

# Where does species size matter the most?

## Stability and interaction strengths in complex food webs

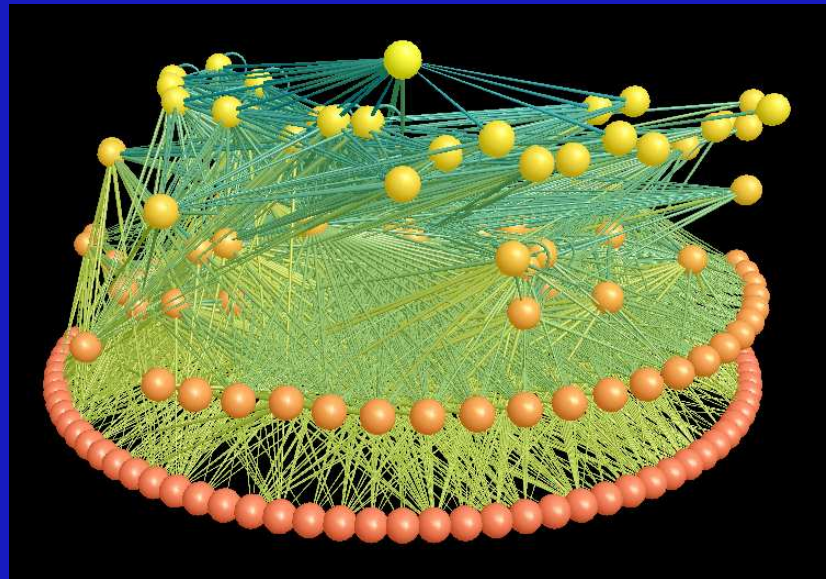
Ulrich Brose

Complex Ecological Networks Lab

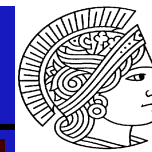
Emmy Noether Group

Darmstadt University of Technology

Lake Tahoe food web



Food web graphics by Web3D © Rich Williams

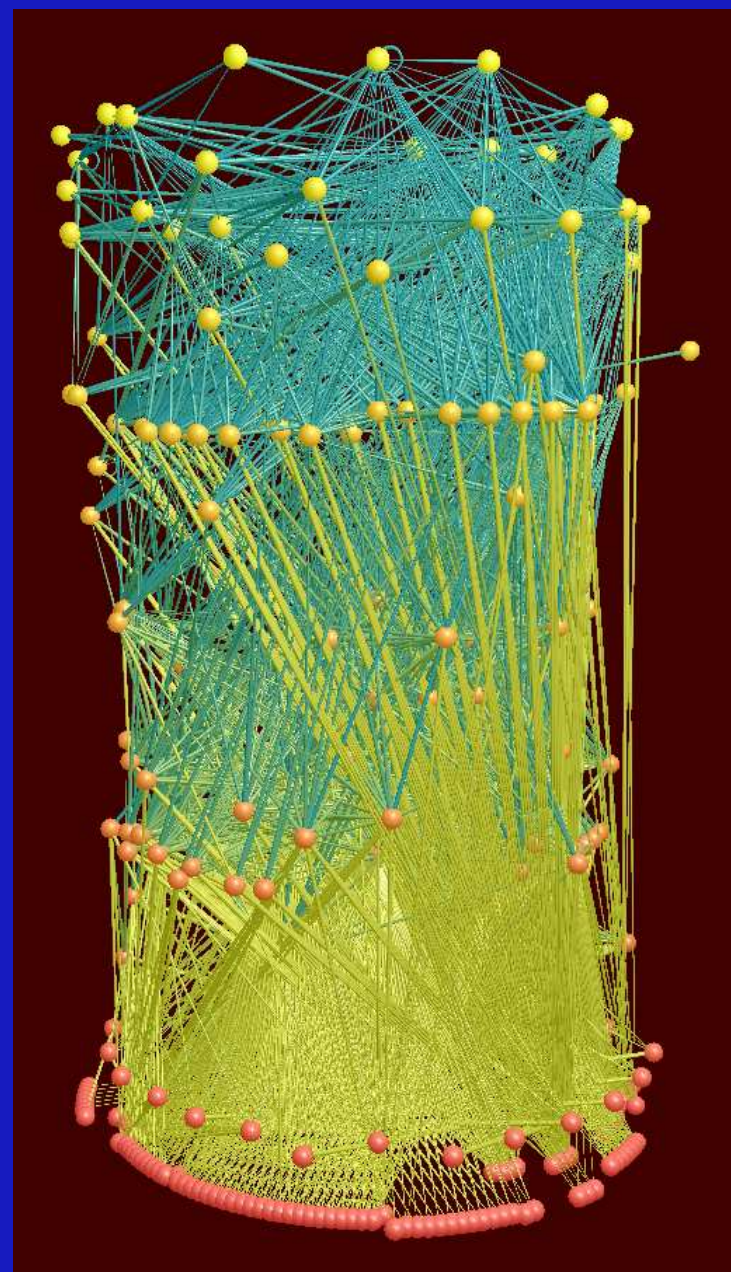


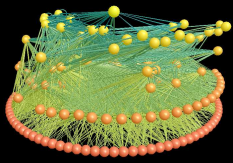
## Complex ecological networks

The Weddell Sea food web Antarctica  
(Jacob et al. unpublished):

492 species, 16137 trophic interactions

Does body size matter?





# Complex ecological networks



## Body size affects food-web structure

*Proc. R. Soc. Lond. B* **224**, 421–448 (1985)  
*Printed in Great Britain*

### A stochastic theory of community food webs I. Models and aggregated data

BY J. E. COHEN<sup>1</sup> AND C. M. NEWMAN<sup>2</sup>

