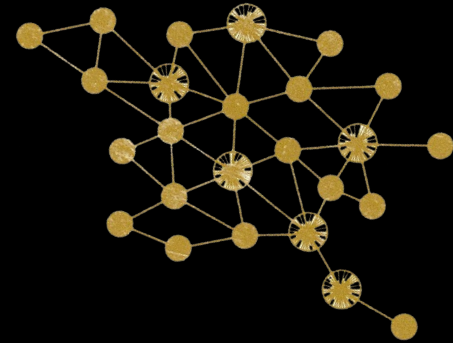


# Multilayer ecological networks

Sonia Kéfi



SANTA FE  
INSTITUTE



# Black out : ce 28 septembre 2003, l'Italie plonge dans l'obscurité

Le pays ayant abandonné le nucléaire en 1987 est alors jugé trop dépendant de ses importations électriques. Depuis, il a misé sur les énergies renouvelables

Temps de lecture estimé : 1 minute

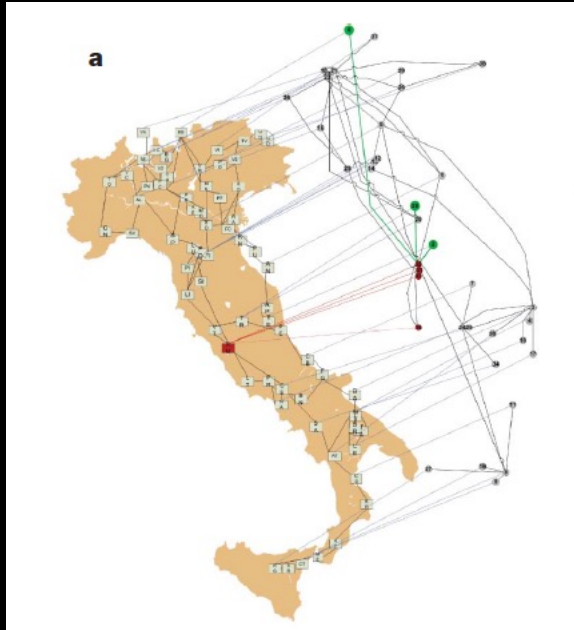
Publié le 12 décembre 2016 à 17:48 - Maj 24 octobre 2021 à 20:49



Blackout en Italie en 2003 - Sipa Press

# Interdependent networks

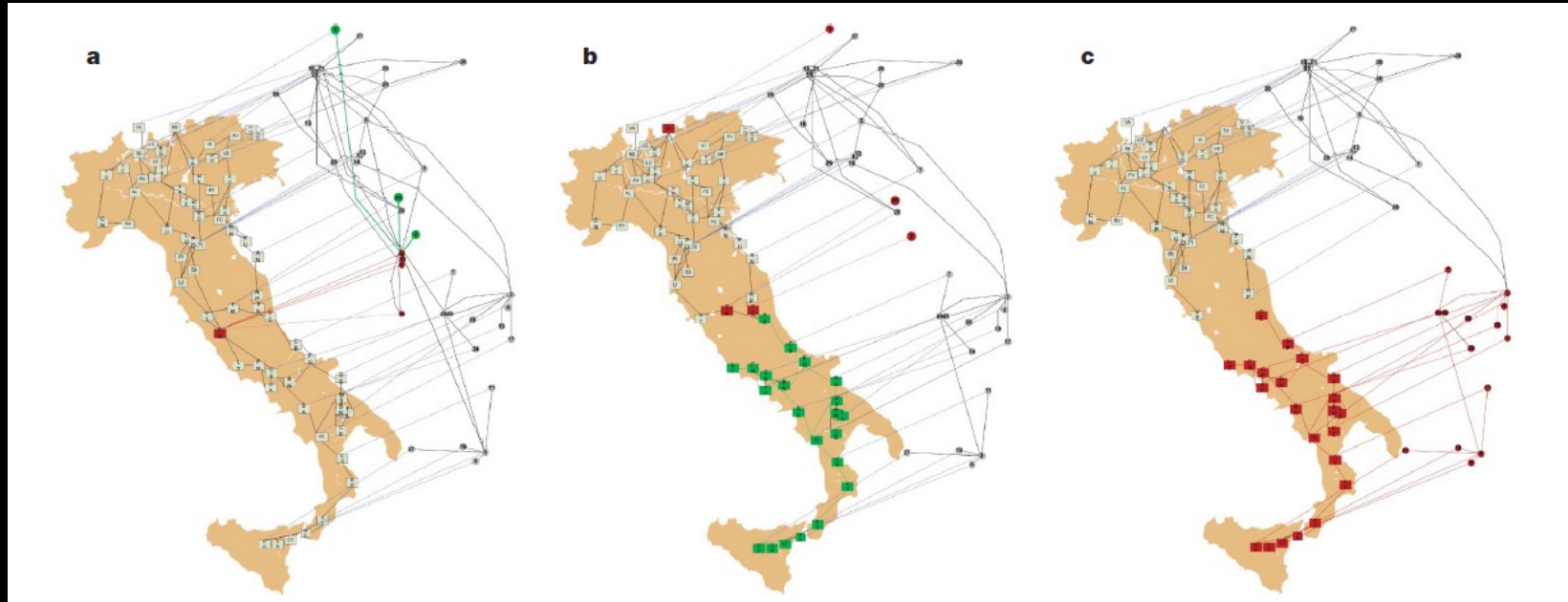
power network



Internet network

- One power station removed (red)
- nodes removed from internet network (red)
- Isolated power station removed next (green)

power network

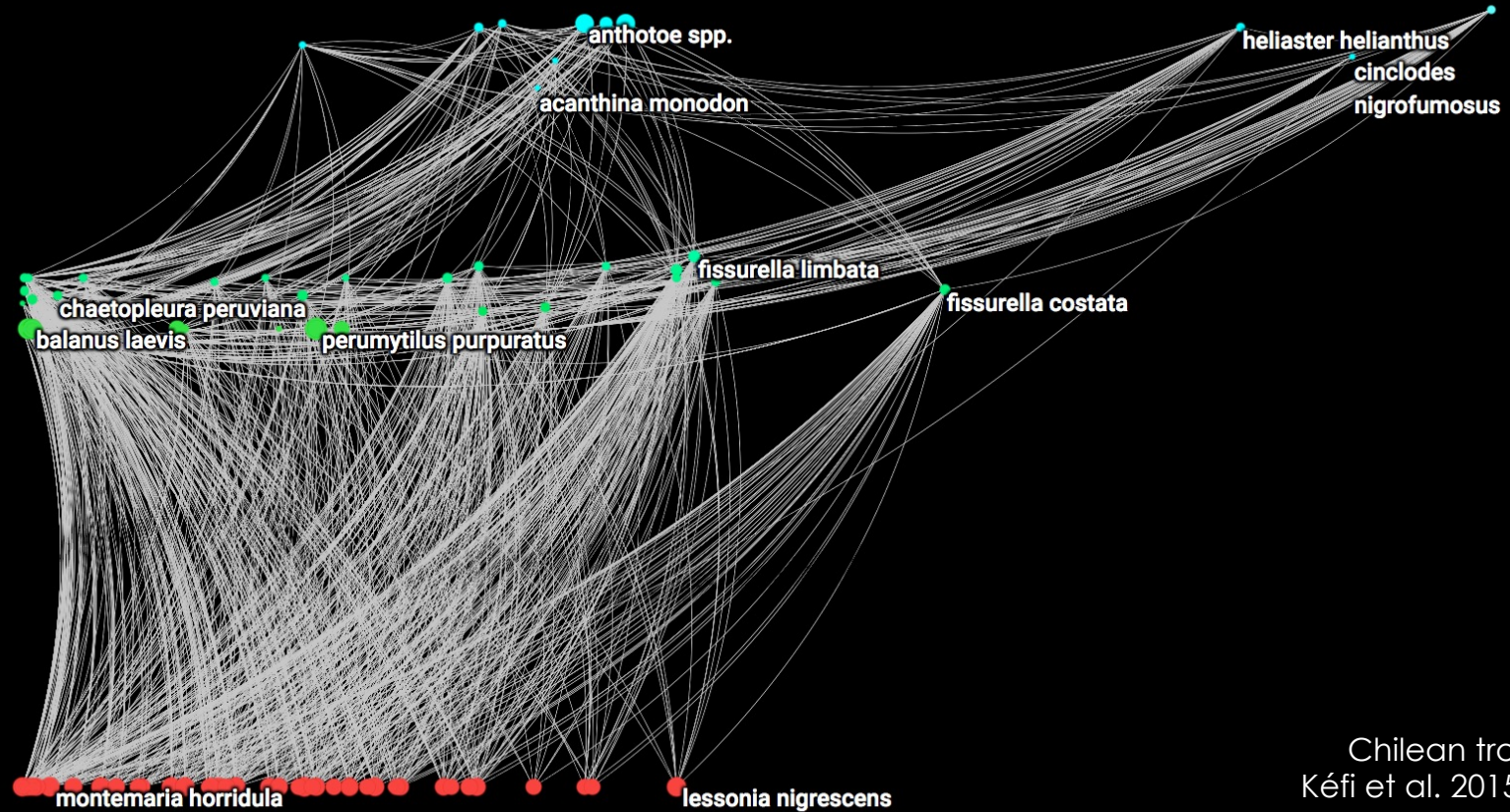


Internet network



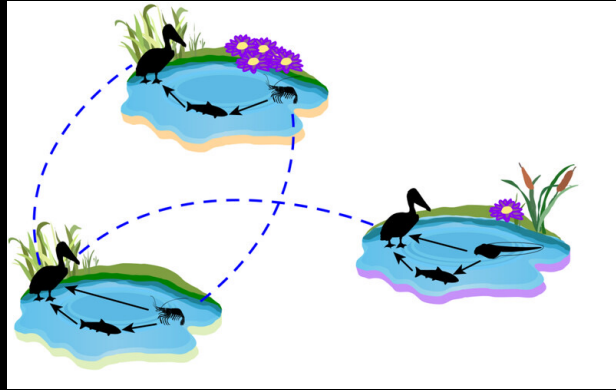
Modern systems are interdependent networks  
→ Cascades of failures possible

What about ecological networks?

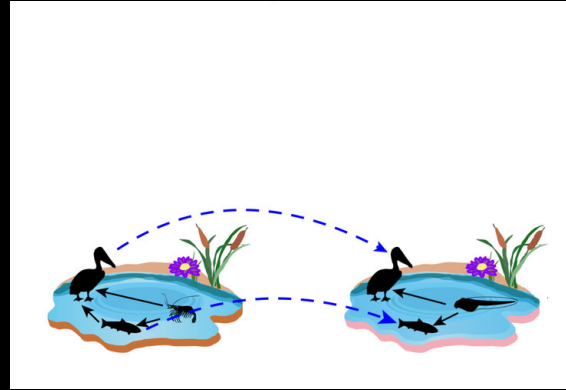


Chilean trophic web  
Kéfi et al. 2015, Ecology  
plotted with mappr

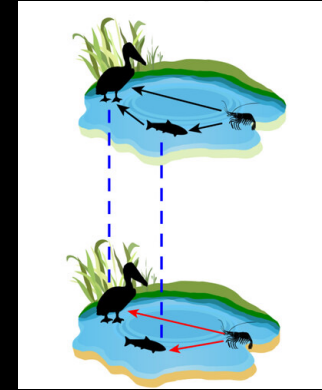
Spatial



Temporal



Multi-interactions



# multilayer ecological networks

## Mathematical Formulation of Multilayer Networks

Manlio De Domenico,<sup>1</sup> Albert Solé-Ribalta,<sup>1</sup> Emanuele Cozzo,<sup>2</sup> Mikko Kivela,<sup>3</sup> Yamir Moreno,<sup>2,4,5</sup>  
Mason A. Porter,<sup>6</sup> Sergio Gómez,<sup>1</sup> and Alex Arenas<sup>1</sup>

*Journal of Complex Networks* (2014) 2, 203–271

doi:10.1093/comnet/cnu016

Advance Access publication on 14 July 2014

### Multilayer networks

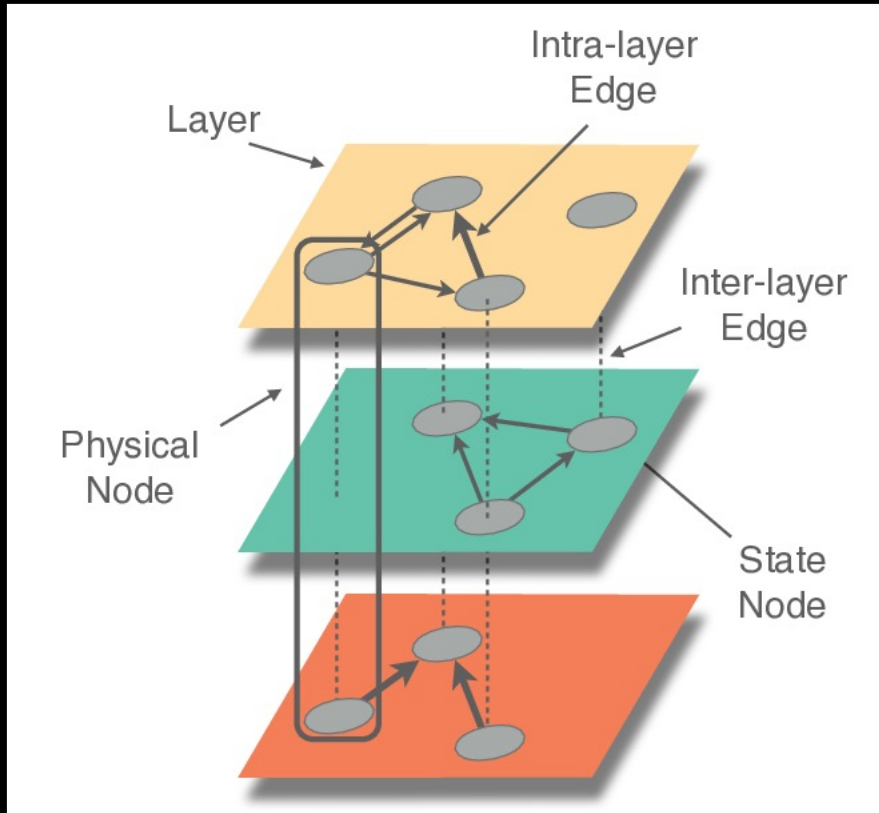
MIKKO KIVELÄ

*Oxford Centre for Industrial and Applied Mathematics, Mathematical Institute, University of Oxford,  
Oxford OX2 6GG, UK*

### The structure and dynamics of multilayer networks



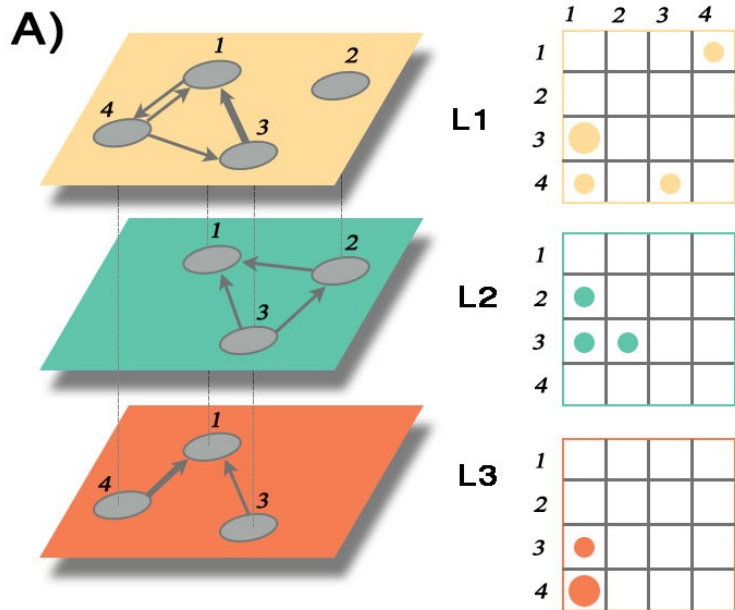
S. Boccaletti<sup>a,b,\*</sup>, G. Bianconi<sup>c</sup>, R. Criado<sup>d,e</sup>, C.I. del Genio<sup>f,g,h</sup>,  
J. Gómez-Gardeñes<sup>i</sup>, M. Romance<sup>d,e</sup>, I. Sendiña-Nadal<sup>j,e</sup>, Z. Wang<sup>k,l</sup>,  
M. Zanin<sup>m,n</sup>



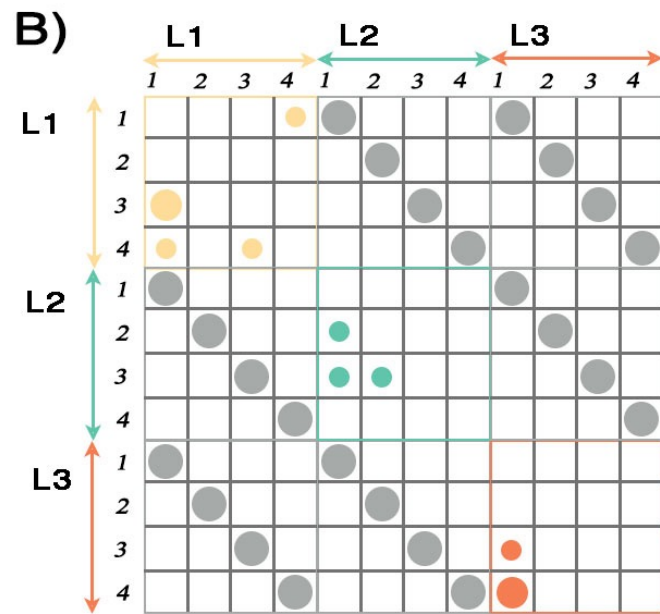
#### 4 components:

- layers (patches, interaction types, time points)
- nodes (physical vs state)
- intralayer links
- **interlayer links**





