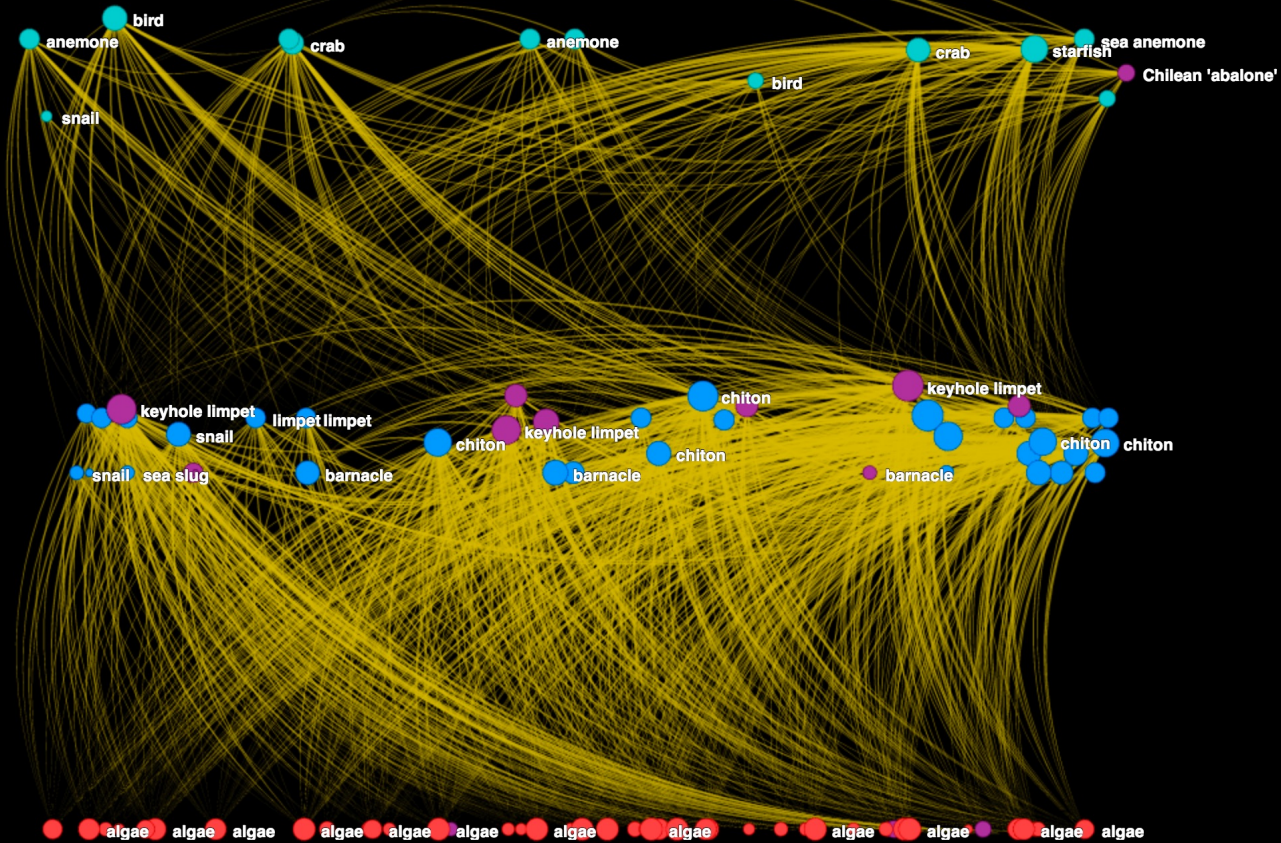
1456	Feeding
155	Non-Feeding Positive

1 2 3

TL

Rand

# CHILEAN MARINE FOOD WEB



TL

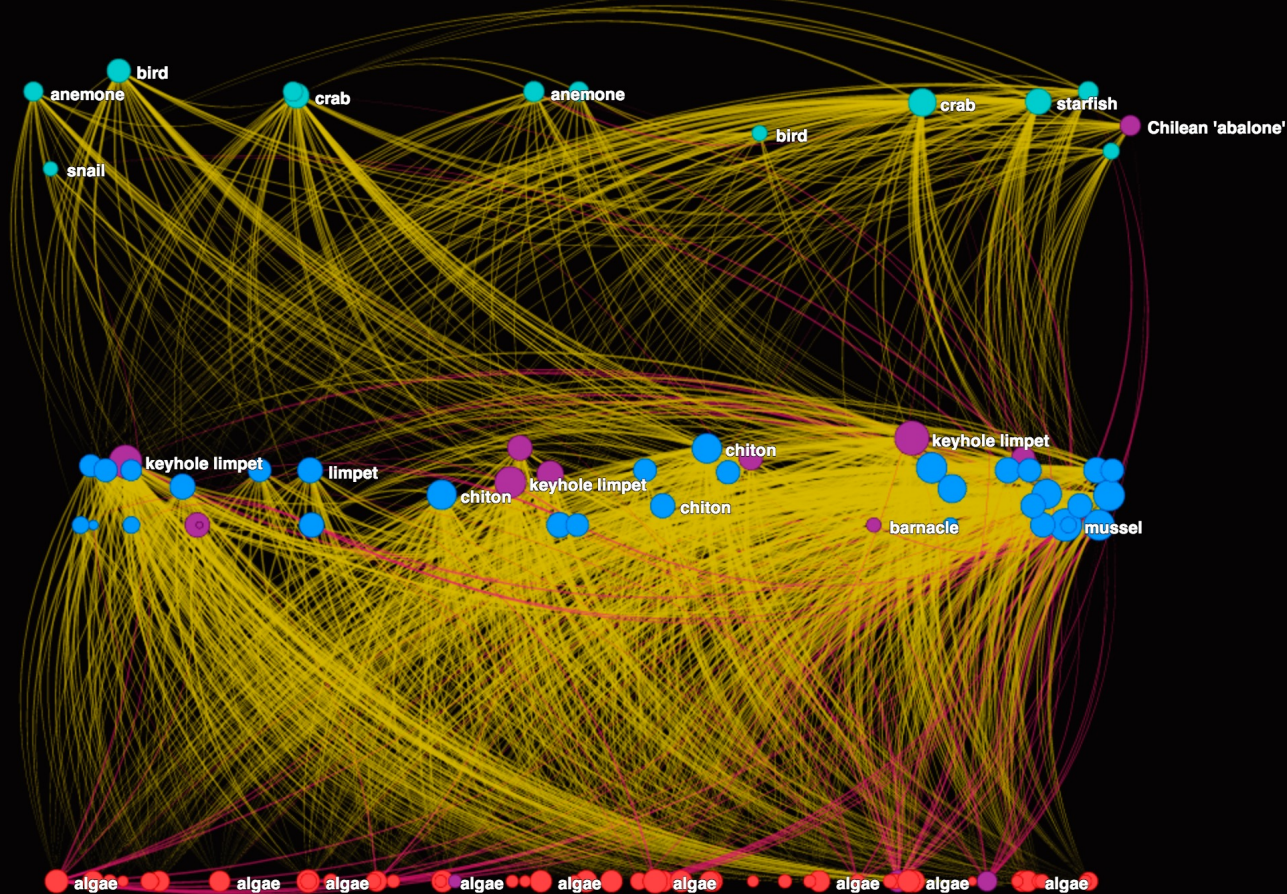
Rand

**NODES 104**

<span style="color: red;">●</span>	46	Basal
<span style="color: blue;">●</span>	32	Intermediate
<span style="color: cyan;">●</span>	12	Top
<span style="color: purple;">●</span>	14	zHarvested

1 2

# CHILEAN MARINE ECOLOGICAL NETWORK



## NODES 104

- 46 Basal