Cohen & Newman 1985 PRSLB

Cascade model

Feeding hierarchy amongst species

Michael G. Neubert · Steven C. Blumenshine  
Daniel E. Duplisea · Tomas Jonsson · Brenda Rashleigh

### **Body size and food web structure: testing the equiprobability assumption of the cascade model**

Neubert et al 2000

Oecologia

Feeding hierarchy and  
body size

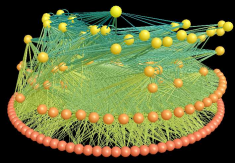
### **Simple rules yield complex food webs**

Richard J. Williams & Neo D. Martinez

Williams & Martinez 2000

Niche model

Interval feeding ranges on niche  
axis



# Complex ecological networks

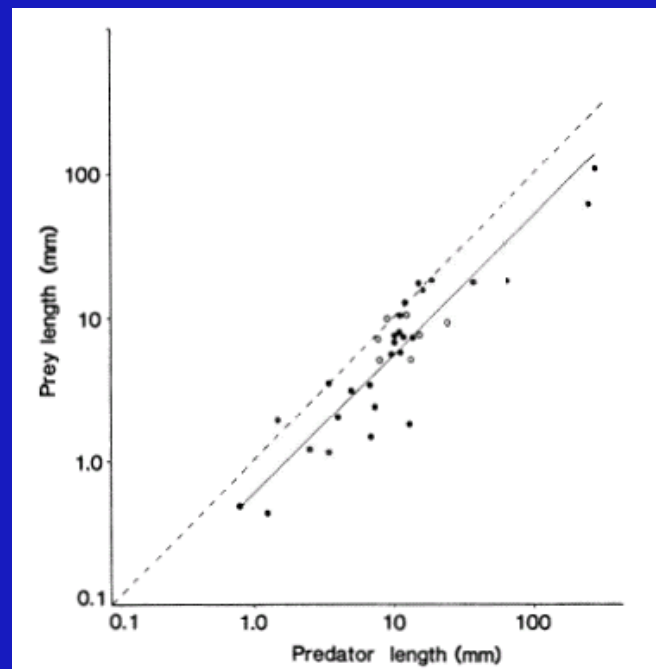


## Body size affects food-web structure

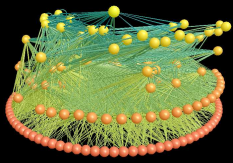
**Invertebrate predator-prey body size relationships:  
an explanation for upper triangular food webs and patterns  
in food web structure?**