Interconnected  
Multiplex Network



Supra-adjacency Matrix

## Non-interconnected

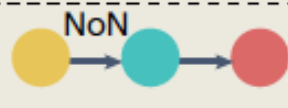


Edge-coloured

## Interconnected



Categorical



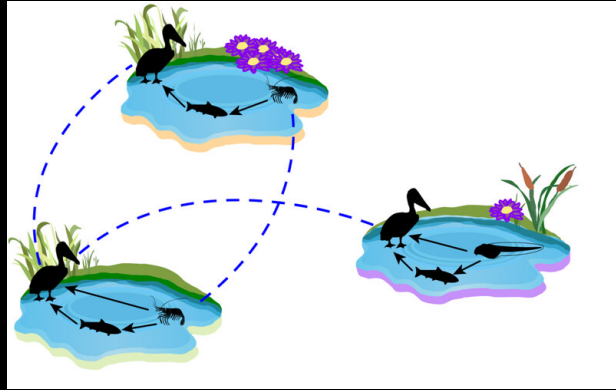
Temporal



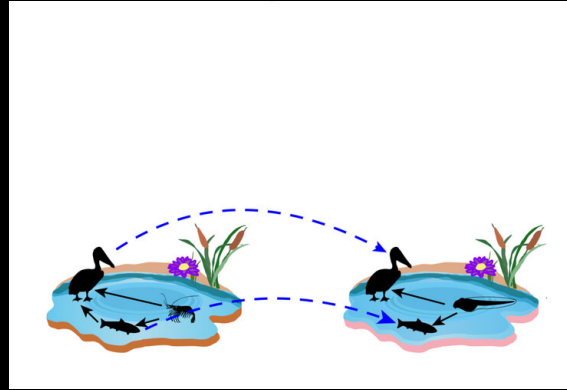
Interdependent

Multiplex

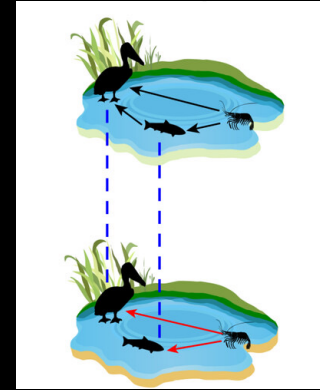
Spatial



Temporal



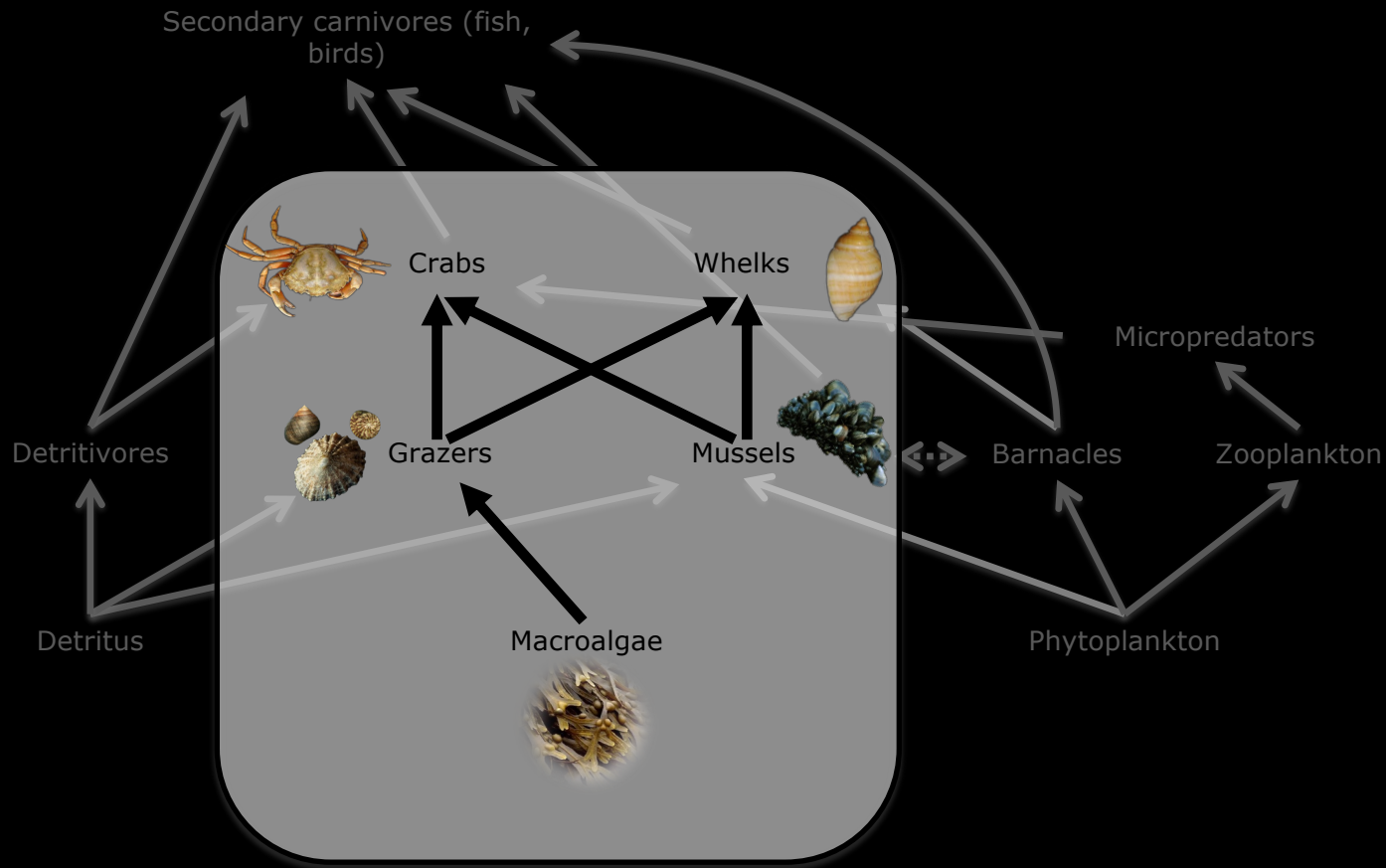
Multi-interactions



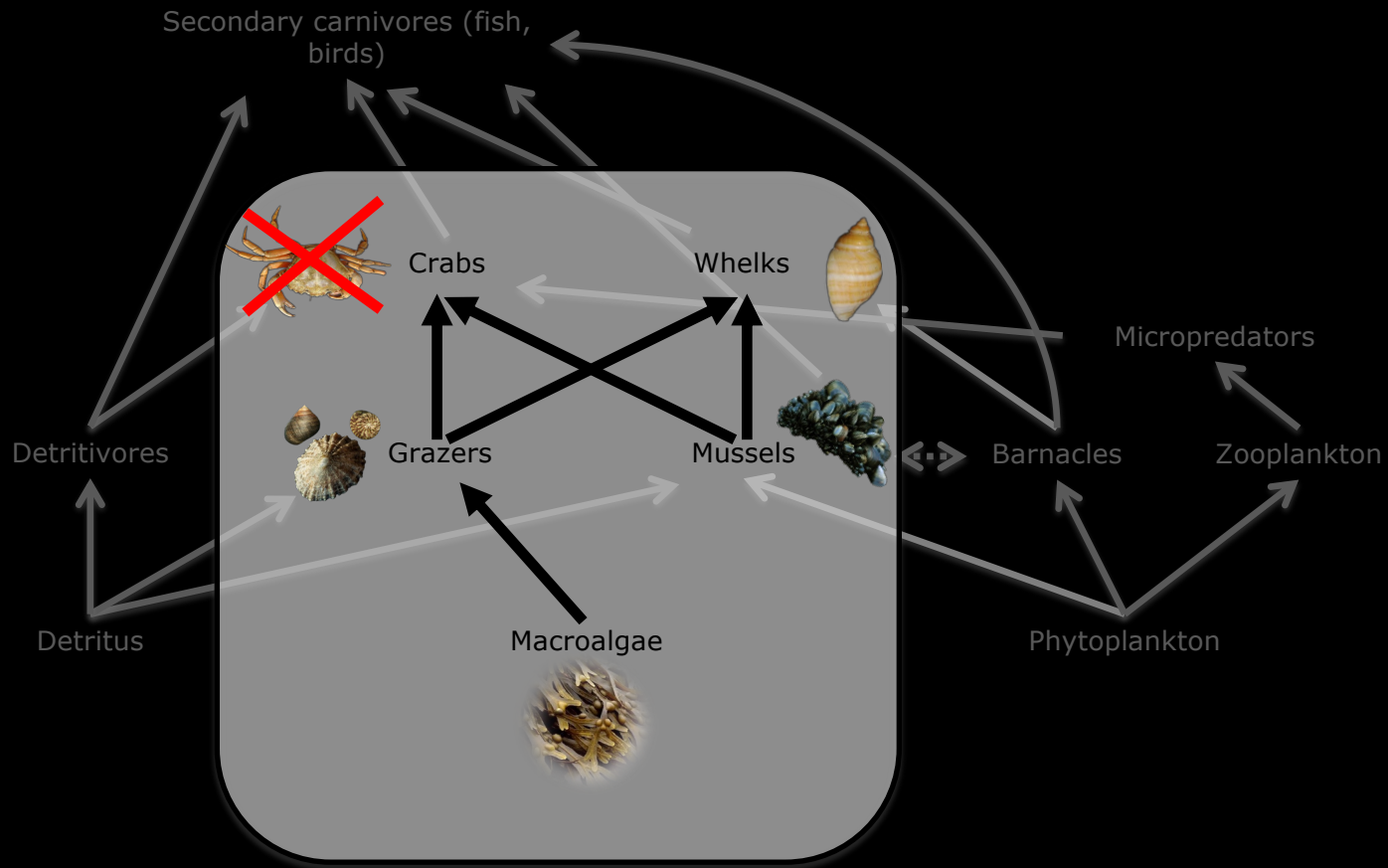
multi-interaction networks



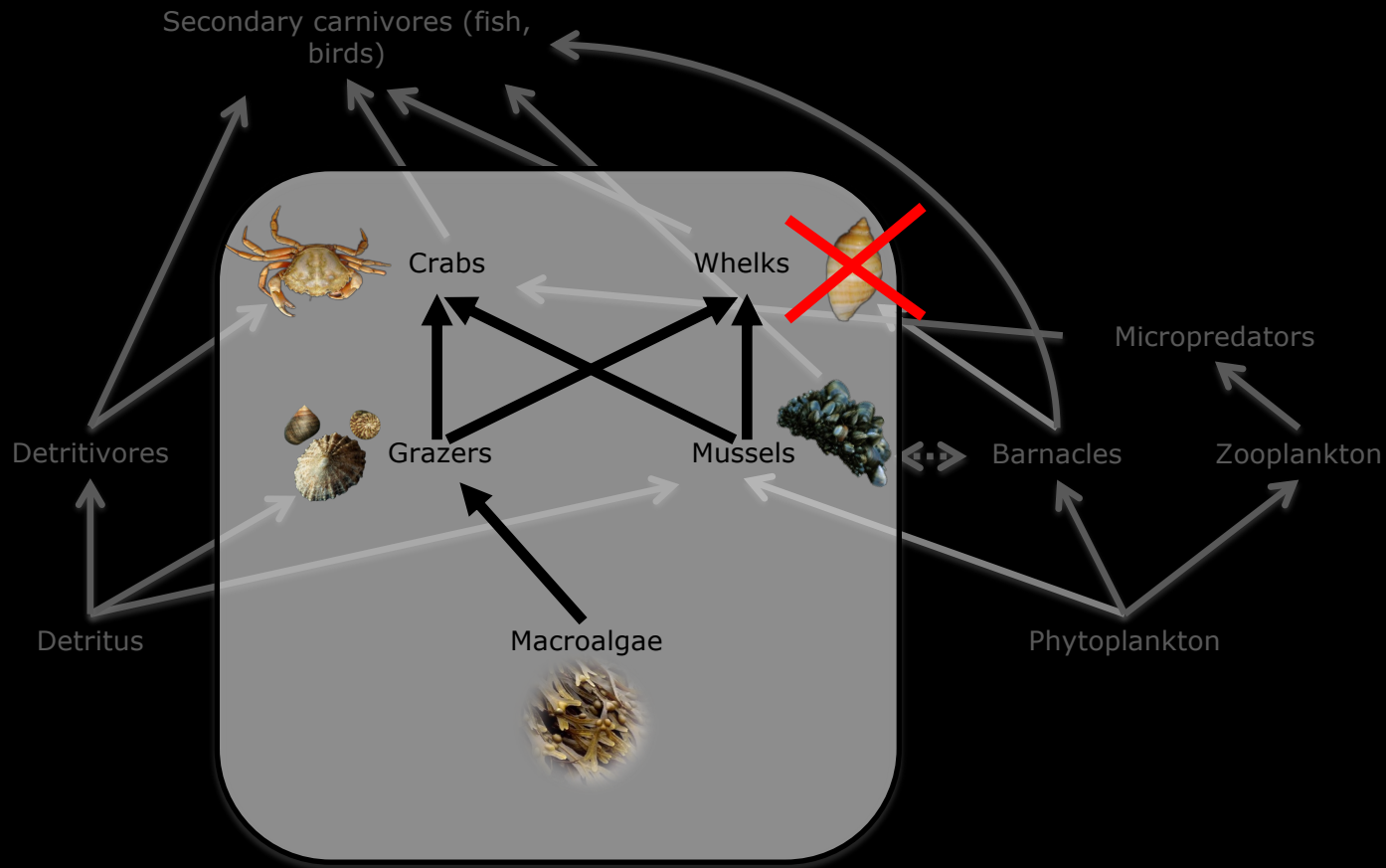
@ian Donohue

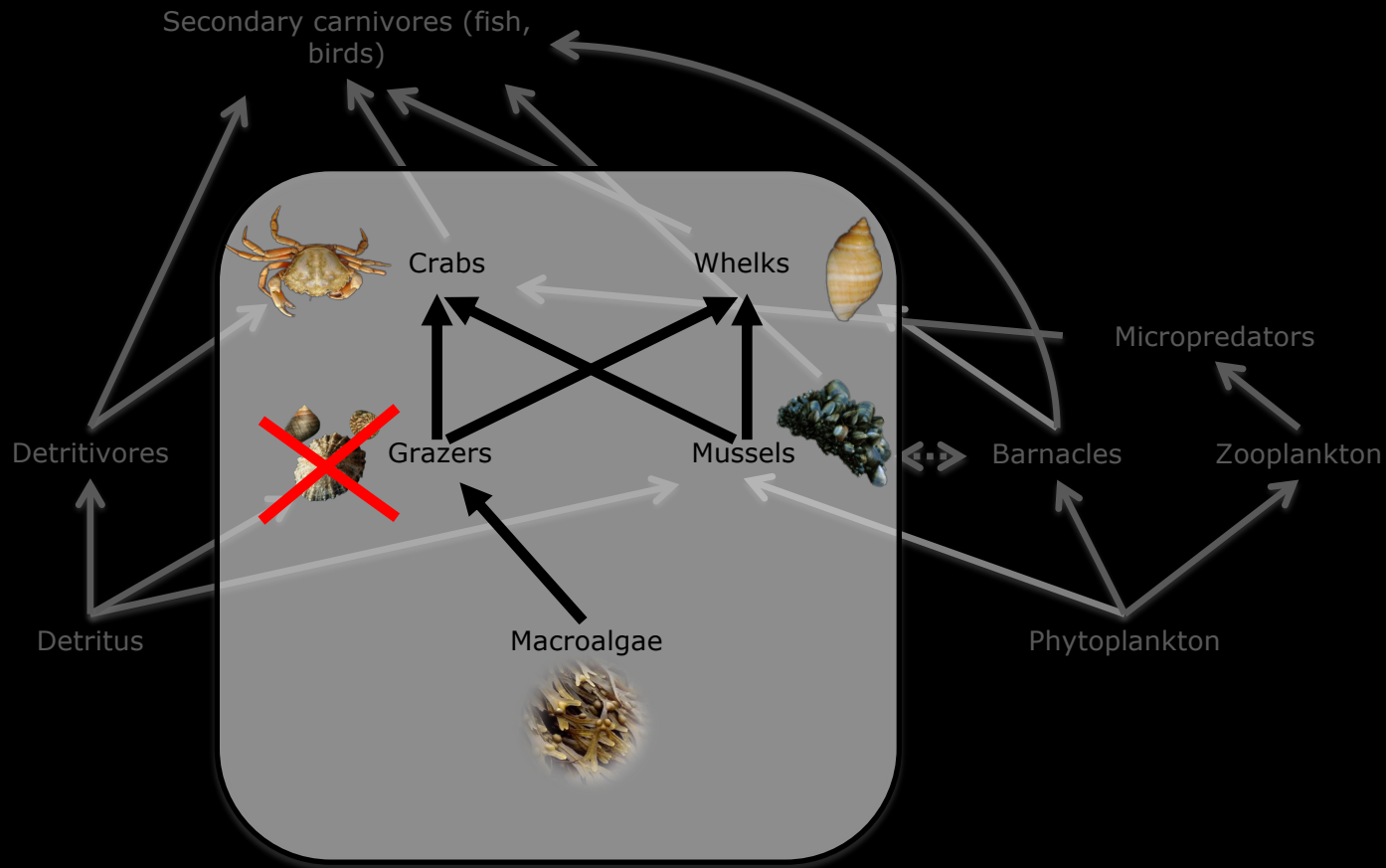