- 32 Intermediate
- 12 Top
- 14 zHarvested

## EDGES 1611

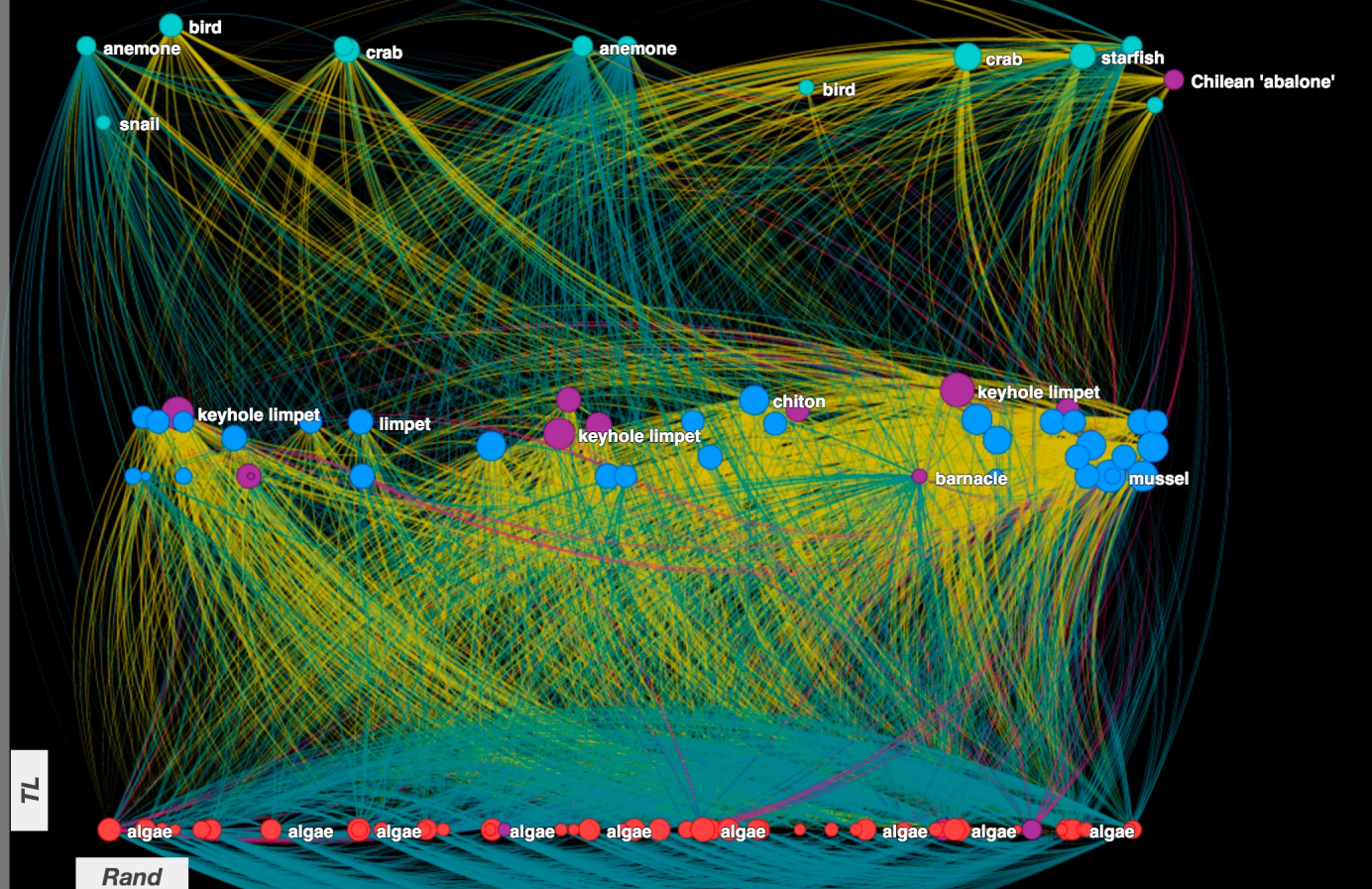
- 1456 Feeding
- 155 Non-Feeding Positive

1 2 3

TL

Rand

# CHILEAN MARINE ECOLOGICAL NETWORK



**NODES 104**

46	Basal
32	Intermediate
12	Top
14	zHarvested

**EDGES 4720**

1424	Feeding
3141	Non-Feeding Negative
155	Non-Feeding Positive

1 2 3

Do species collapse into a smaller set of  
multiplex clusters?