P.H. Warren and J.H. Lawton

Department of Biology, University of York, Heslington, York YO1 5DD, UK



*Warren & Lawton 1987 Oecologia*



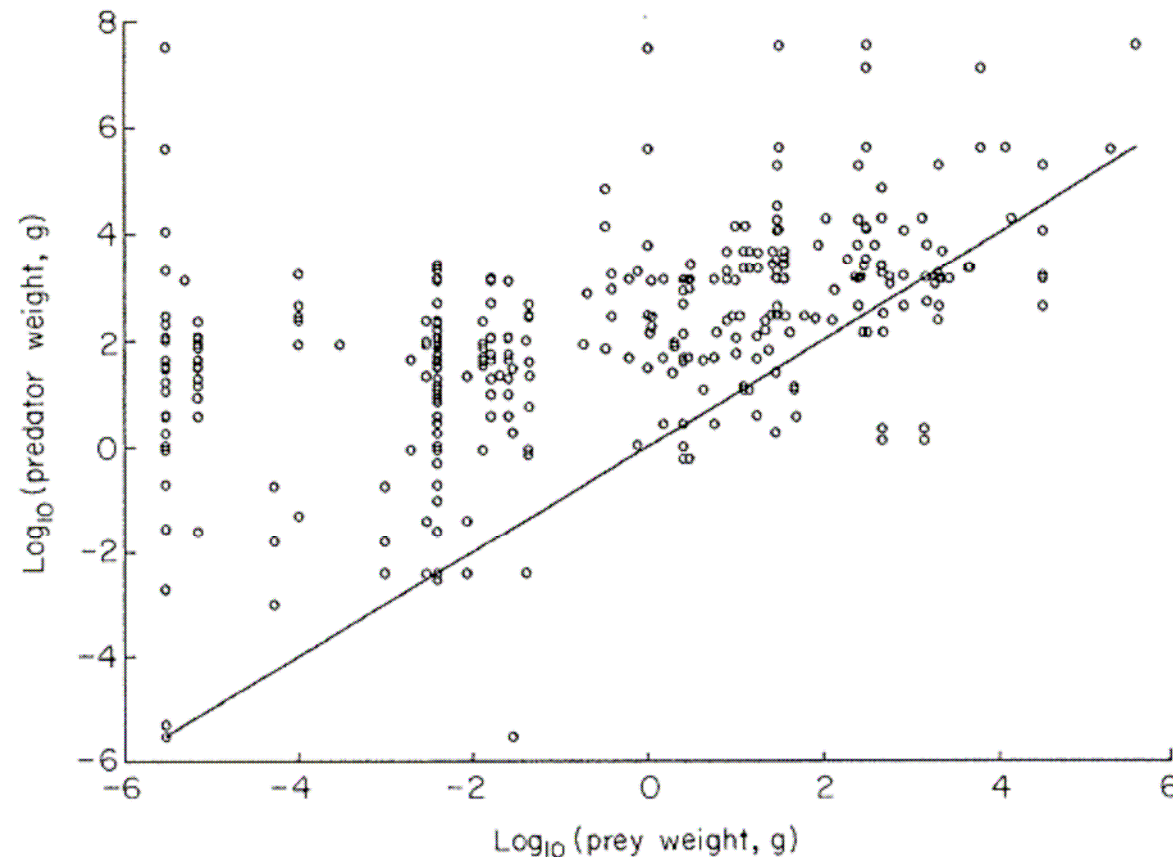
# Complex ecological networks

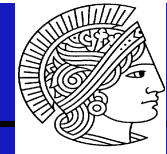
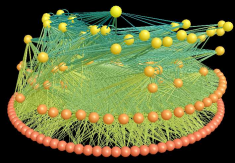
## Body size affects food-web structure