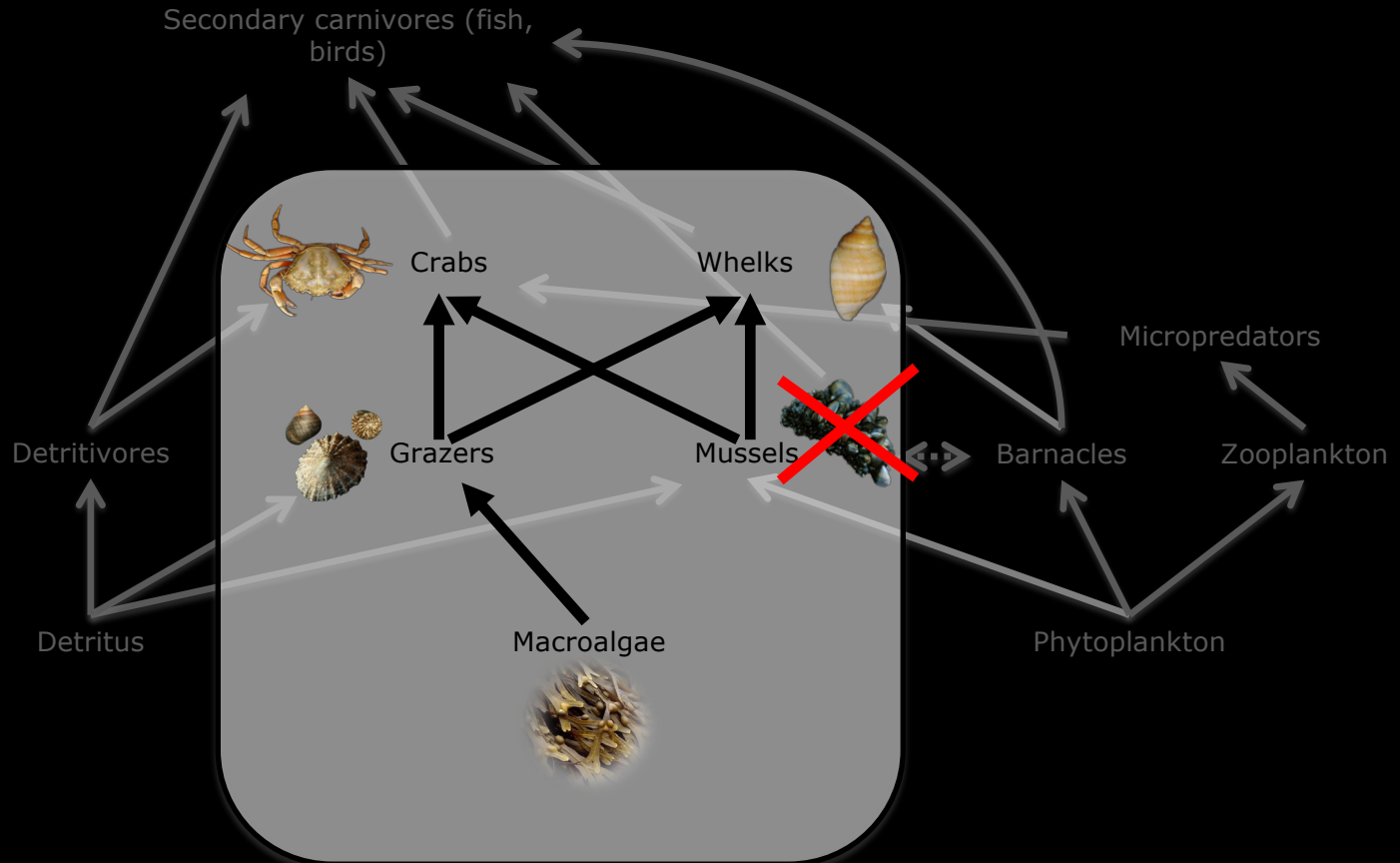


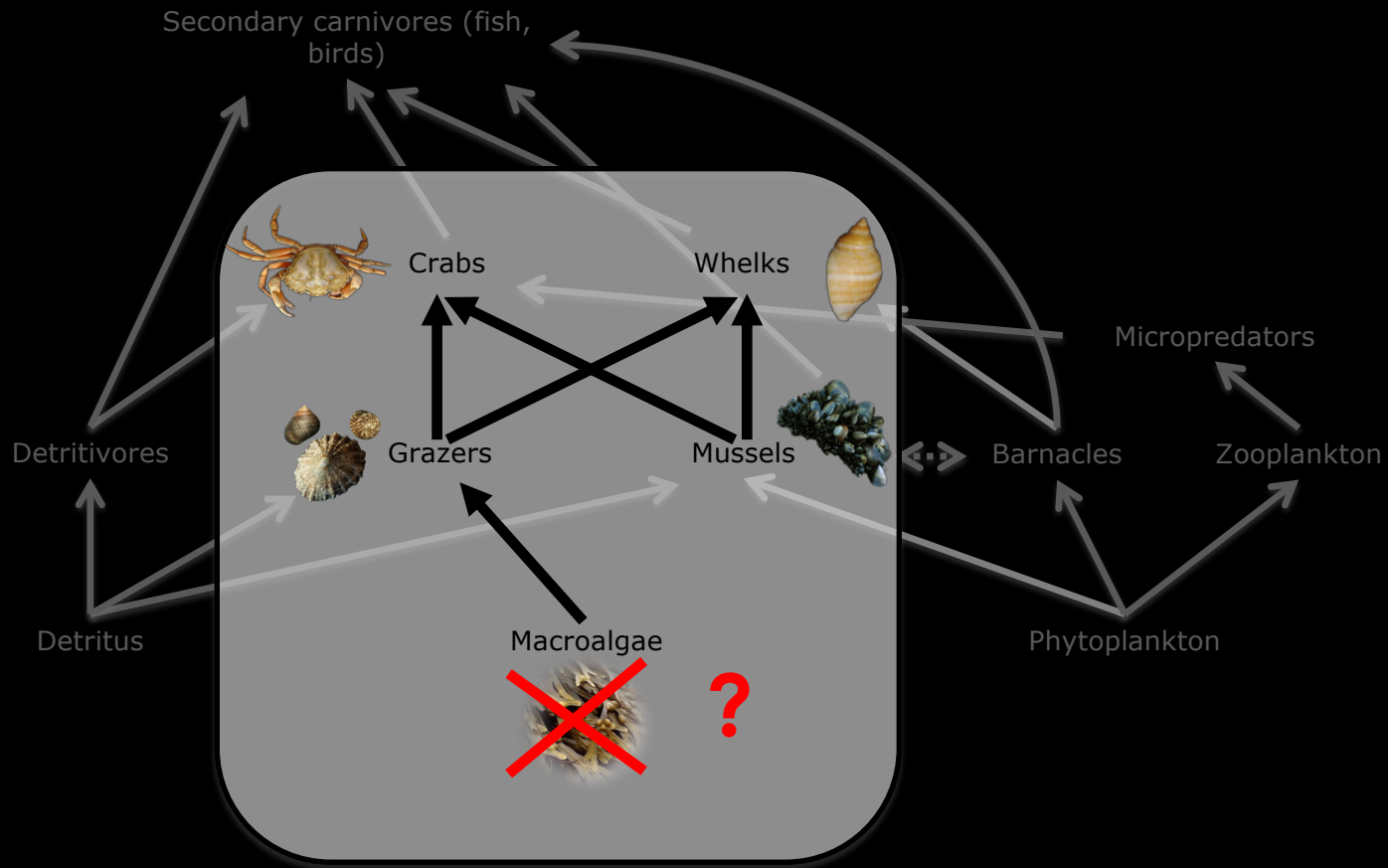


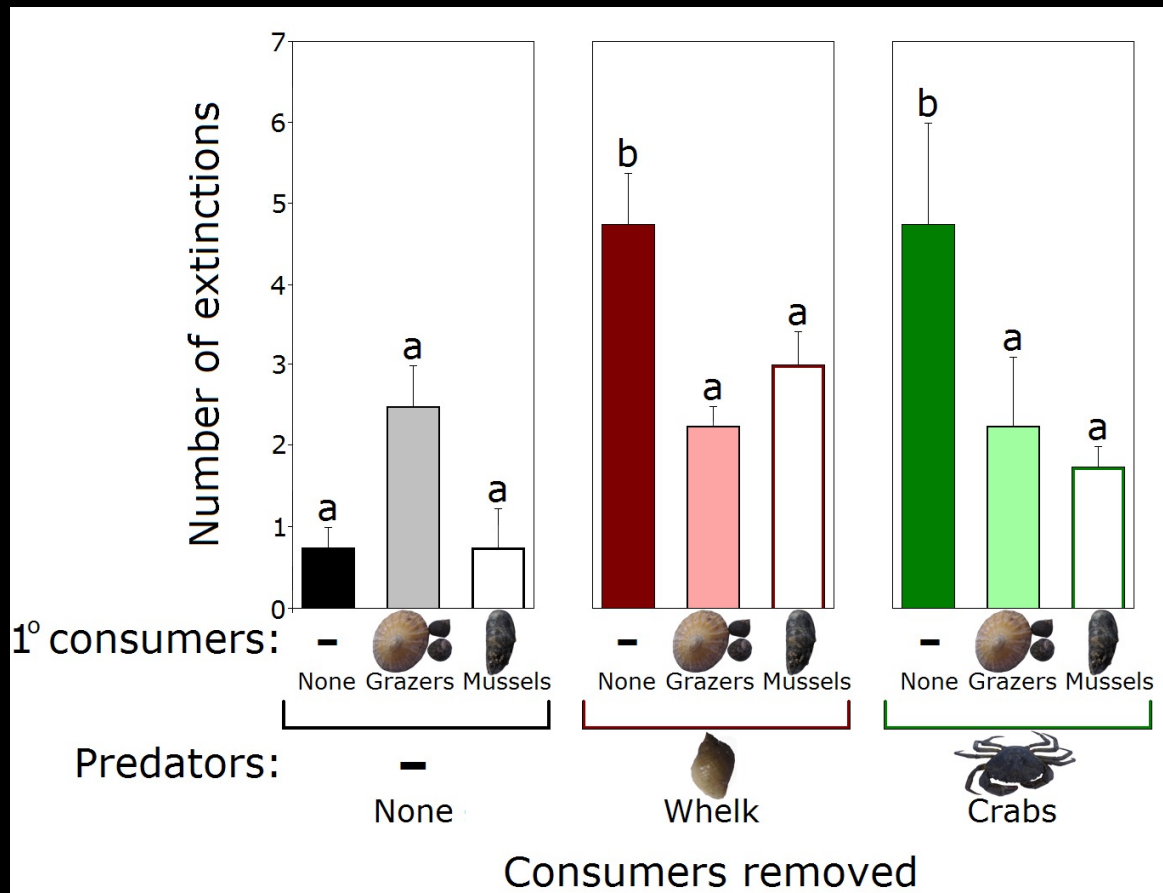












1/3 of the macroalgal taxa lost following the removal of either predator species

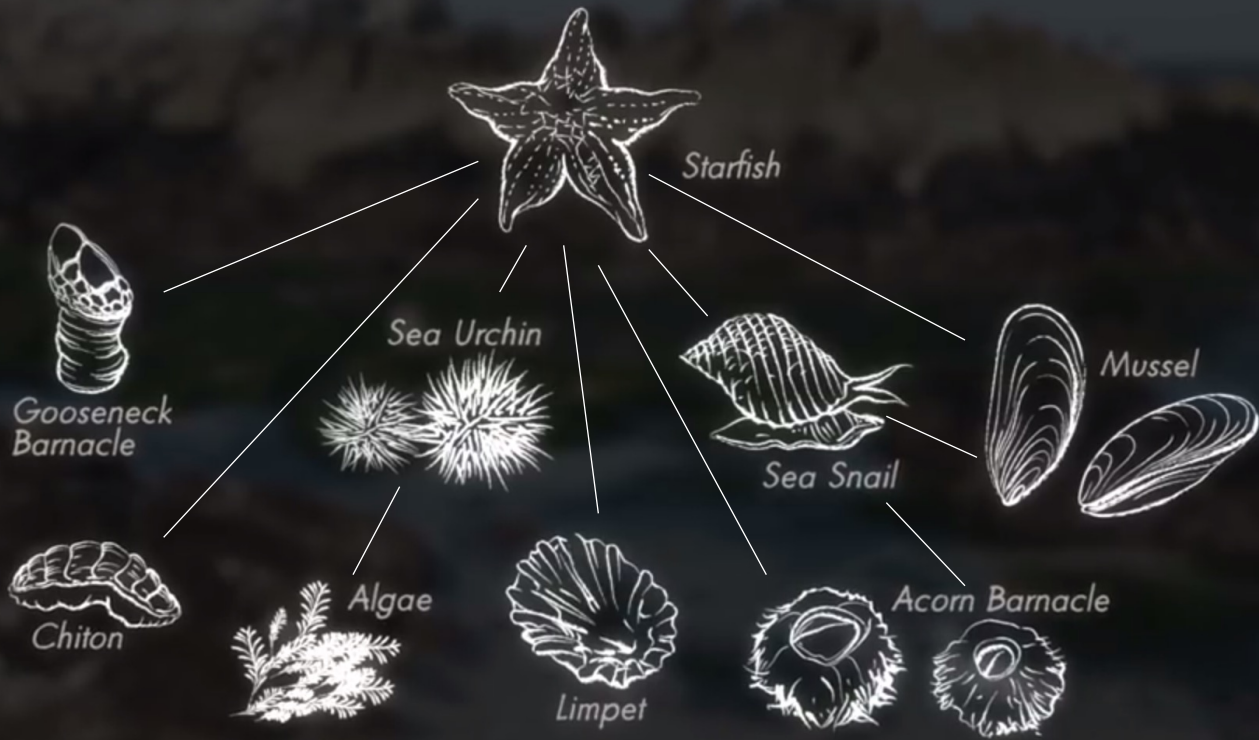
an order of magnitude greater than in models

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

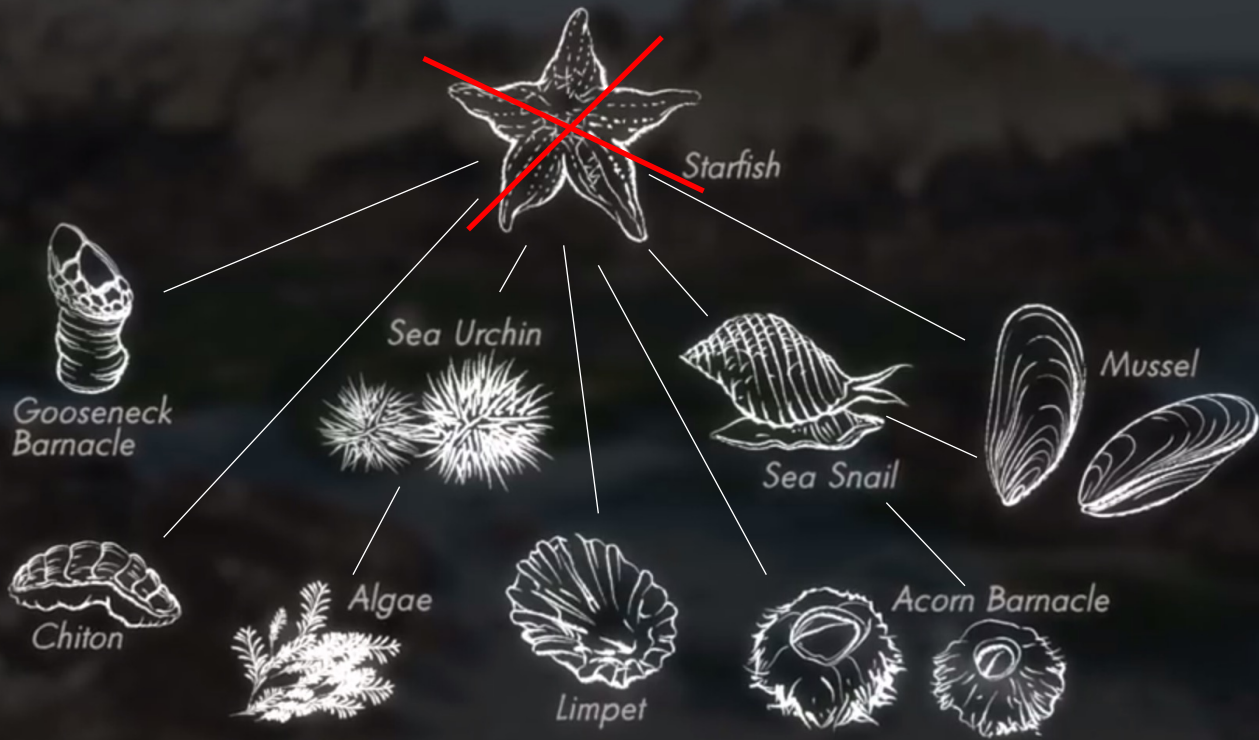




Robert Paine  
Credit: Alamy. Telegraph obituary



hhmi biointeractive  
« Some Animals Are More Equal than Others: Keystone Species and Trophic Cascades »