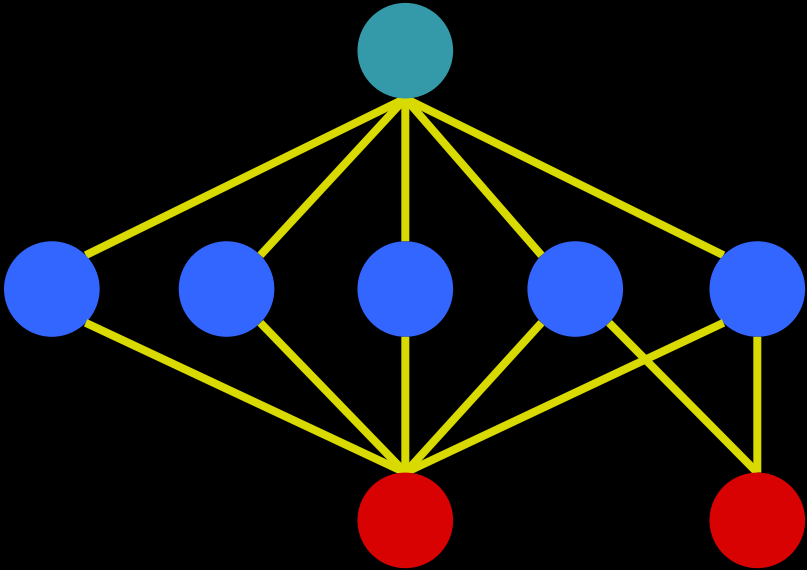
# stochastic block model

Newman and Leicht 2007

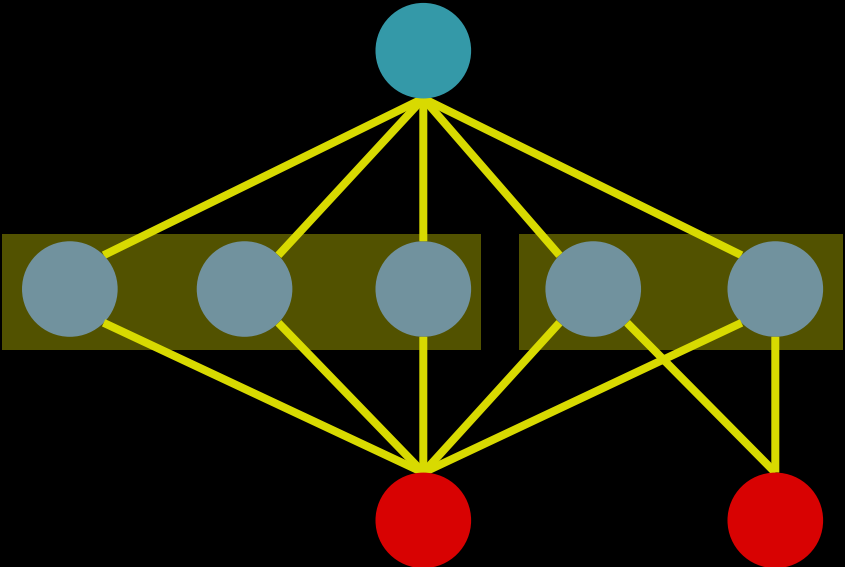
Daudin *et al.* 2008

Miele *et al.* 2014

— FEEDING



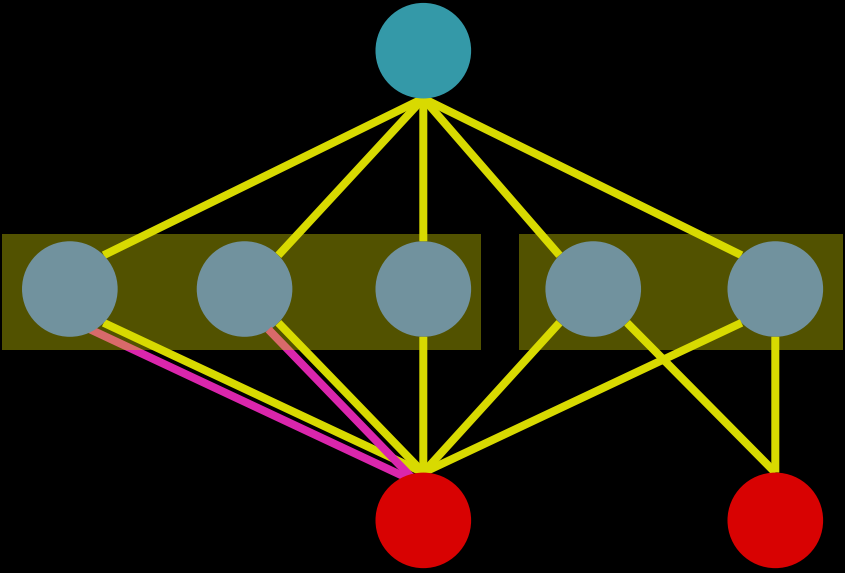
— FEEDING



“TROPIC SPECIES”