*Journal of Animal Ecology* 1993,  
**62**, 67–78

### Body sizes of animal predators and animal prey in food webs

JOEL E. COHEN\*, STUART L. PIMM†, PETER YODZIS‡ and  
JOAN SALDAÑA§





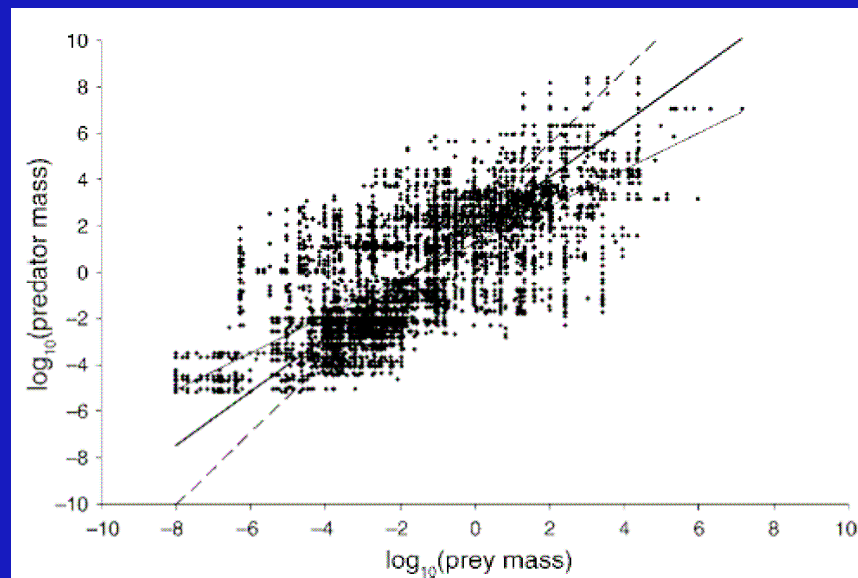
# Complex ecological networks

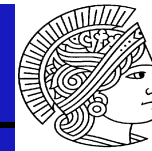
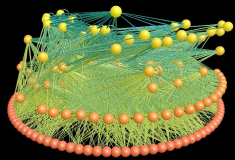
## Body size affects food-web structure

*Ecology*, 87(10), 2006, pp. 2411–2417  
© 2006 by the Ecological Society of America

### CONSUMER–RESOURCE BODY-SIZE RELATIONSHIPS IN NATURAL FOOD WEBS

ULRICH BROSE,<sup>1,2,20</sup> TOMAS JONSSON,<sup>3</sup> ERIC L. BERLOW,<sup>1,2,4</sup> PHILIP WARREN,<sup>5</sup> CAROLIN BANASEK-RICHTER,<sup>1</sup>  
LOUIS-FÉLIX BERSIER,<sup>6</sup> JULIA L. BLANCHARD,<sup>7</sup> THOMAS BREY,<sup>8</sup> STEPHEN R. CARPENTER,<sup>9</sup>  
MARIE-FRANCE CATTIN BLANDENIER,<sup>10</sup> LARA CUSHING,<sup>2</sup> HASSAN ALI DAWAH,<sup>11</sup> TONY DELL,<sup>12</sup> FRANCOIS EDWARDS,<sup>13</sup>  
SARAH HARPER-SMITH,<sup>14</sup> UTE JACOB,<sup>8</sup> MARK E. LEDGER,<sup>13</sup> NEO D. MARTINEZ,<sup>2</sup> JANE MEMMOTT,<sup>15</sup>  
KATJA MINTENBECK,<sup>8</sup> JOHN K. PINNEGAR,<sup>7</sup> BJÖRN C. RALL,<sup>1</sup> THOMAS S. RAYNER,<sup>12</sup> DANIEL C. REUMAN,<sup>16</sup>  
LILIANE RUESS,<sup>17</sup> WERNER ULRICH,<sup>18</sup> RICHARD J. WILLIAMS,<sup>2,21</sup> GUY WOODWARD,<sup>19</sup> AND JOEL E. COHEN<sup>16</sup>