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



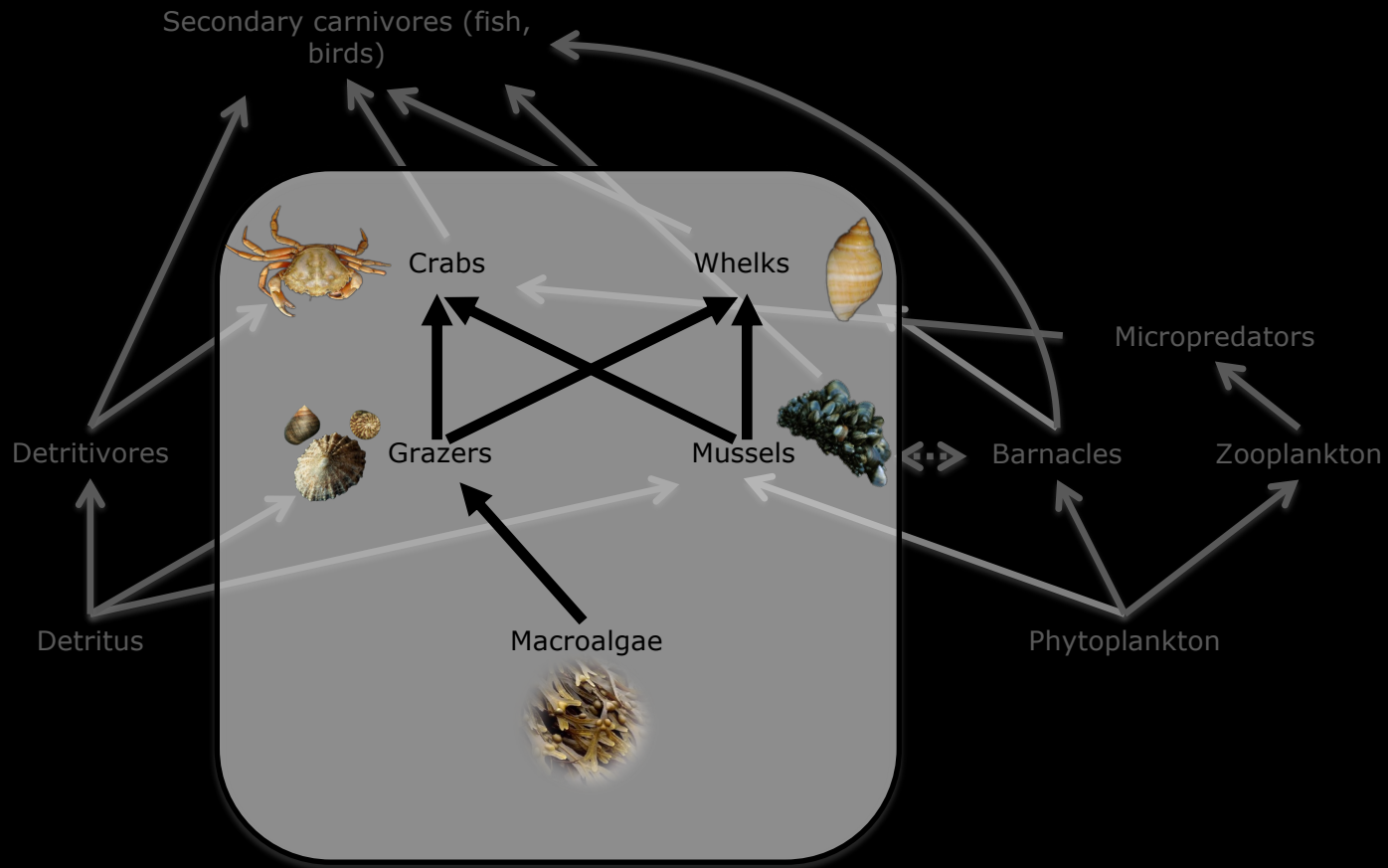


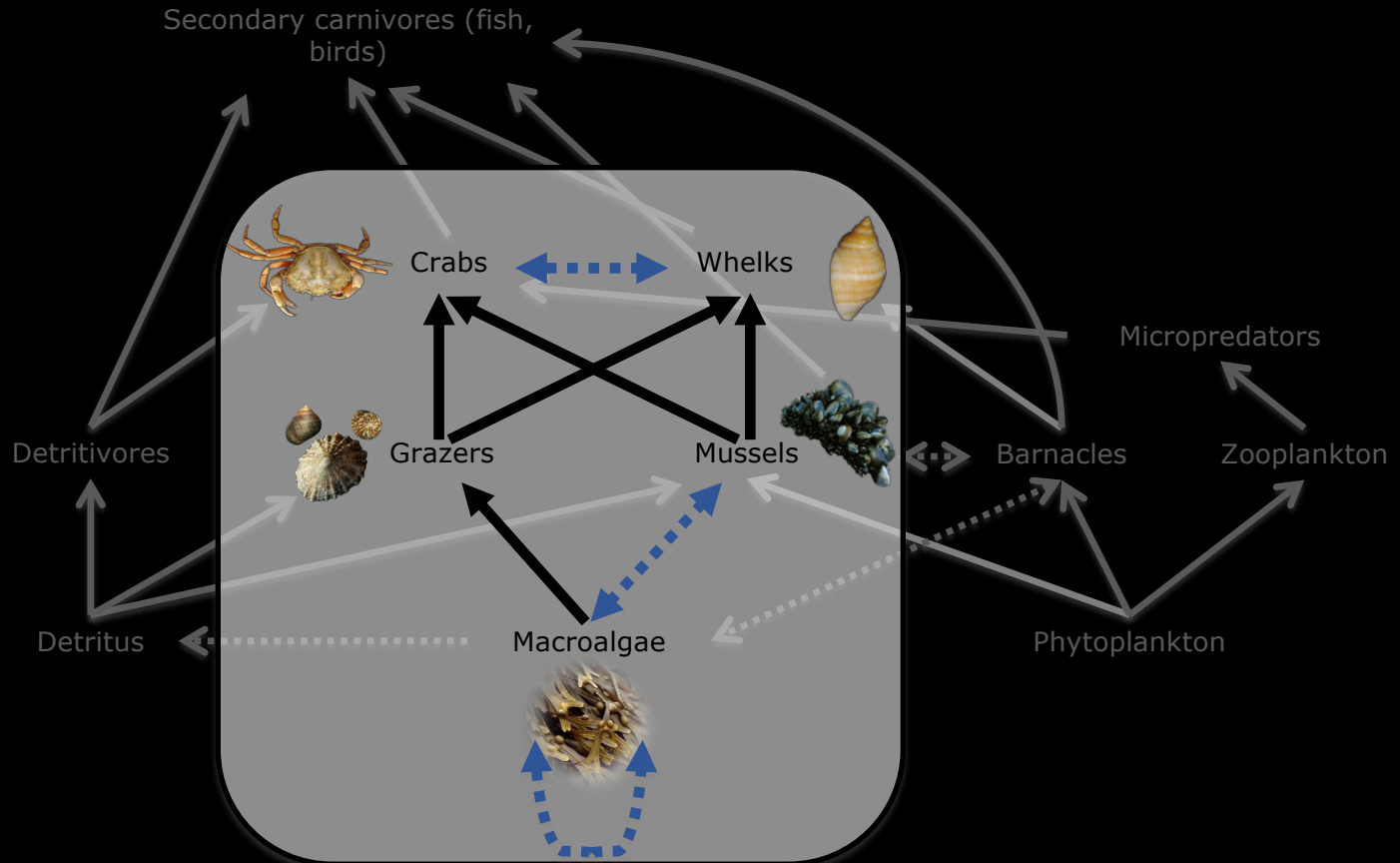












dynamical model  
[bioenergetic consumer-resource model]



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

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

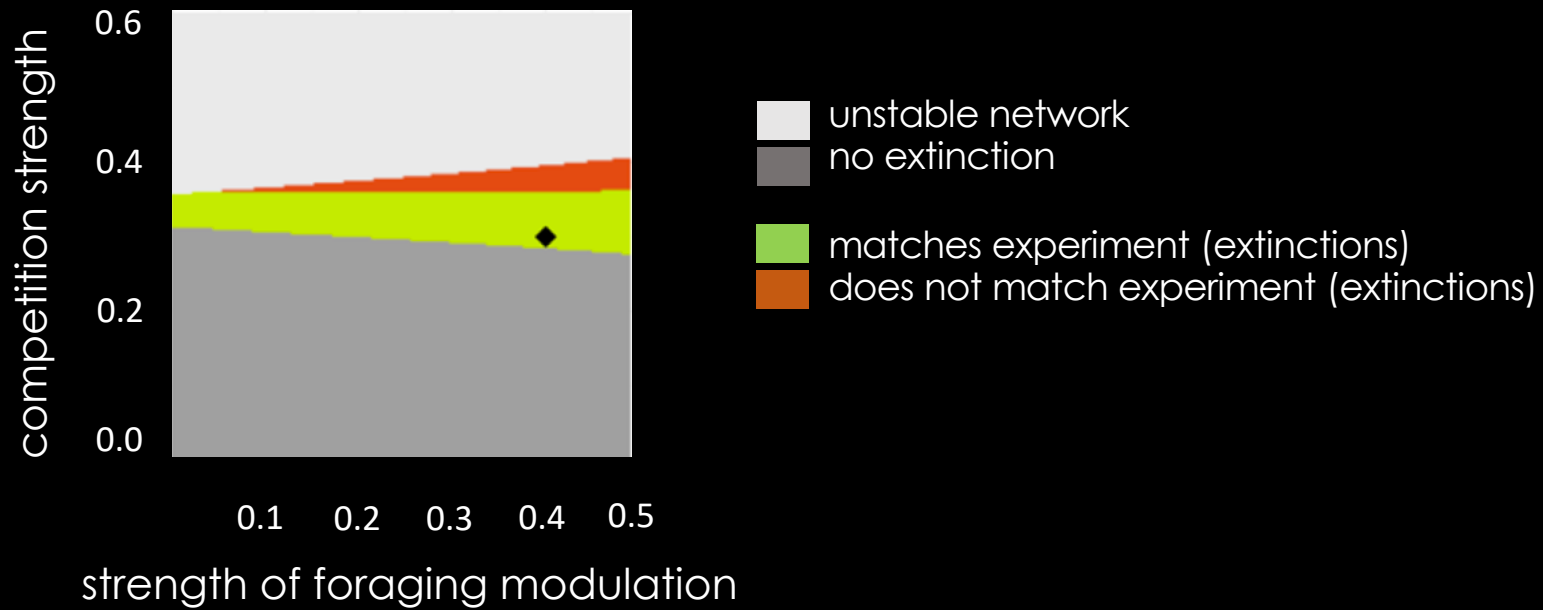
$$\frac{dB_i}{dt} = \underbrace{r_i \left(1 - \frac{B_i}{K_i}\right) B_i}_{\text{growth}} + \underbrace{e B_i \sum_j F_{ij}}_{\text{consumption (eats)}} - \underbrace{\sum_k F_{ki} B_k}_{\text{consumption (is eaten)}} - \underbrace{x_i B_i}_{\text{metabolism}}$$

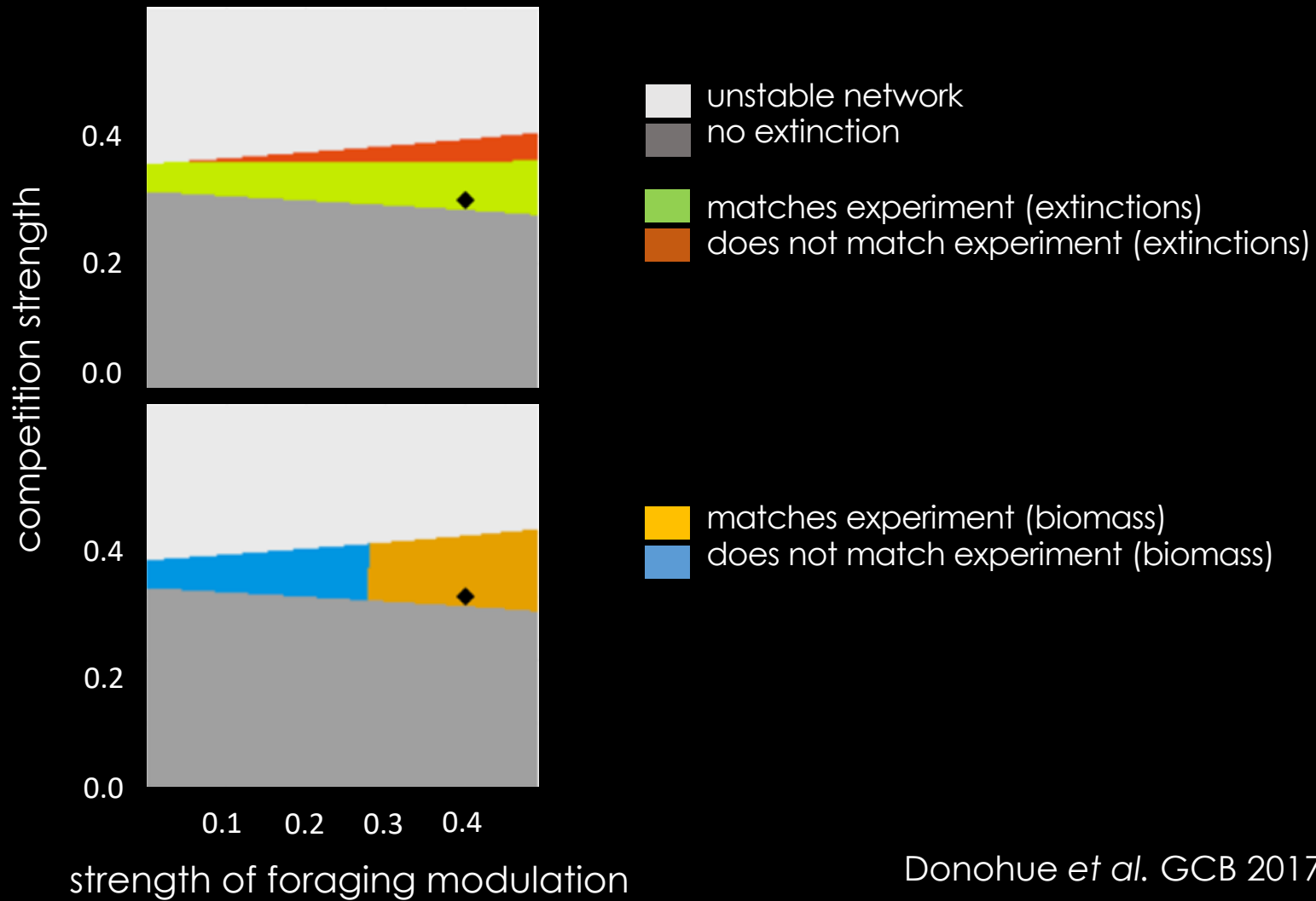
$$F_{ij} = \frac{w_i b_{ij} B_j^{1+q}}{1 + w_i h_i \sum_k b_{ik} B_k^{1+q}}$$

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

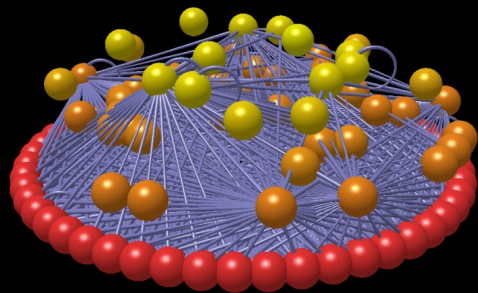
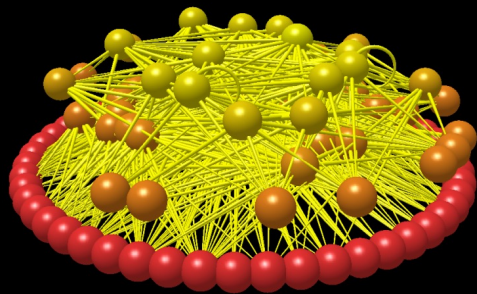
dynamical model  
[bioenergetic consumer-resource model]

+ non-trophic interactions  
competition for space  
foraging modulation

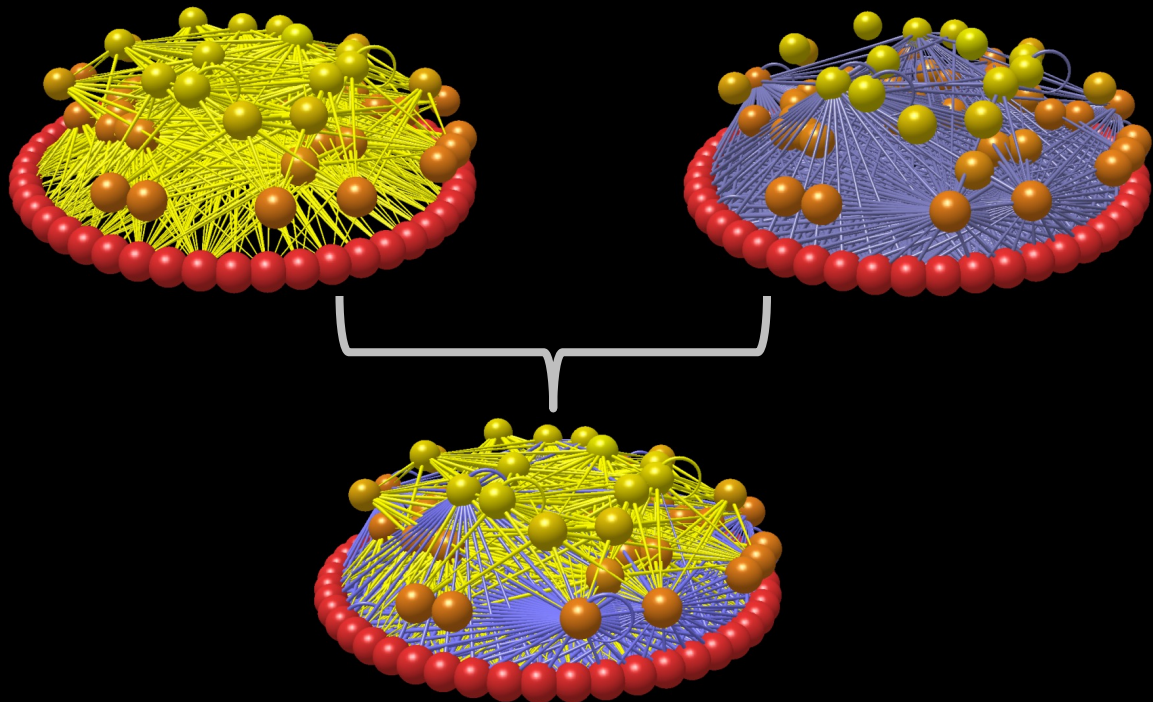


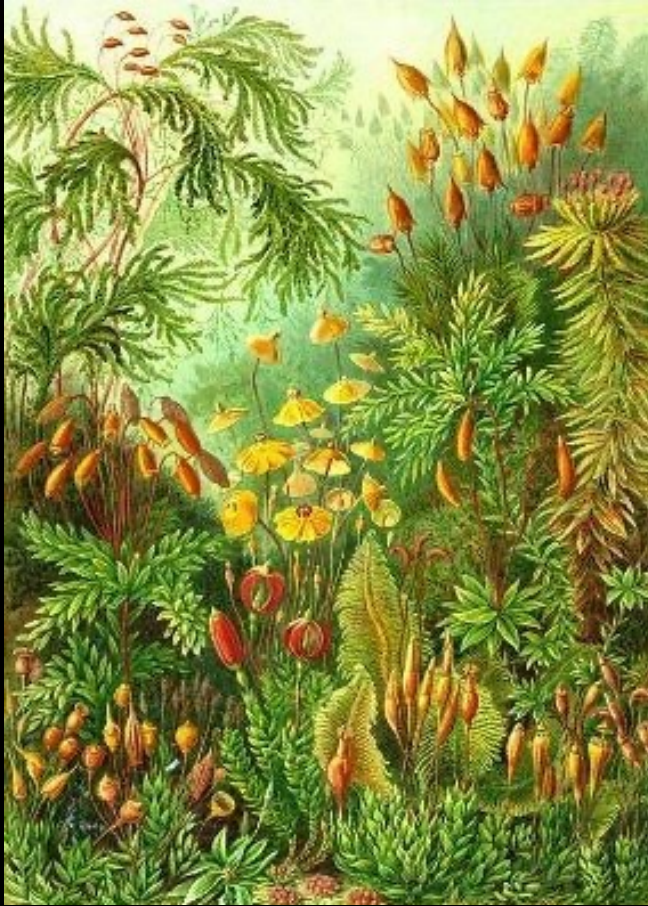


The diversity of interaction types is needed to reproduce the results of the experiments