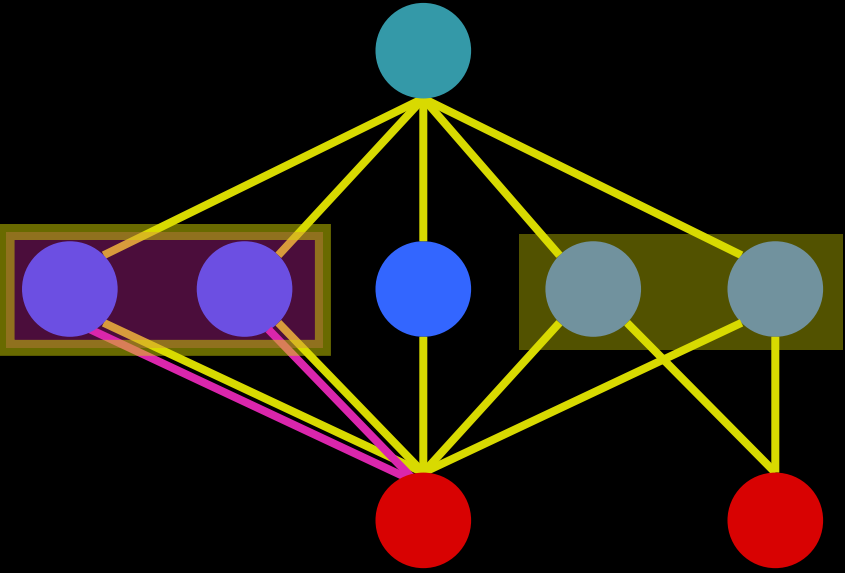
— FEEDING  
— FACILITATION



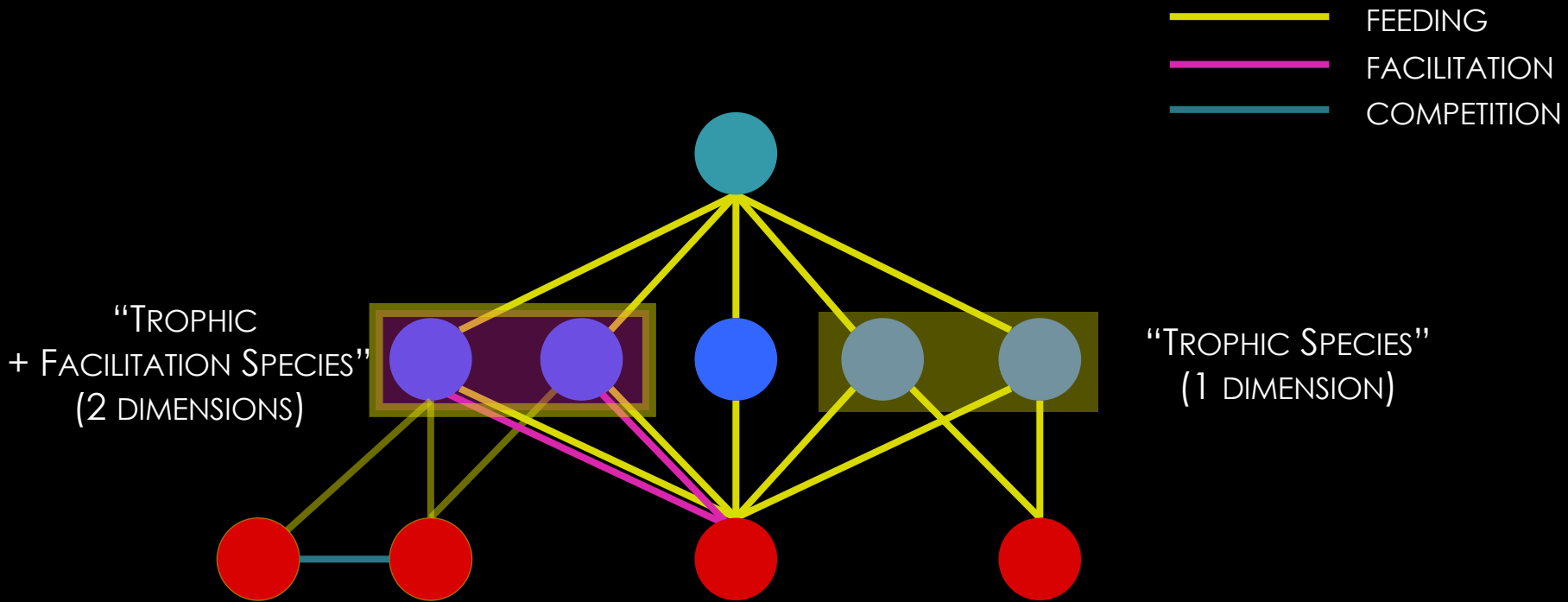
“TROPHIC SPECIES”  
(1 DIMENSION)