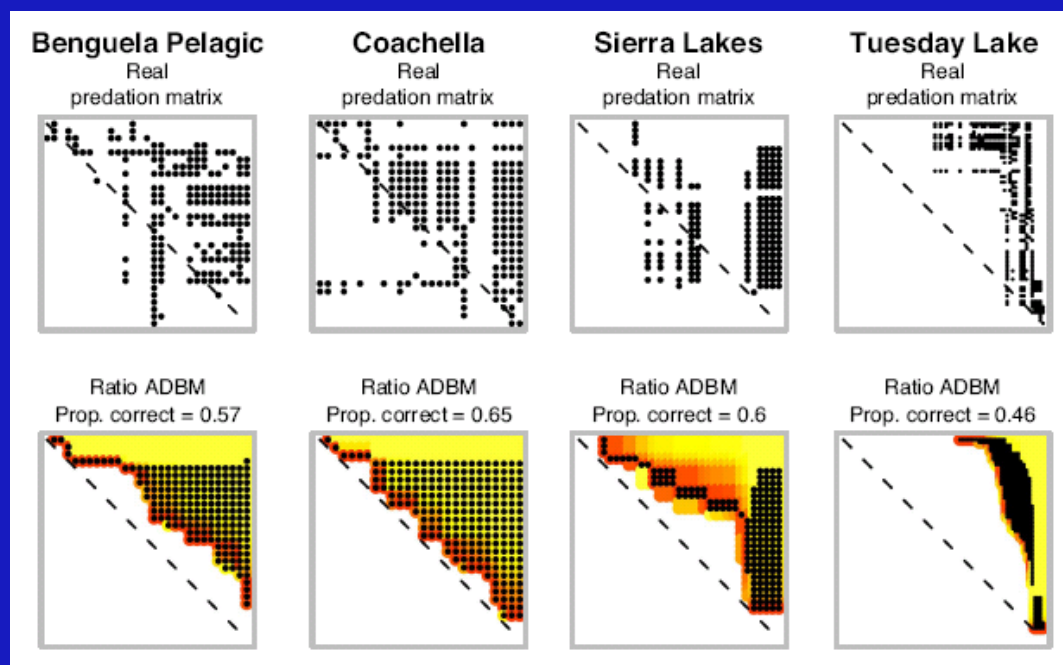


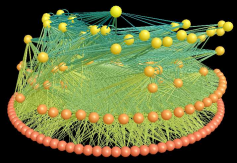
# Complex ecological networks

## Body size affects food-web structure

### Size, foraging, and food web structure

Owen L. Petchey<sup>\*†</sup>, Andrew P. Beckerman<sup>\*</sup>, Jens O. Riede<sup>‡</sup>, and Philip H. Warren<sup>\*</sup>