« So dependent on each other  
in so complex a manner »

Charles Darwin, 1859

DARWIN'S "ENTANGLED BANK" (HAECKEL, CIRCA 1904)

A need for **integrating** several interaction types  
in ecological network studies

Berlow et al. 2004  
Ings et al. 2009  
Olf et al. 2009  
Fontaine et al. 2011  
Kéfi et al. 2012

How does the diversity of interaction types affect functioning?

dynamical model  
[bioenergetic consumer-resource model]

+ non-trophic interactions

Competition for space

Predator interference

Recruitment facilitation

Refuge provisioning

Positive and negative effects on survival

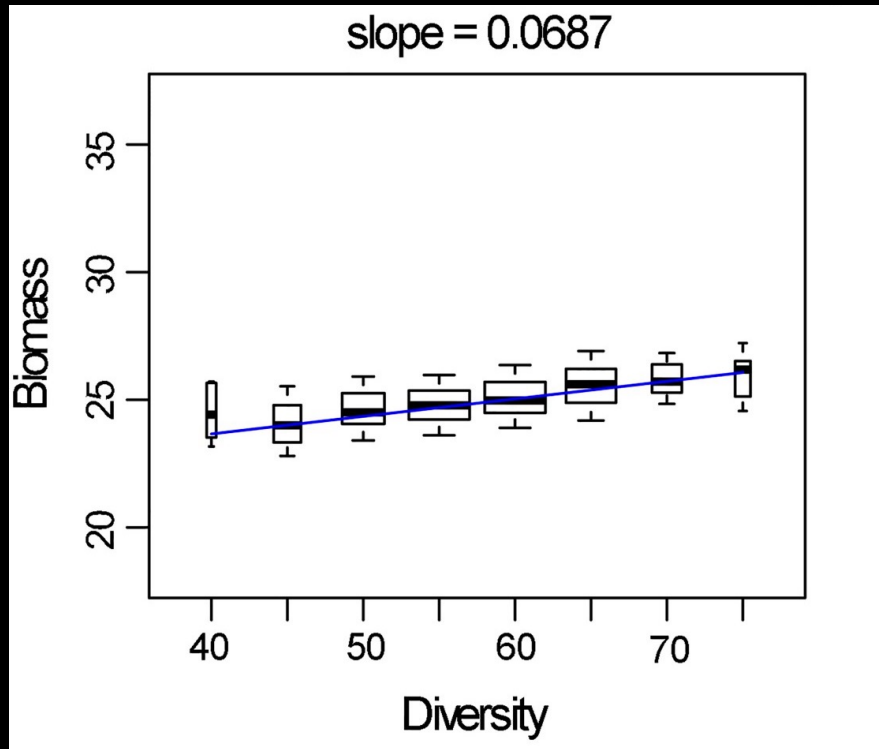
# Simulations

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



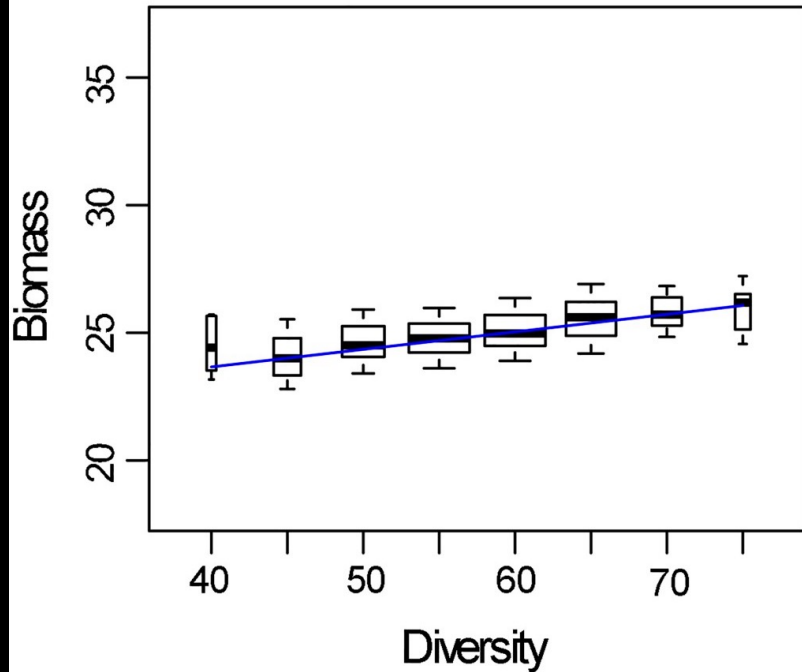
Calculate species diversity and total biomass

# One interaction type (trophic)



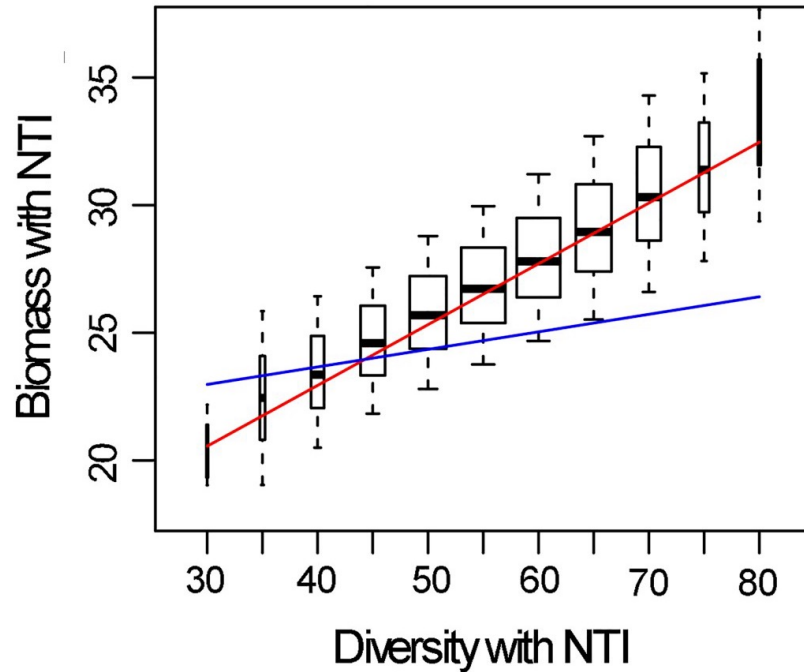
## One interaction type (trophic)

slope = 0.0687



## Diverse interactions types (multiplex)

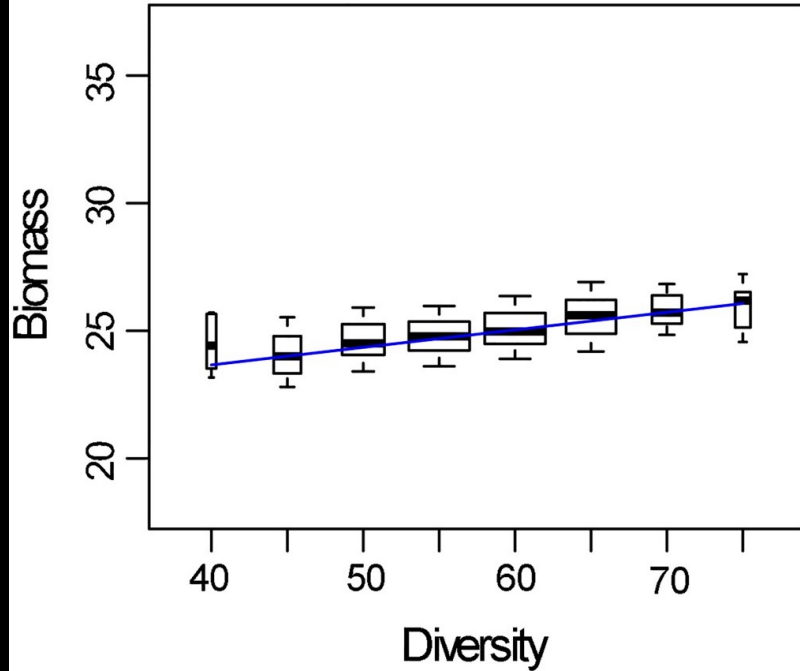
slope = 0.238





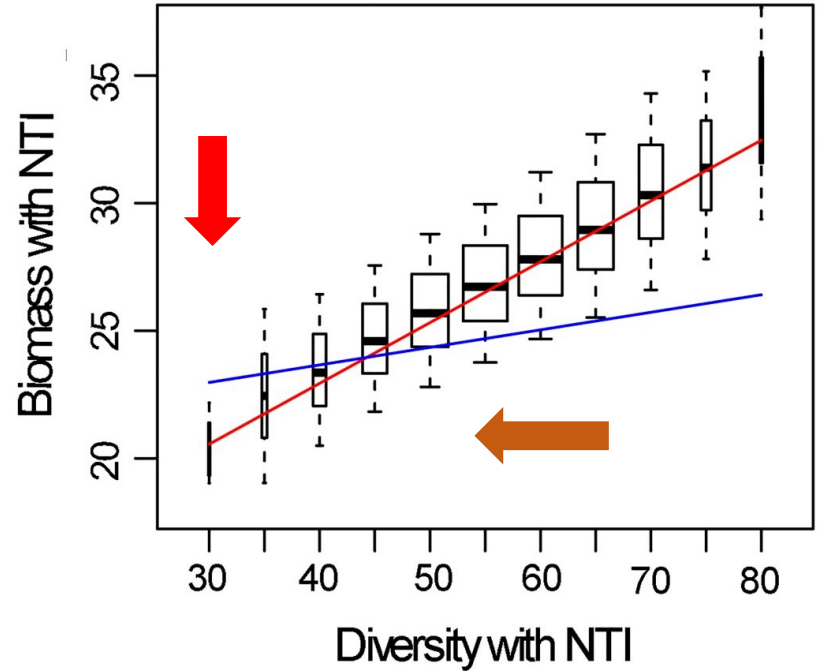
## One interaction type (trophic)

slope = 0.0687



## Diverse interactions types (multiplex)

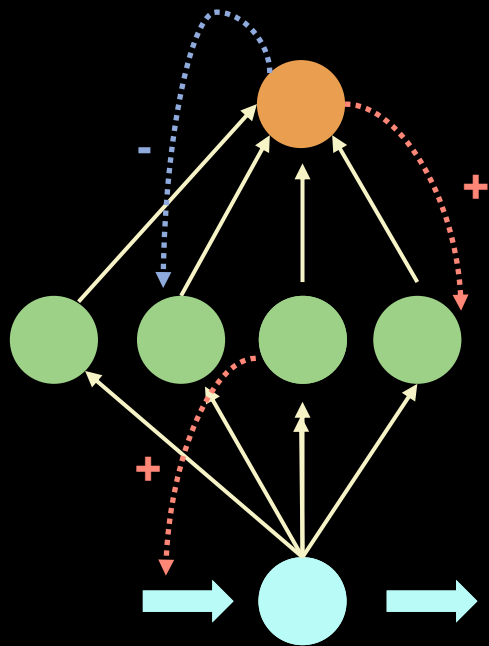
slope = 0.238



NTIs affect species diversity, community  
functioning and their relationship

How do different interaction types map  
onto each other?

What's the relative abundance of different interaction types?