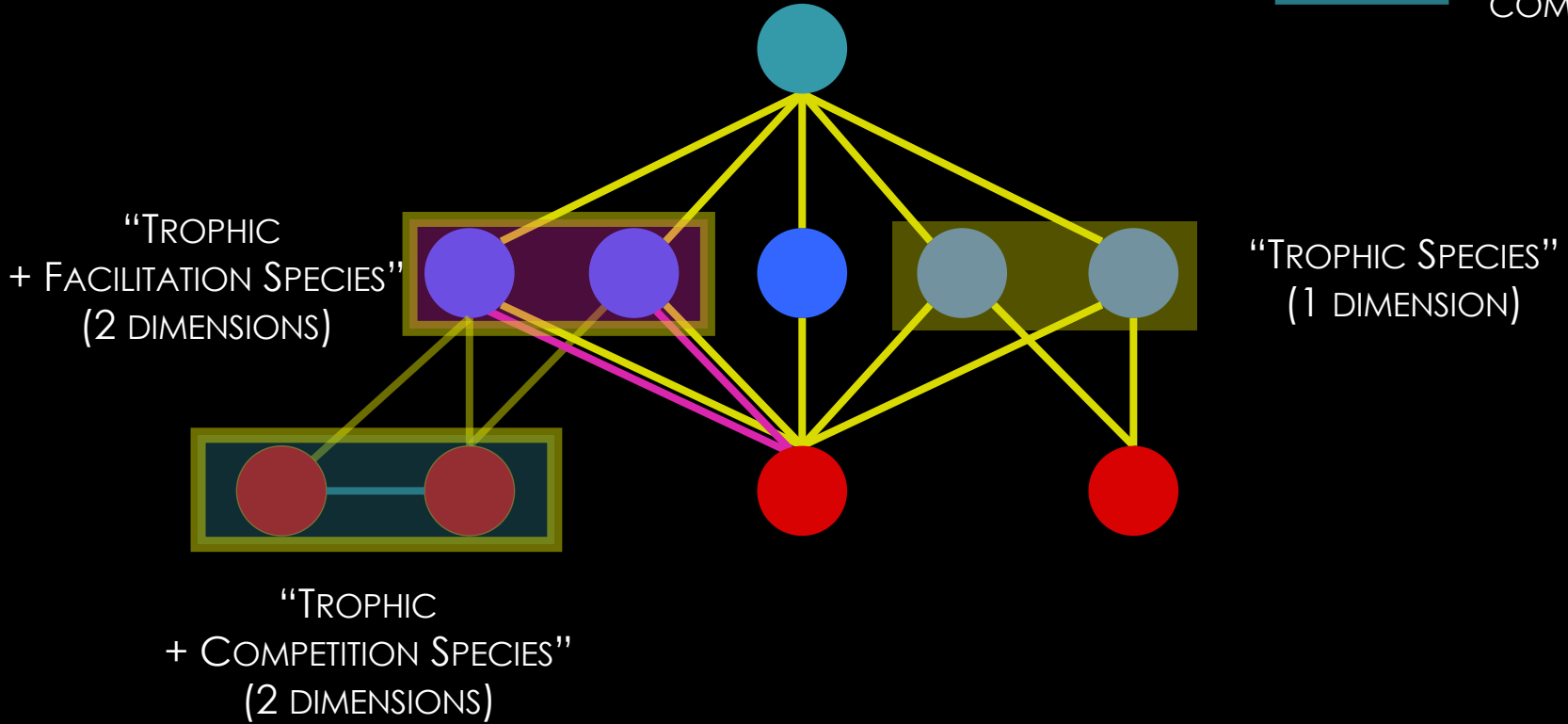
— FEEDING  
— FACILITATION

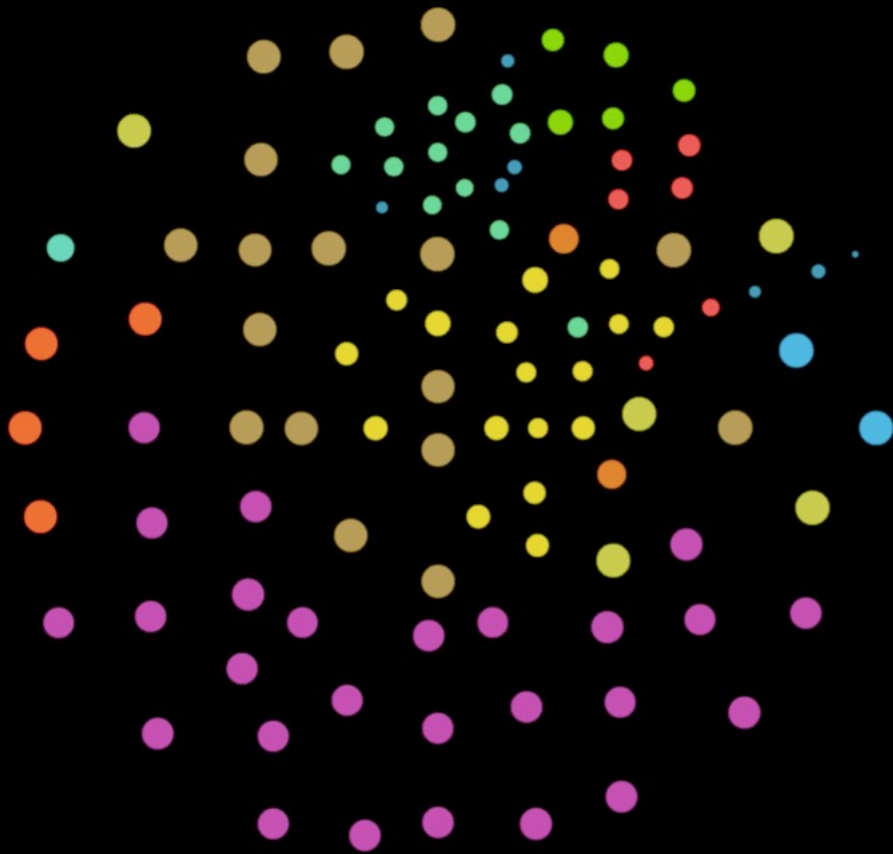
“TROPHIC  
+ FACILITATION SPECIES”  
(2 DIMENSIONS)



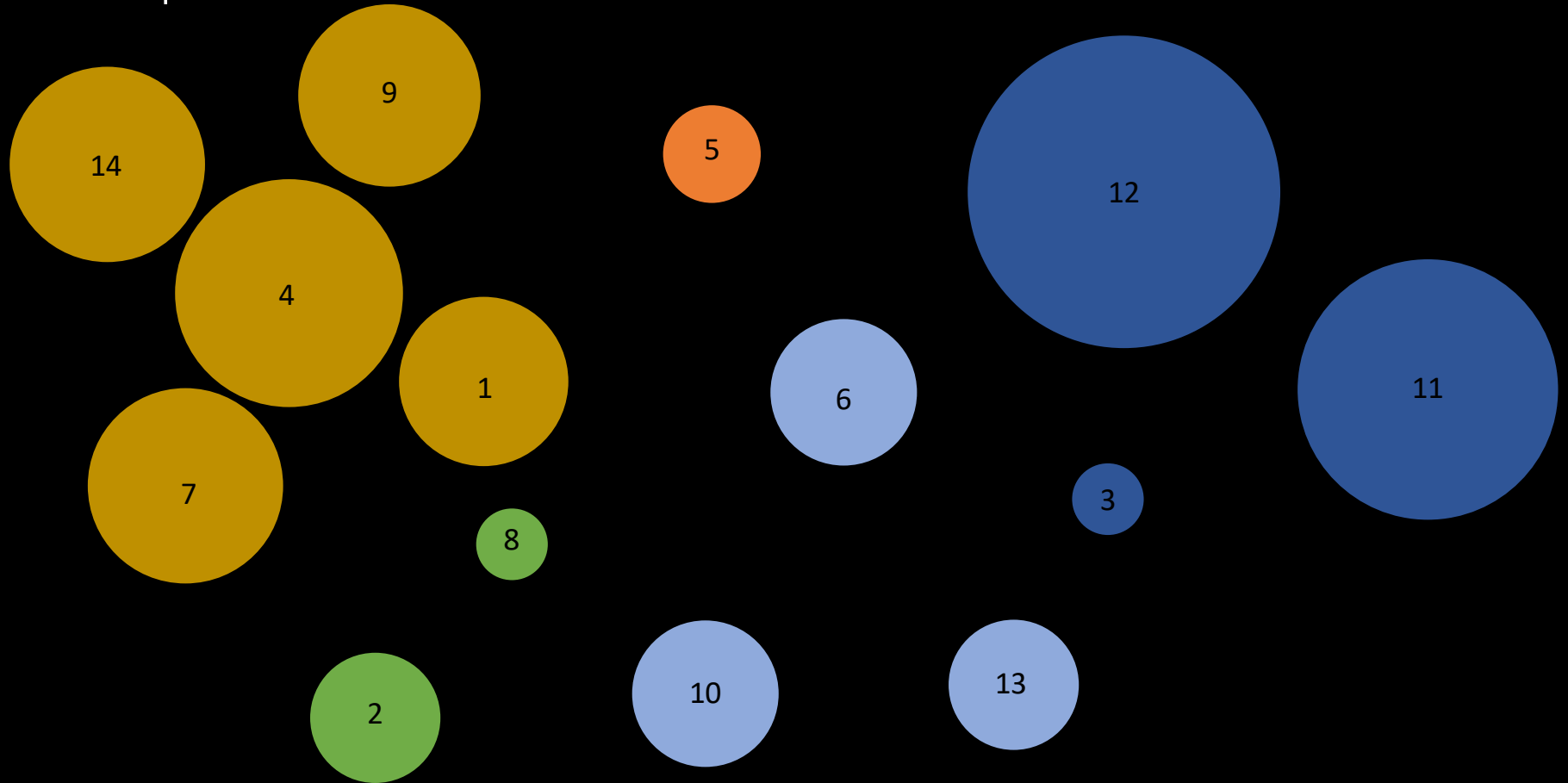
“TROPHIC SPECIES”  
(1 DIMENSION)