# Complex ecological networks



## Dynamic food webs:

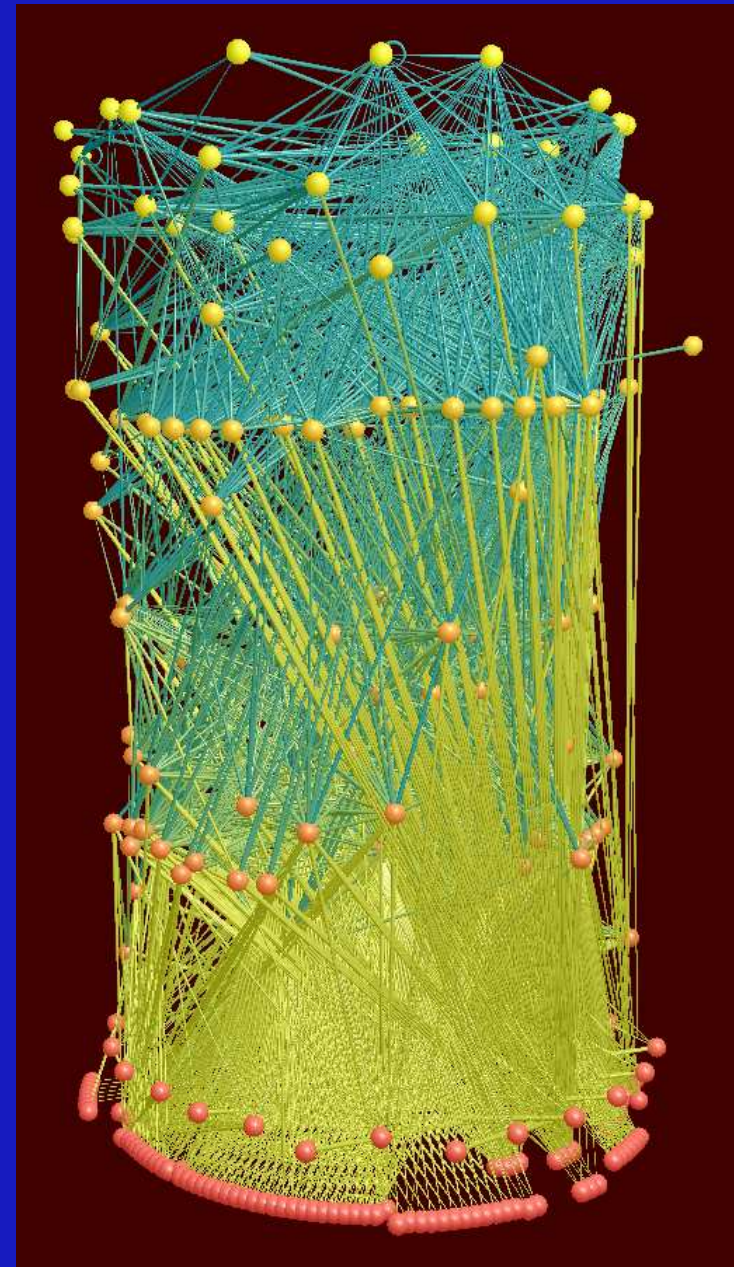
Where does body size matter?

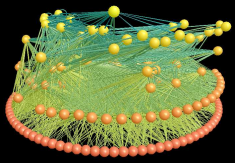
### Methodology:

Dynamic allometric network model

### Questions:

- How do all these species coexist (food-web stability)?
- What are the consequences of species extinctions (interaction strengths)?





# Complex ecological networks

## Dynamic network model

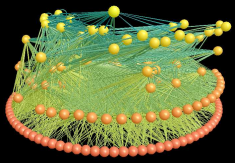
Biomass change  $\sim$  growth – metabolism + consumption – being consumed

$$B_i'(t) = r_i G_i(\vec{B}) - x_i B_i(t) + \sum_{j=1}^n \left( x_i y_{ij} F_{ij}(\vec{B}) B_i(t) - x_j y_{ji} F_{ji}(\vec{B}) B_j(t) / e_{ji} \right)$$