multiplex ecological network



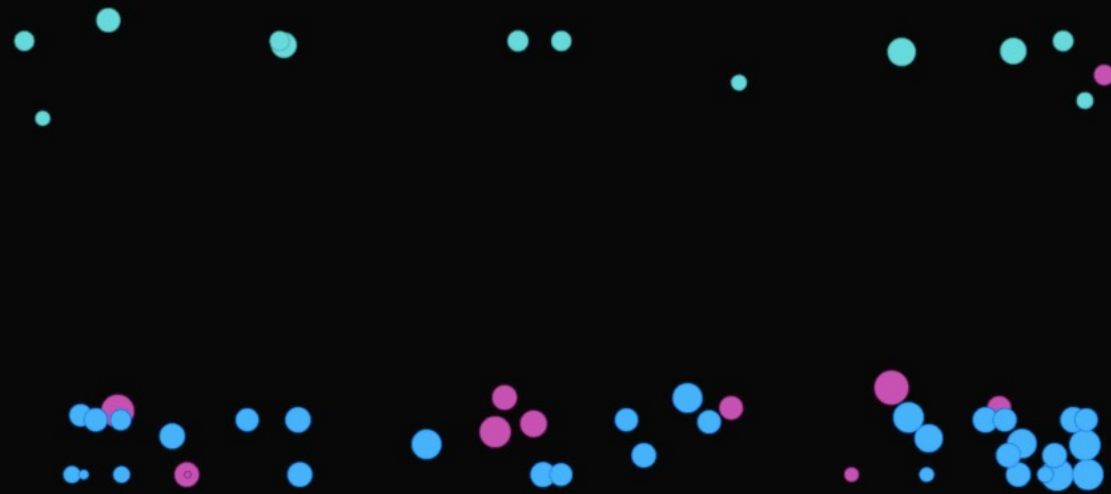
Sergio Navarrete,  
Evie Wieters

*Kéfi et al. 2015*





# CHILEAN MARINE ECOLOGICAL NETWORK



## 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

## EDGES 1611

1456	Feeding
155	Non-Feeding Positive

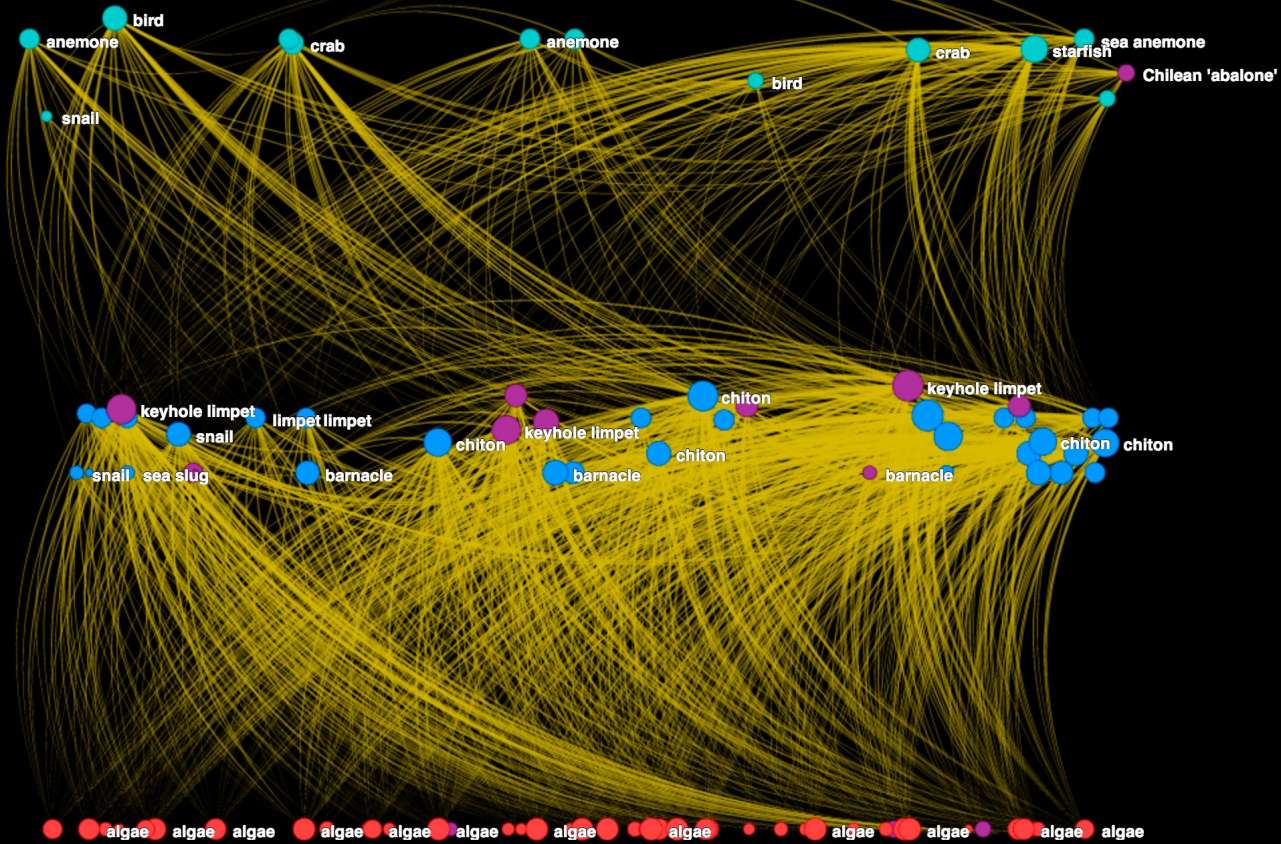
1 2 3

TL

Rand



# CHILEAN MARINE FOOD WEB



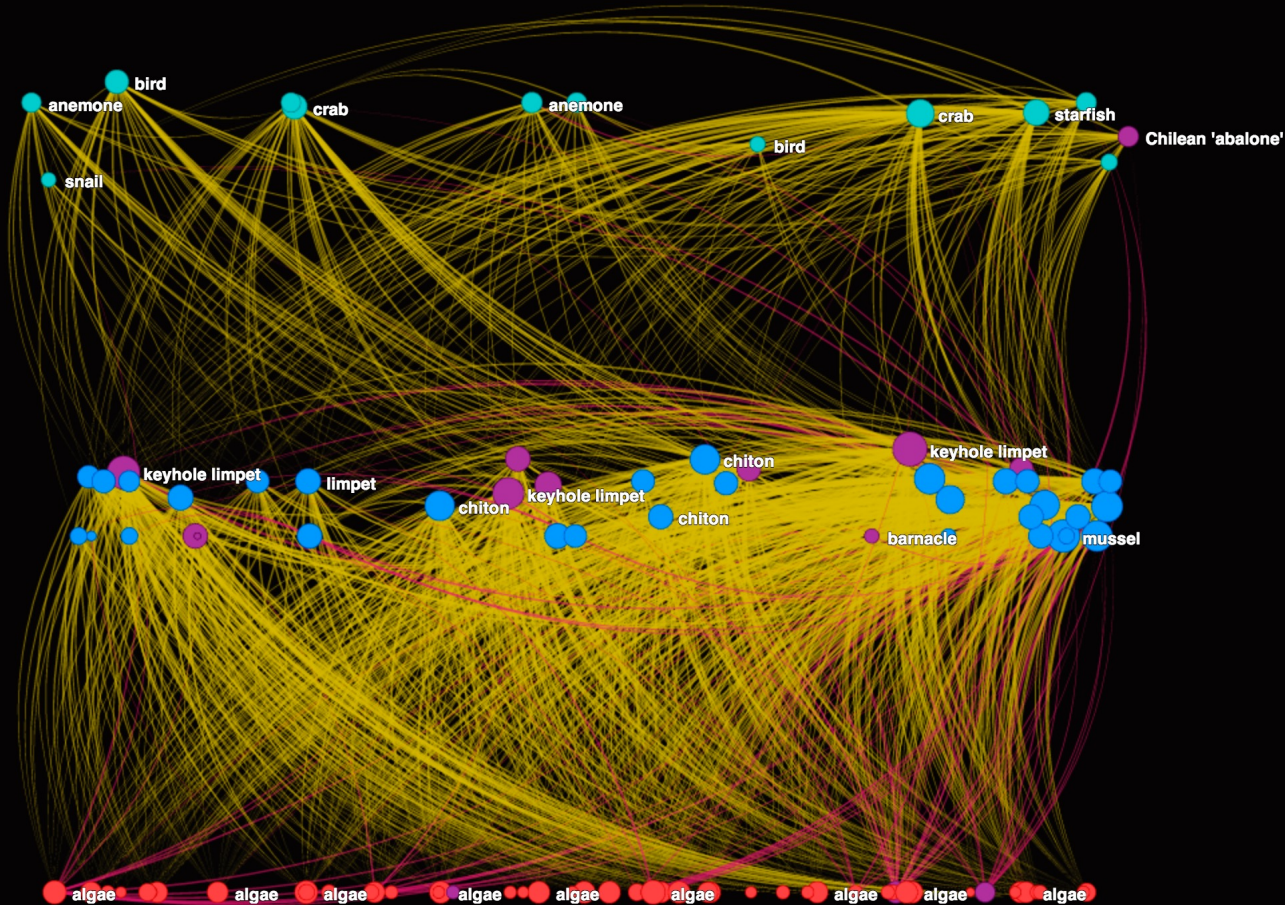
**NODES 104**

<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

TL

Rand

# CHILEAN MARINE ECOLOGICAL NETWORK



## NODES 104

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

## EDGES 1611

- 1456 Feeding
- 155 Non-Feeding Positive

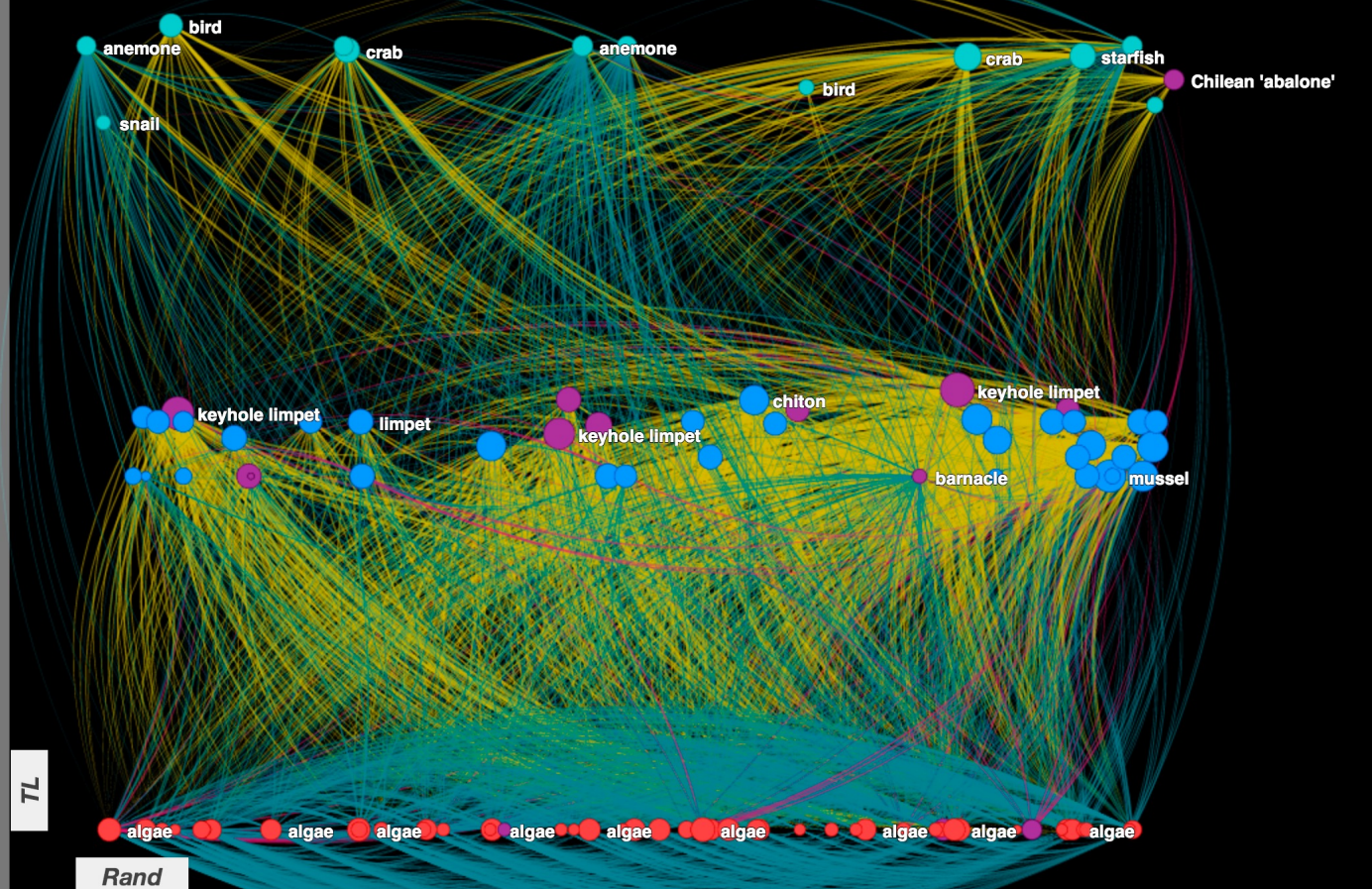
1 2 3

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?

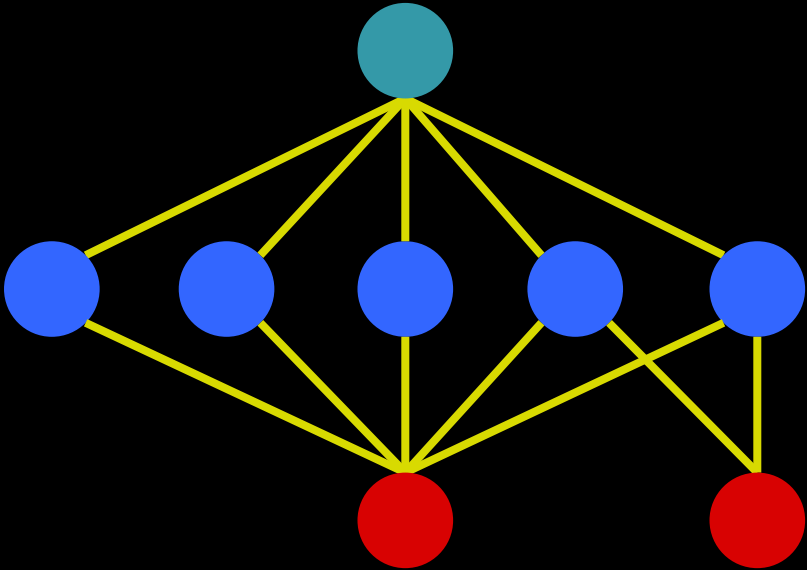
# stochastic block model

Newman and Leicht 2007

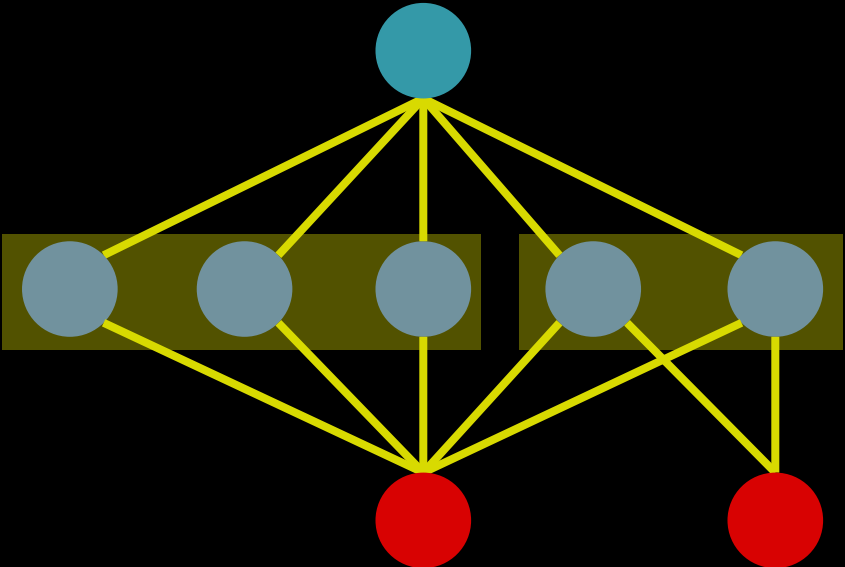
Daudin *et al.* 2008

Miele *et al.* 2014

———— FEEDING

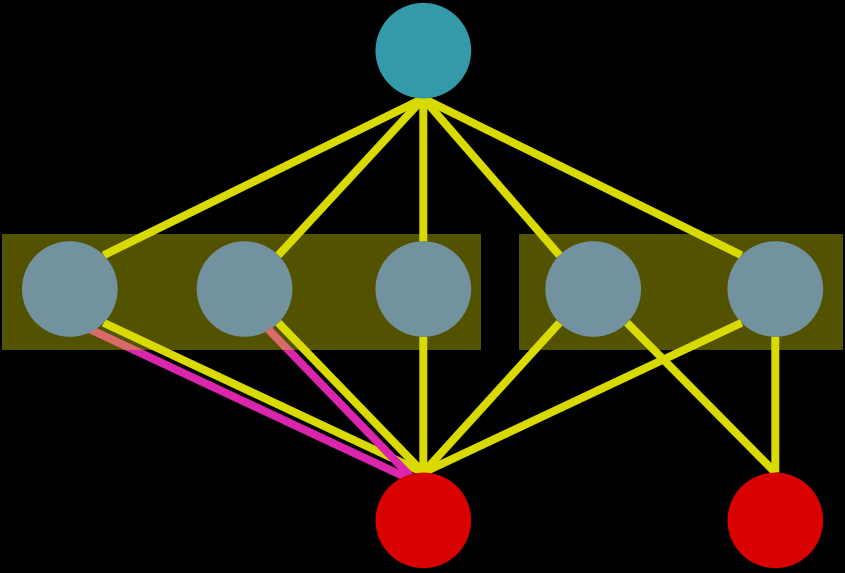


— FEEDING



“TROPHIC SPECIES”

— FEEDING  
— FACILITATION

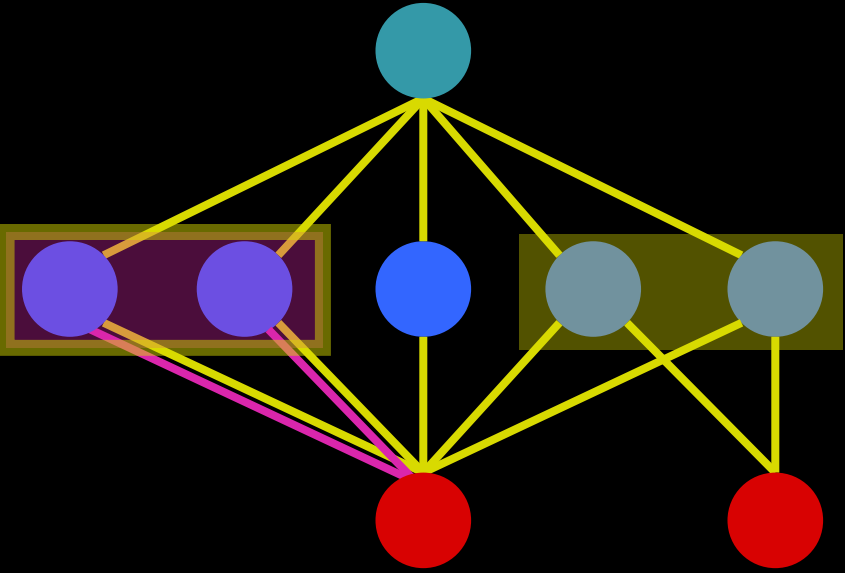


“TROPIC SPECIES”  
(1 DIMENSION)

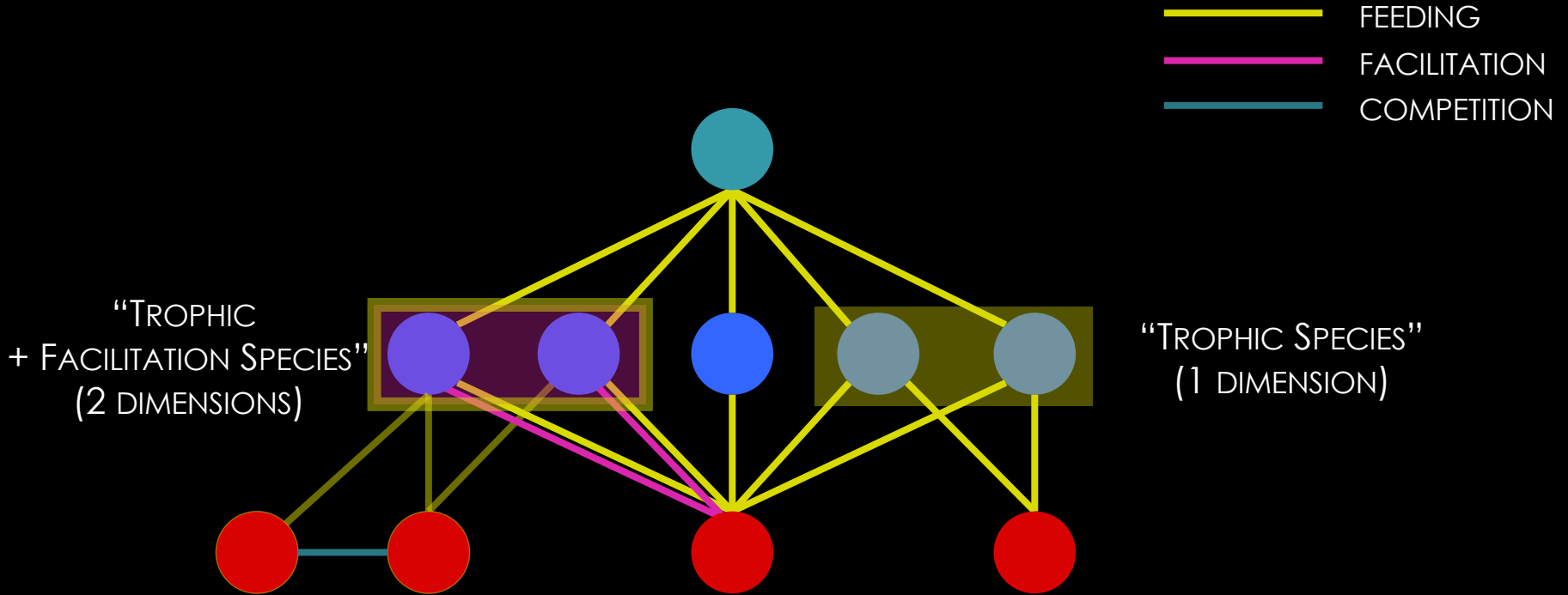


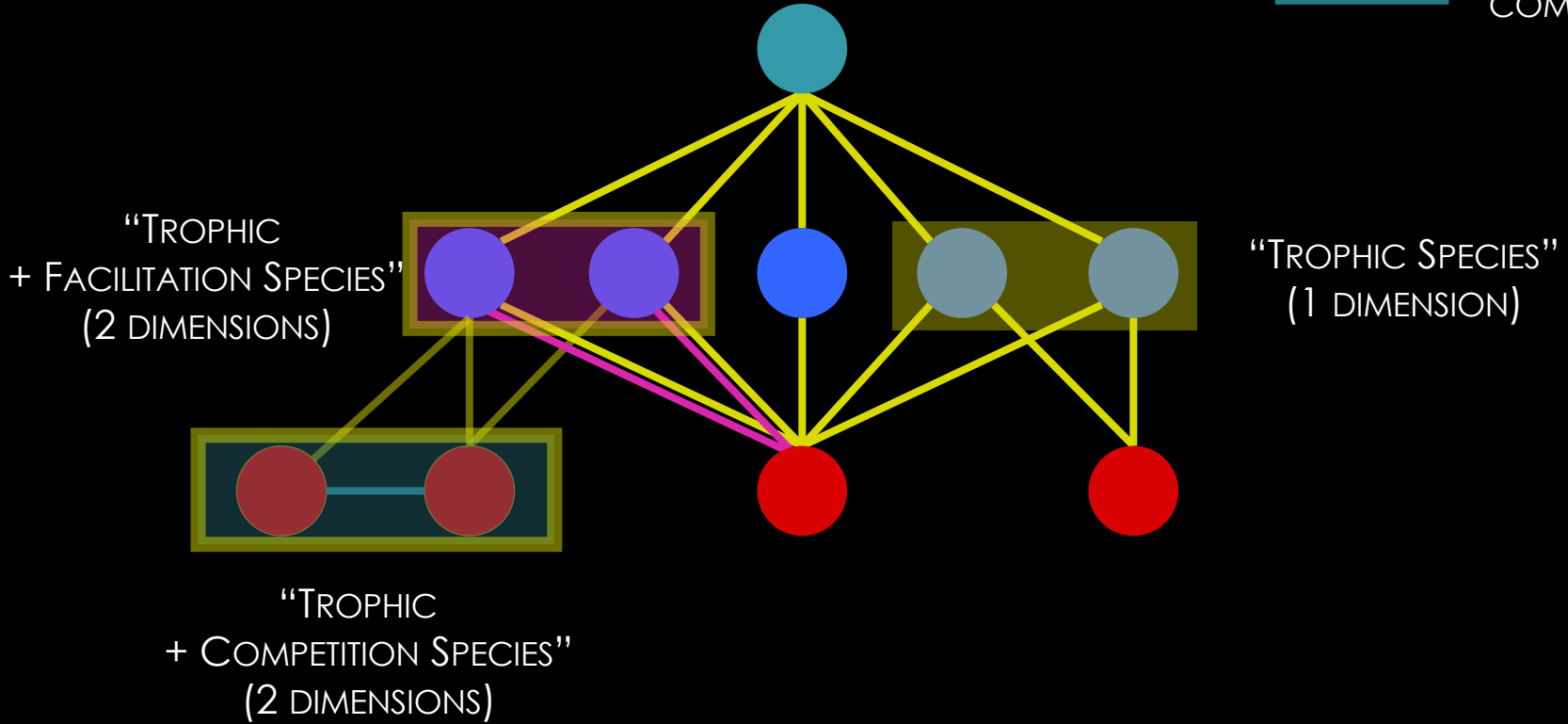
— FEEDING  
— FACILITATION

“TROPHIC  
+ FACILITATION SPECIES”  
(2 DIMENSIONS)