# 14 multiplex clusters



Species collapse into a small set of  
multiplex clusters

What are the functional consequences of  
the 3-dimensional connectivity pattern?



dynamical model  
[bioenergetic consumer-resource model]

dynamical model  
[bioenergetic consumer-resource model]

+ non-trophic interactions

Competition for space

Predator interference

Recruitment facilitation

Refuge provisioning

Positive and negative effects on survival

# Simulations

**14 nodes**

('typical' species of  
the cluster)

# Simulations


**14 nodes**  
(‘typical’ species of  
the cluster)



(i) Connectivity of the Chilean web

# Simulations

**14 nodes**  
(‘typical’ species of  
the cluster)

- 
- (i) Connectivity of the Chilean web
  - (ii) 500 random networks  
(keep degree sequence)

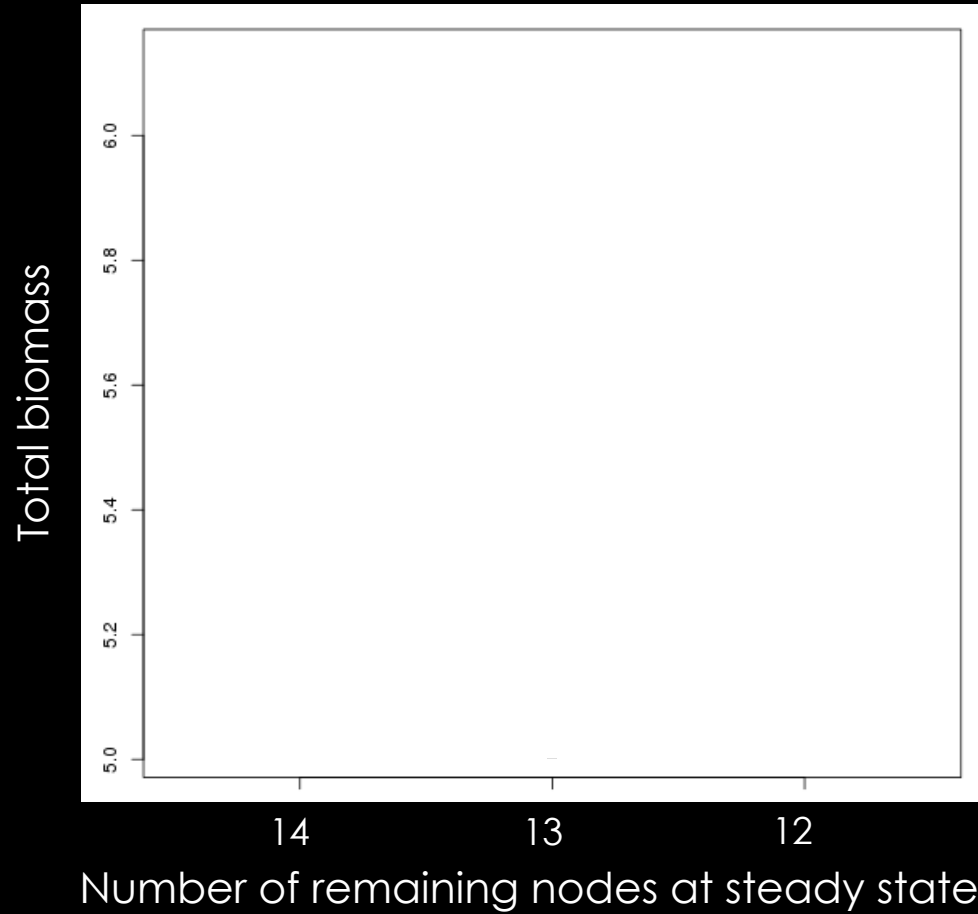
# Simulations

**14 nodes**  
(‘typical’ species of  
the cluster)

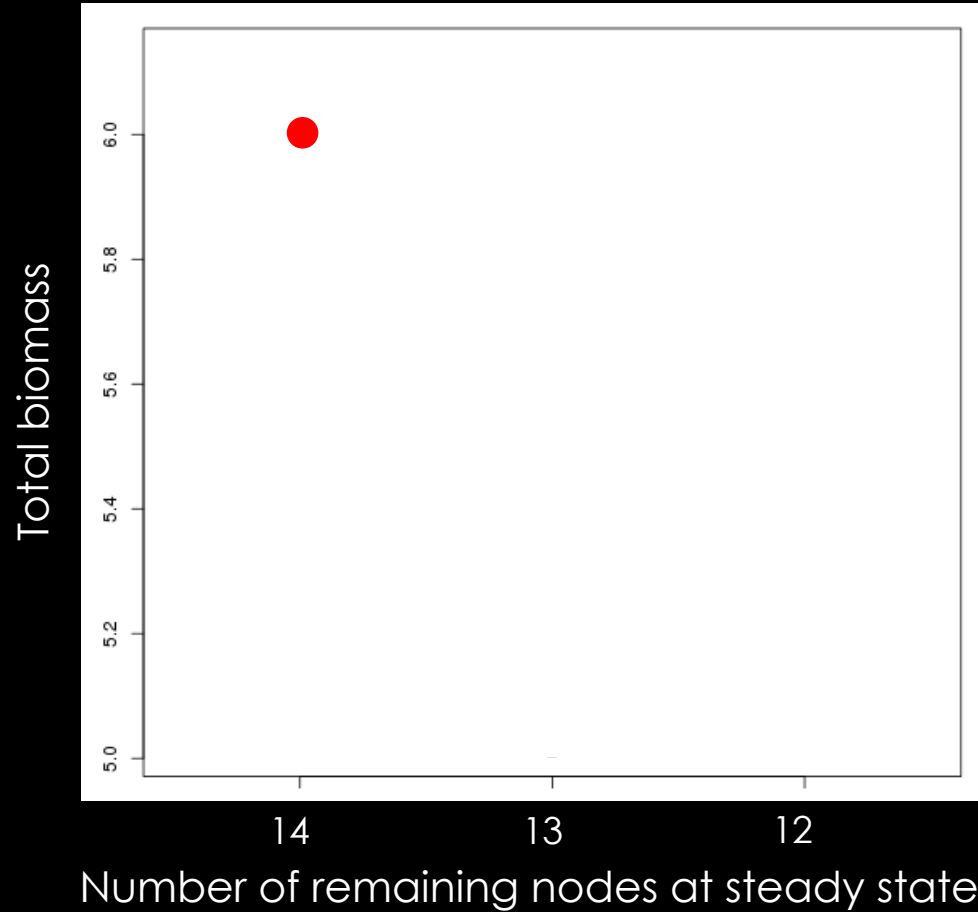
- 
- ```
graph TD; A["14 nodes  
(‘typical’ species of  
the cluster)"] --> B["(i) Connectivity of the Chilean web"]; A --> C["(ii) 500 random networks  
(keep degree sequence)"]; B --> D["Calculate species diversity and total biomass"]; C --> D;
```
- (i) Connectivity of the Chilean web
  - (ii) 500 random networks  
(keep degree sequence)