Growth  
rate

Metabolic  
rate

Maximum  
consumption rate

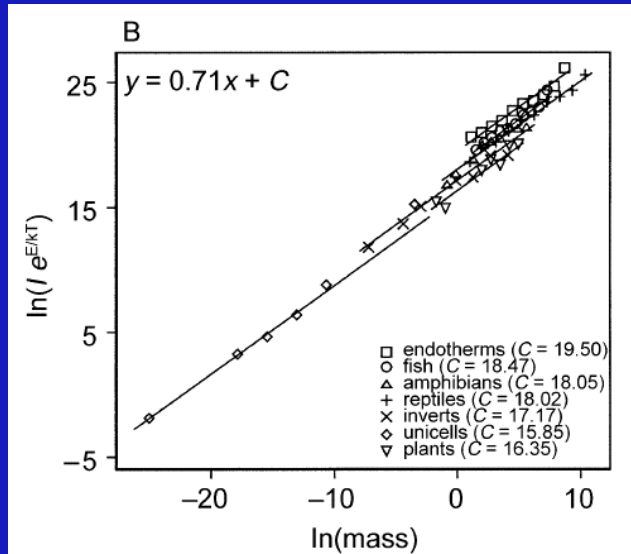


# Complex ecological networks



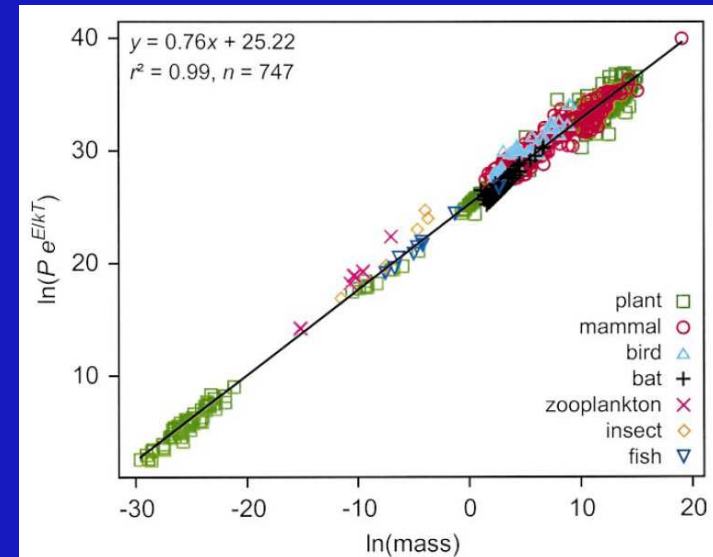
## Allometric scaling of biological rates

ln metabolic rate



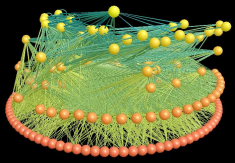
ln body mass

ln production rate



ln body mass

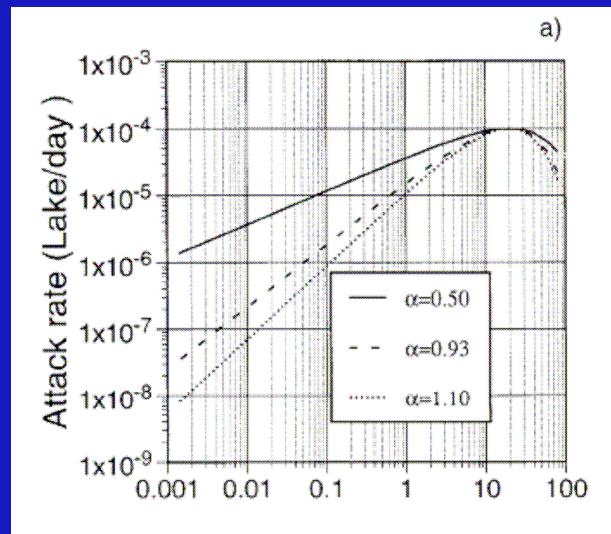
$\frac{3}{4}$  power-law scaling of metabolism, and production