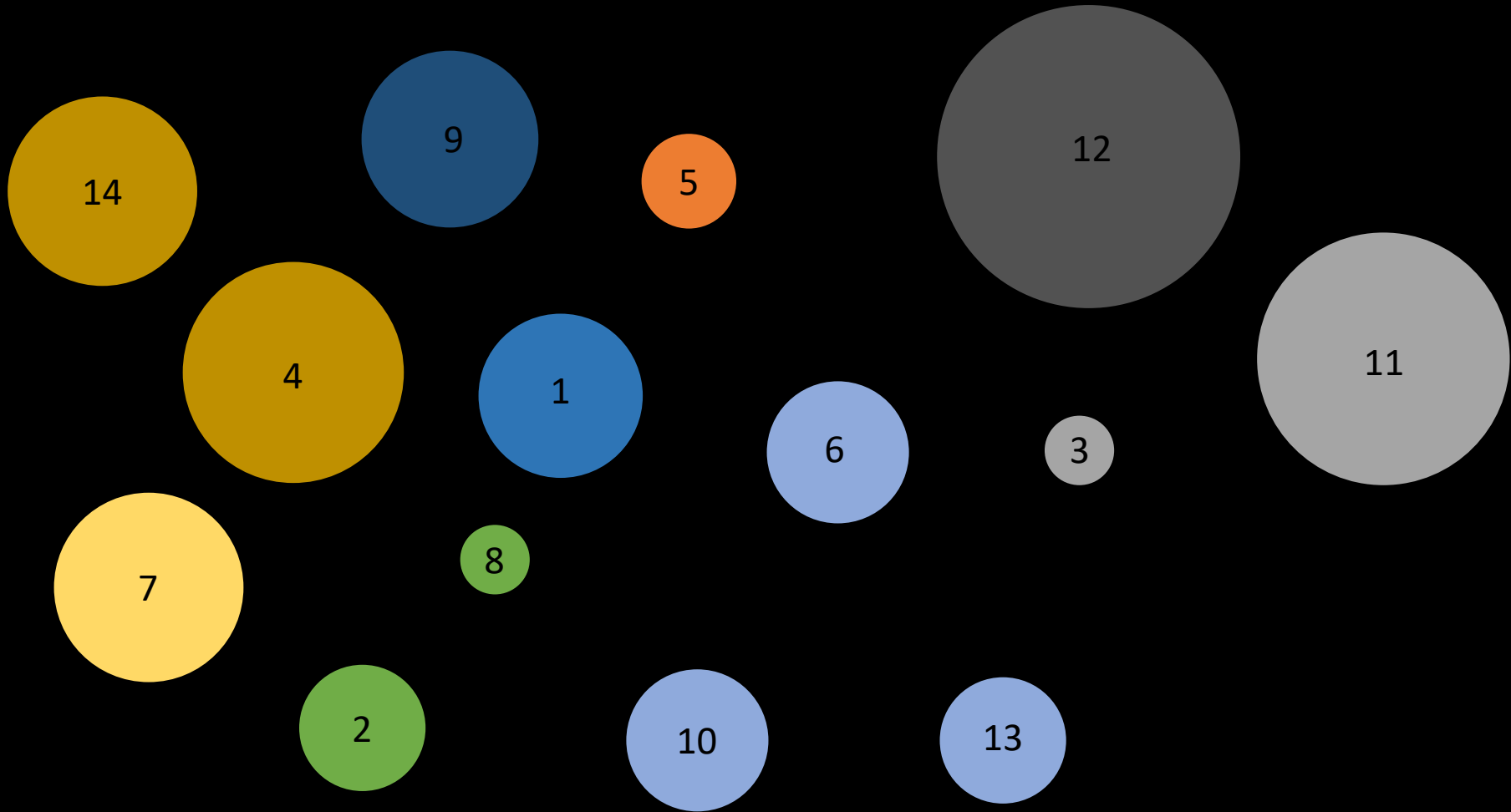


“TROPHIC SPECIES”  
(1 DIMENSION)