Calculate species diversity and total biomass

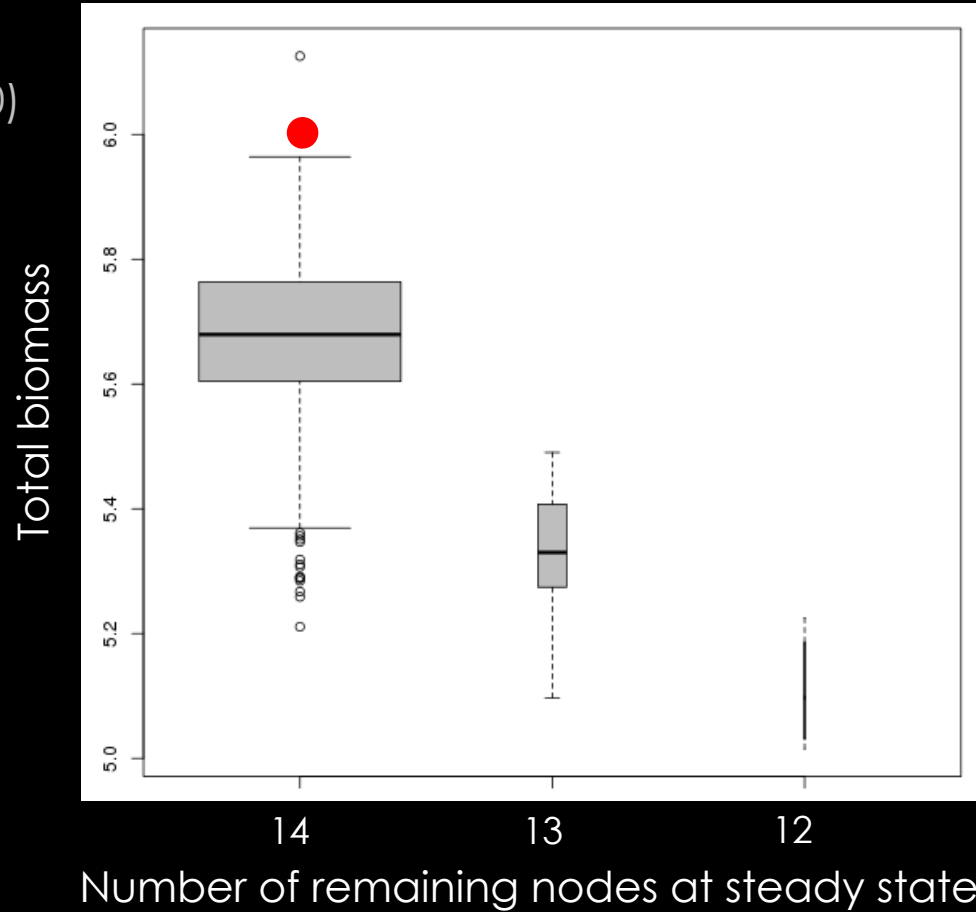


Chilean web





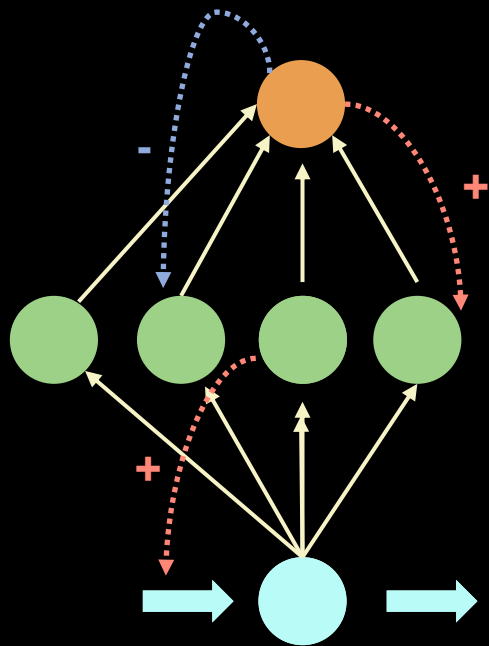
Chilean web  
Random webs (500)



The specific 3-dimensional signature of the clusters  
in the Chilean web promotes:

- high species persistence
- high total biomass



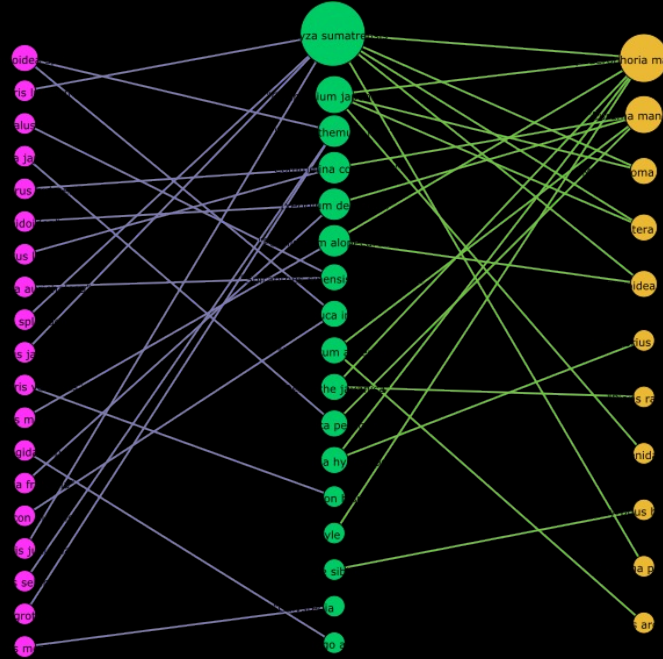


multiplex networks

Herbivores

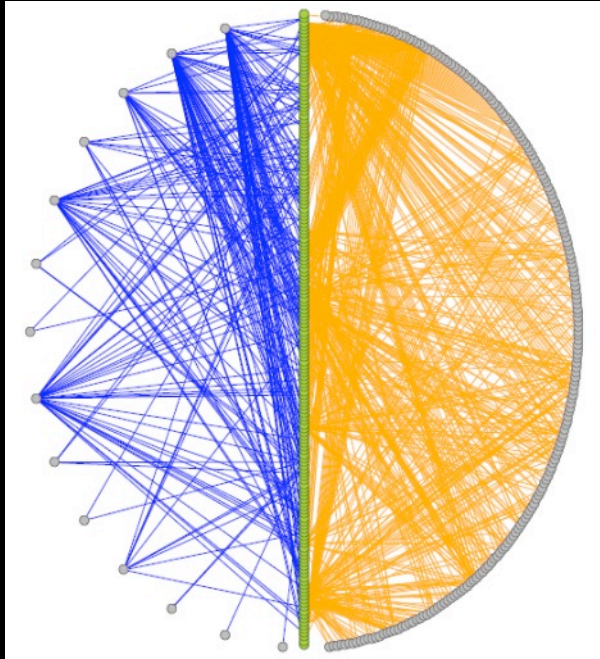
Plants

Pollinators

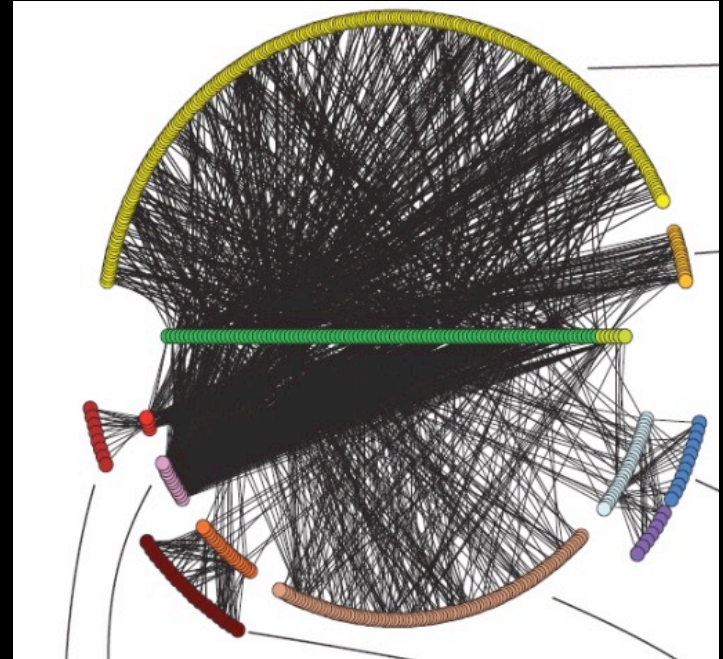


multipartite networks

Antagonistic    Plantes    Mutualistic



Melian et al. 2009  
Donana Biological Reserve, Spain



Pocock et al. 2012  
Norwood Farm, Somerset, UK



# « Complexity begets stability »

Odum 1953

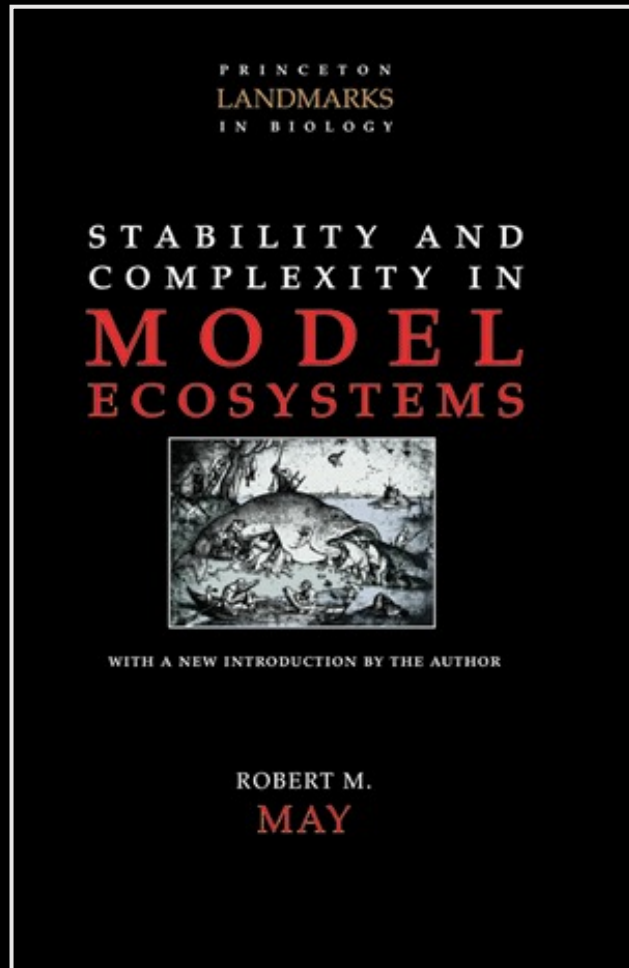
MacArthur 1955

Elton 1958





Robert May



« In general mathematical models of multispecies communities, complexity tends to beget instability »

Robert May, 1973

« In general mathematical models of multispecies communities, complexity tends to beget instability »

Robert May, 1973

« The task, therefore, is to elucidate the **devious strategies** which make for stability in enduring natural systems »

# COMPLEX ECOLOGICAL COMMUNITIES

COMPLEX ECOLOGICAL COMMUNITIES  
MANY SPECIES

COMPLEX ECOLOGICAL COMMUNITIES  
MANY SPECIES  
MANY INTERACTION TYPES

multi-interaction networks

Thank you very much for your attention

Virginia Domínguez-García, Vincent Miele, Sergio Navarrete, Evie Wieters, Eric Berlow, Christian Guill, Rodrigo Ramos-Jiliberto, Ian Donohue, Alexandre Génin, Shai Pilosof, Mason Porter, Mercedes Pascual



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