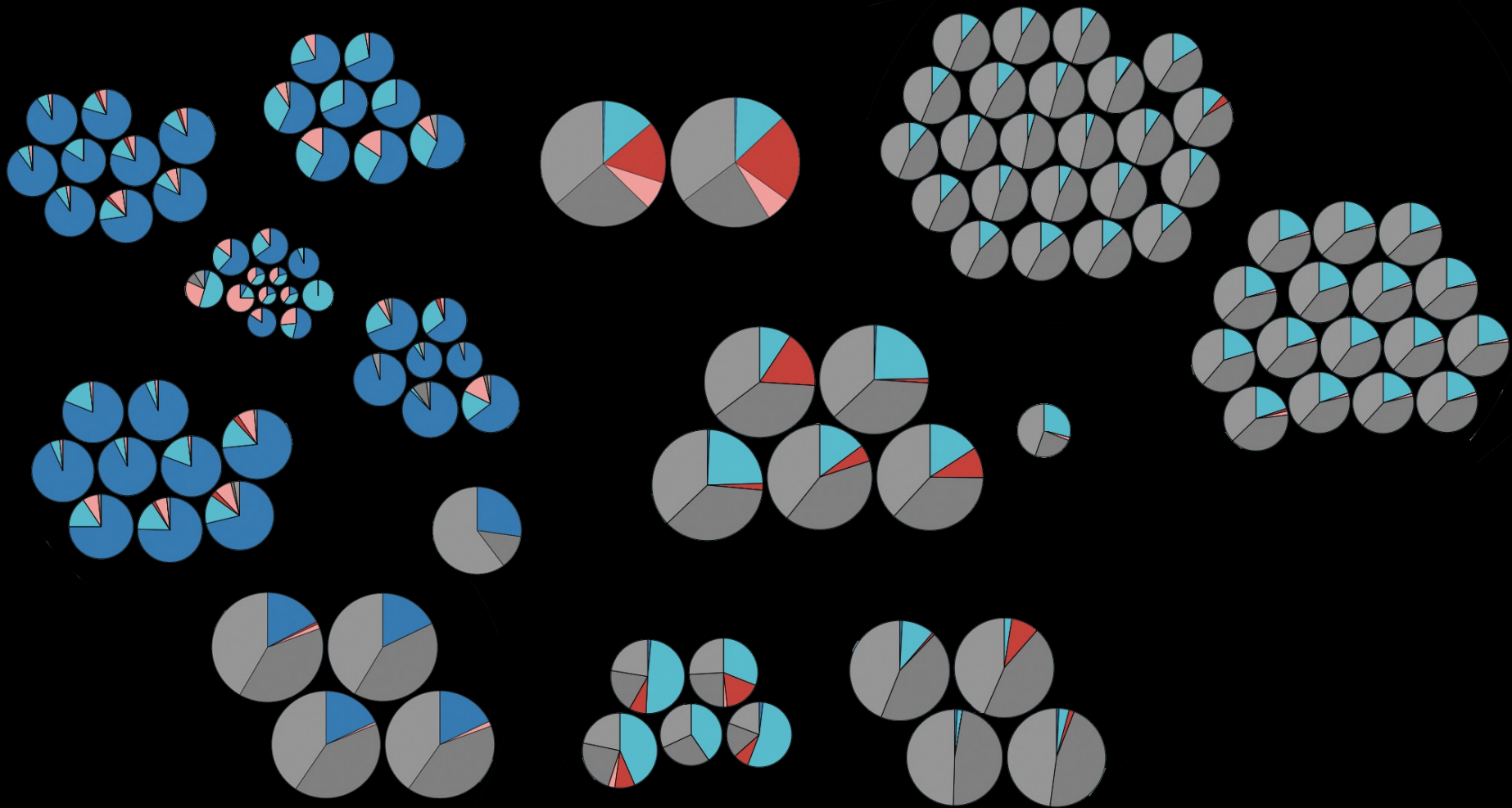




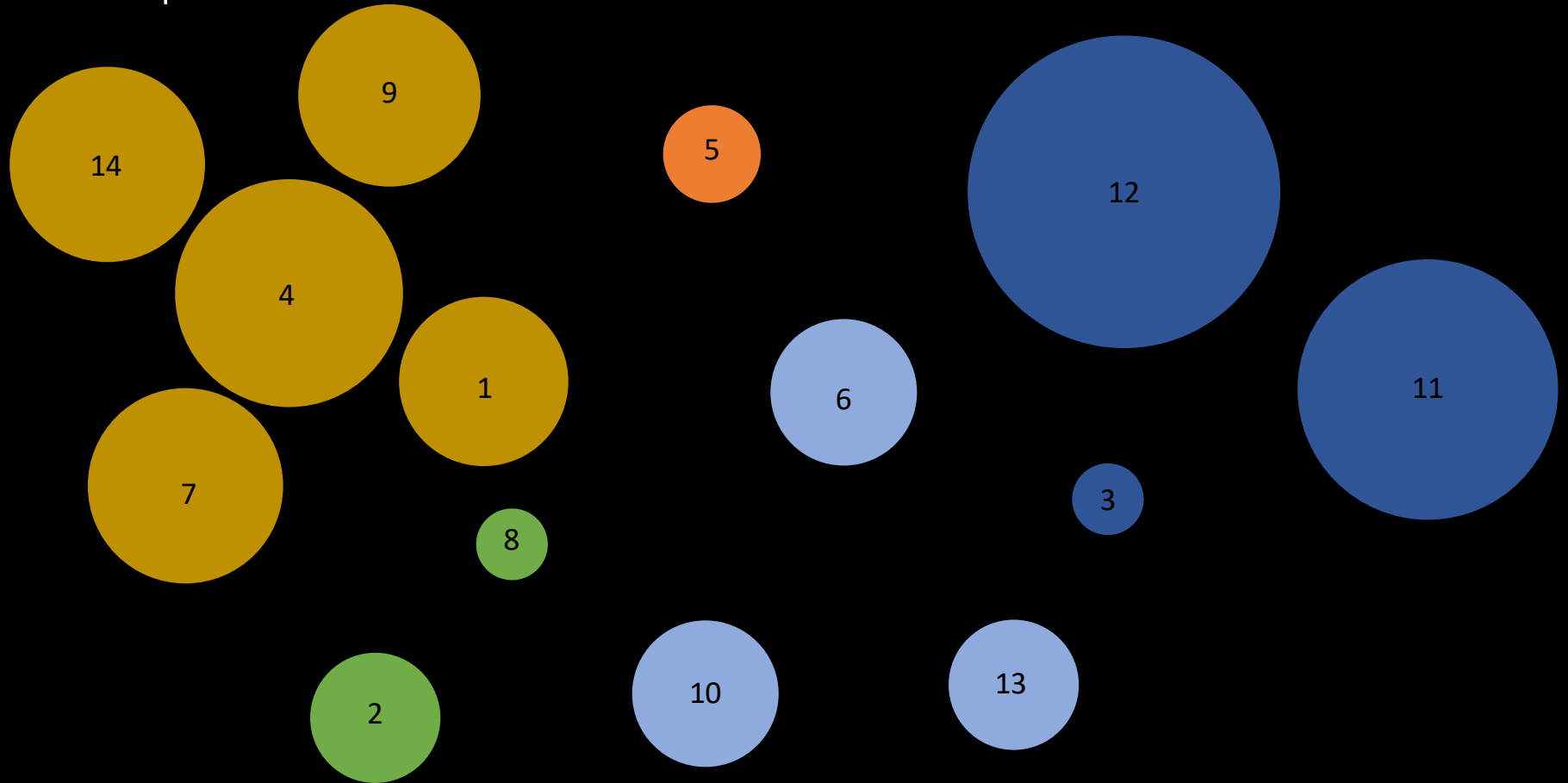




Trophic Out Trophic In Positive Out Positive In Negative Out Negative In



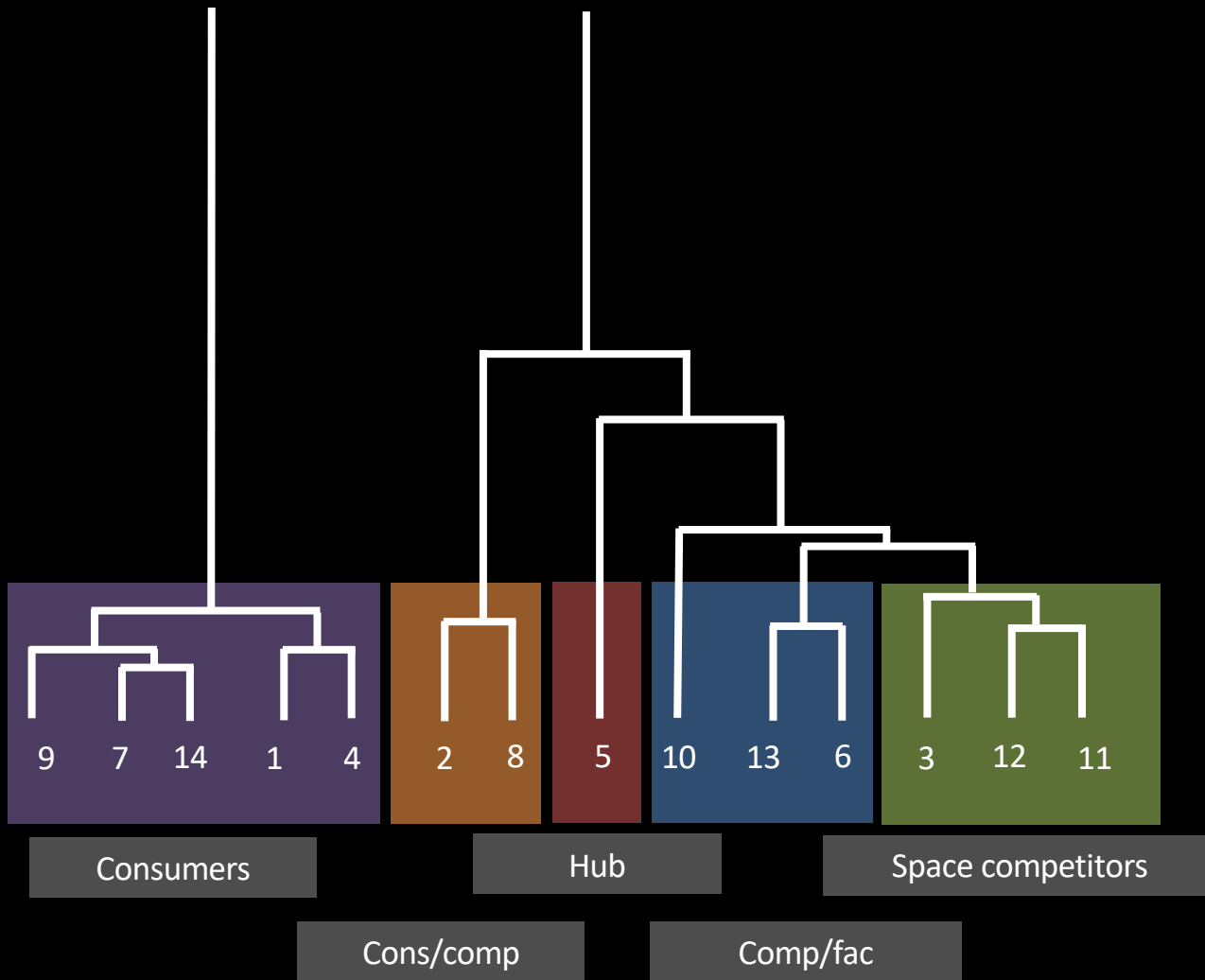
# 14 multiplex clusters



Species collapse into a small set of  
multiplex clusters



Cluster dissimilarity



Consumers

Hub

Space competitors

Cons/comp

Comp/fac

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

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

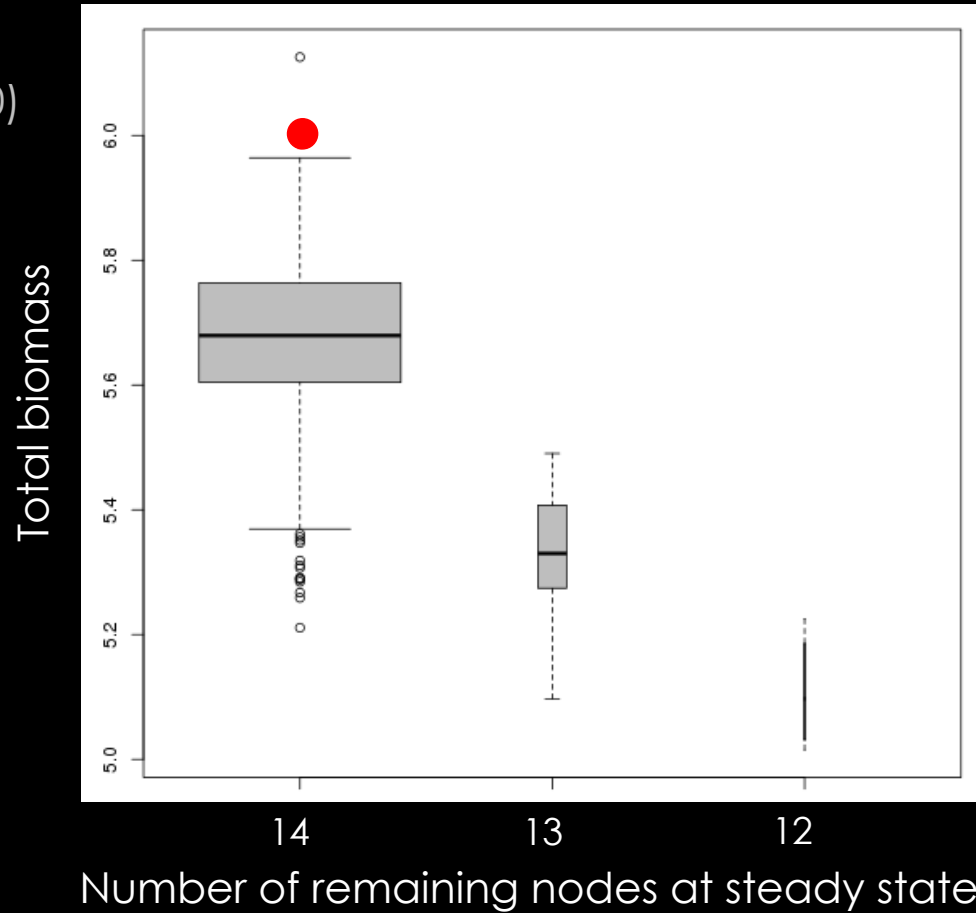
**14 nodes**  
(‘typical’ species of  
the cluster)

- 
- ```
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)

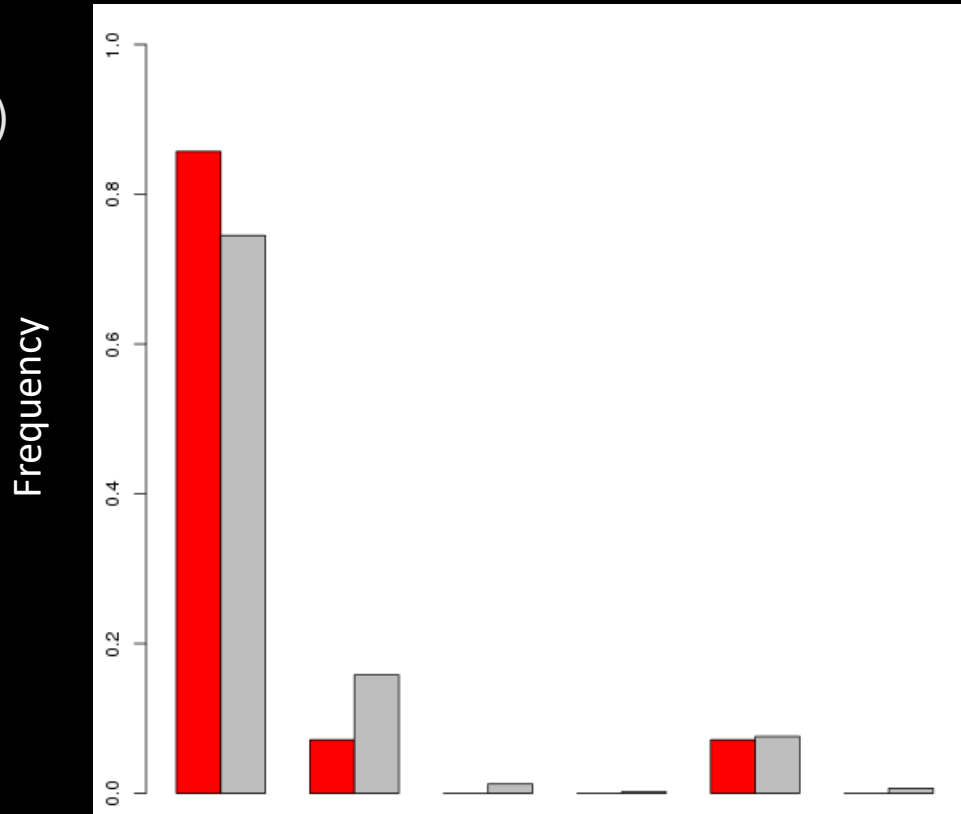


Calculate species diversity and total biomass

Chilean web  
Random webs (500)



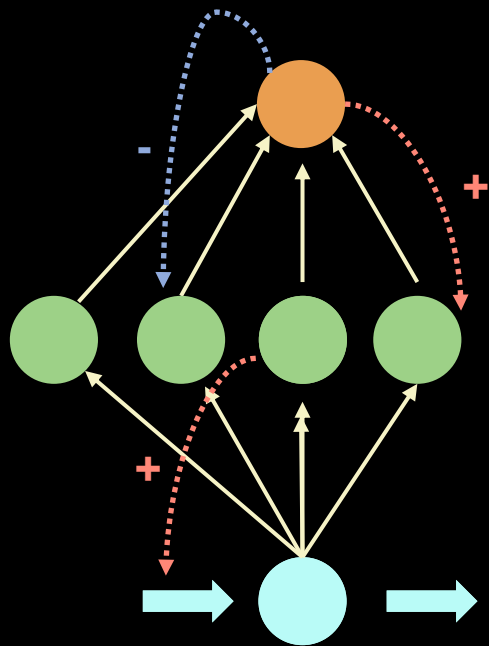
Chilean web  
Random webs (500)



Differential number of clusters after primary extinction

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

- high species persistence
- high total biomass
- tends to decrease the number of secondary extinctions



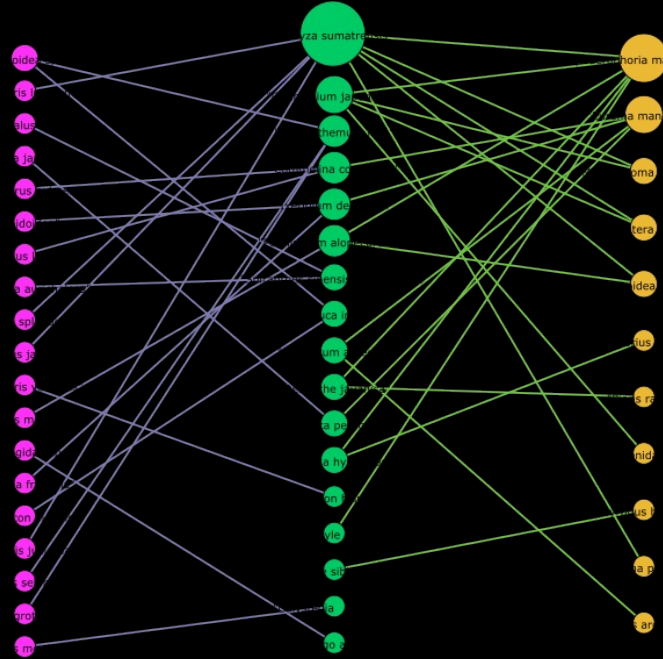
multiplex networks



Herbivores

Plants

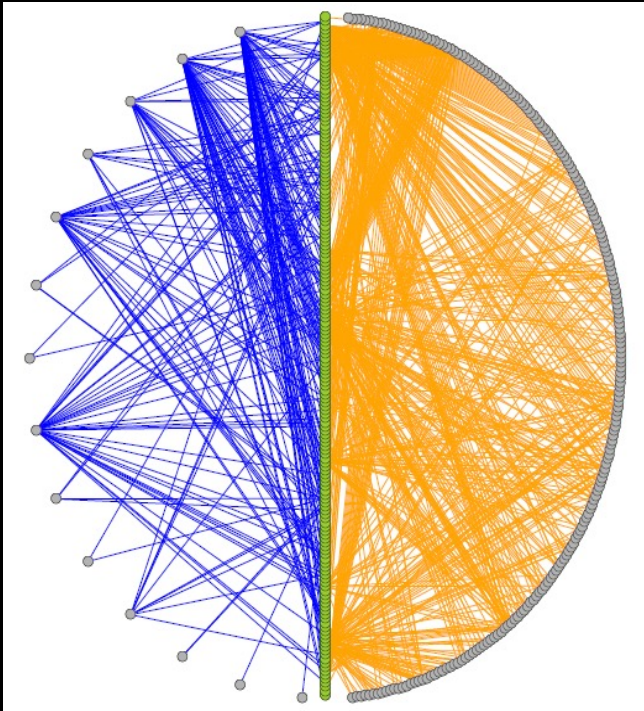
Pollinators



multipartite networks

# Doñana Biological Reserve, Spain

Antagonistic    Plants    Mutualistic



390 species  
(170 plants, 180 pollinators, 26 dispersors, 14 herbivores)

## 2 layers

798 interactions (578 mutualistic, 220 antagonistic)

binary and quantitative links

# Doñana Biological Reserve, Spain

**How are different interactions combined in natural communities?  
How does that affect stability?**

**Two metrics:**

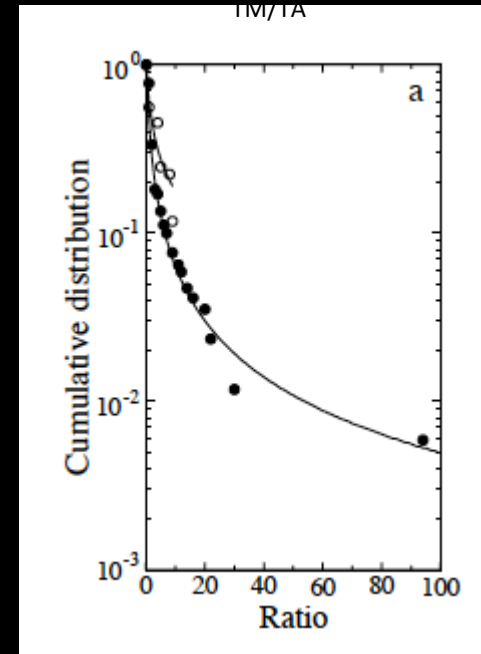
- the presence of the simplest module  
(a plant with a mutualistic and an antagonistic link)
- the ratio of the total number of mutualistic to antagonistic interactions per plant species,  $TM/TA$

Null model:

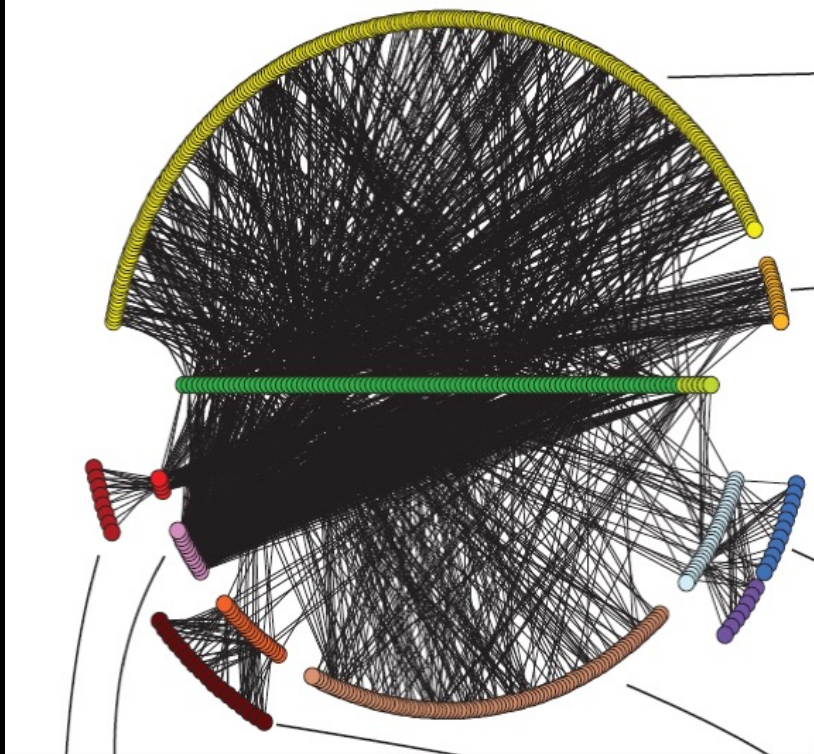
randomize links keeping the nb of links of animal constant (i.e. randomization with respect to the plants)

# Doñana Biological Reserve, Spain

- a few plants are involved in many modules and have a high ratio TM/TA
- very heterogeneous multilayer role of species
- promotes diversity (model)



# Norwood farm, Somerset, UK



560 taxa  
(plants + 11 groups of animals)

## **7 sub-networks**

1501 interactions (trophic, mutualistic, parasitic)

# Norwood farm, Somerset, UK

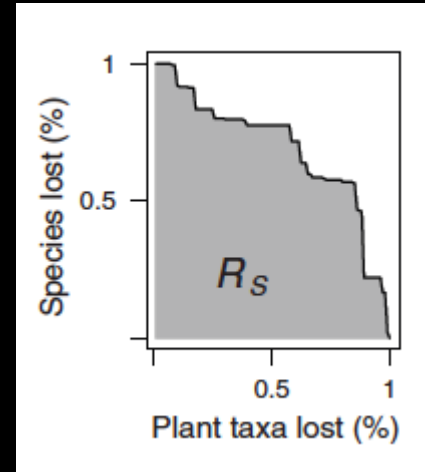
How does the robustness of different species interaction networks vary?

**robustness:**

sequential (random) removal of plant species

→ some sub-networks (layers) are more robust than others

→ Identification of **keystone plants** (that have the most important cascading effects)



# Key results

- Different layers have different structural properties
- Different layers have different robustness
- → id of key species that create a disprop amount of secondary extinctions
  
- species have different roles in different layers
- A few species have disproportional multiplex roles



multi-interaction networks

multilayer ecological networks

temporal networks

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RESEARCH ARTICLE

Journal of Animal Ecology



## Core-periphery dynamics in a plant-pollinator network

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### How does species role change through time?

Dynamic stochastic Block model (on 6 years of data)

→ Core-periphery structure stable through time

→ But role of species variable through time



spatial networks

ARTICLE

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# Multilayer networks reveal the spatial structure of seed-dispersal interactions across the Great Rift landscapes

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- seed–dispersal interactions across the Gorongosa National Park, Mozambique
- id of highly versatile species that disperse many plant species across multiple habitats
- Not predicted by monolayer approaches

# « Complexity begets stability »

Odum 1953

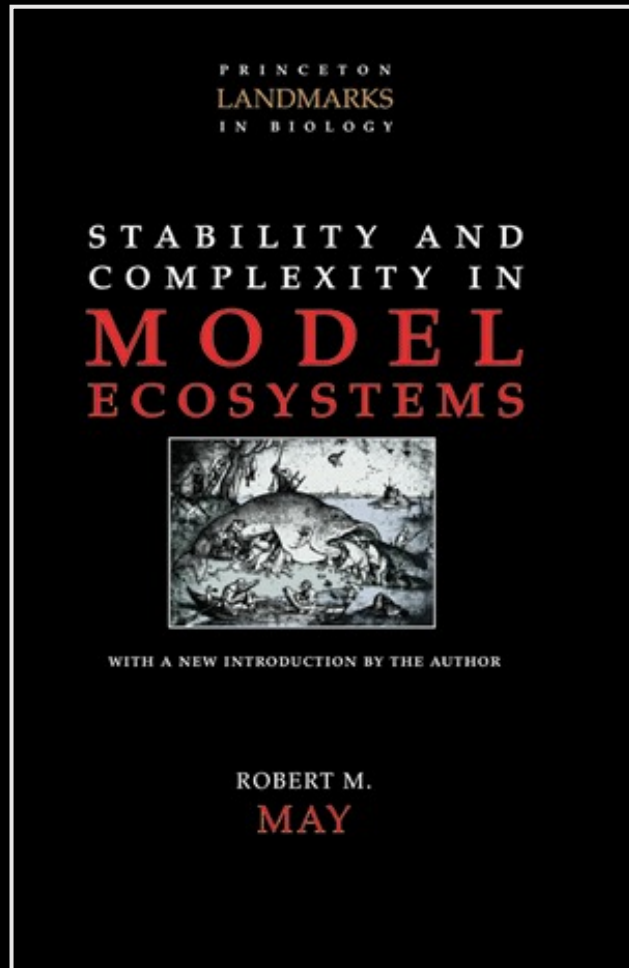
MacArthur 1955

Elton 1958





Robert May



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

Robert May, 1973

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

COMPLEX ECOLOGICAL COMMUNITIES  
MANY SPECIES  
MANY INTERACTION TYPES  
SPATIO-TEMPORAL DYNAMICS

Thank you very much for your attention



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