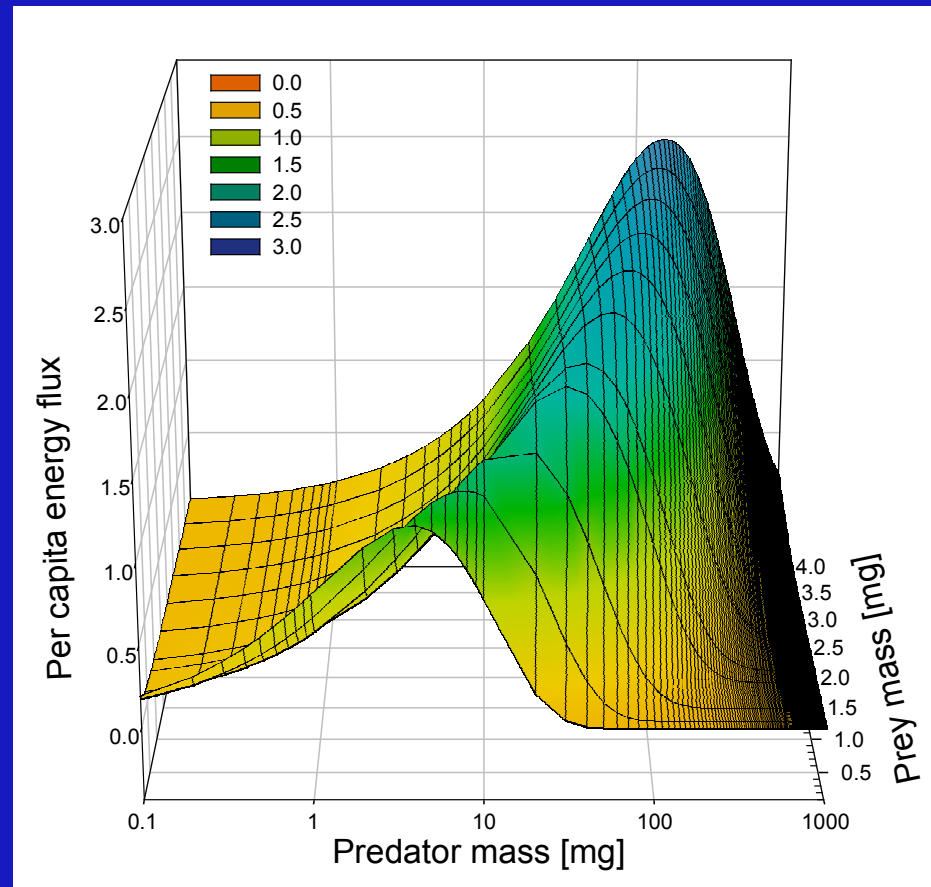
# Complex ecological networks

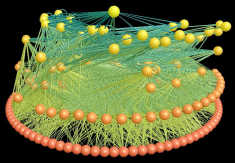


## Allometric scaling of consumption rates



body mass

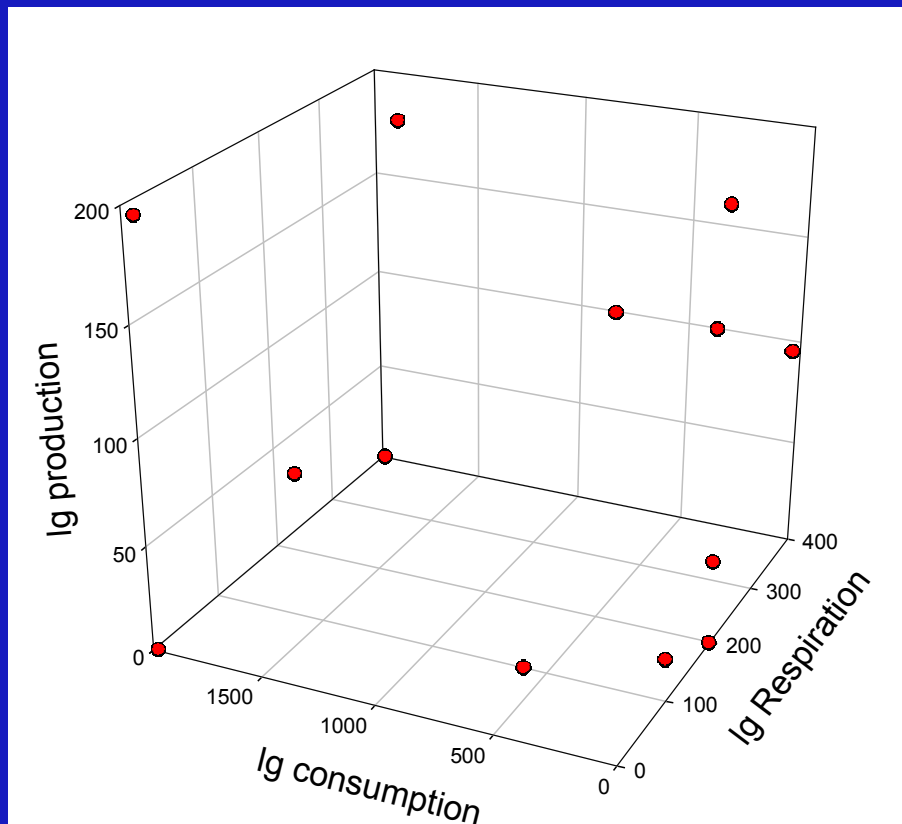




# Complex ecological networks



## Random parameters

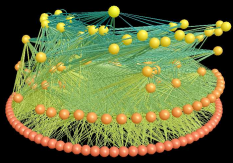


In many population dynamic models:

Parameters of respiration, production and consumption are sampled randomly and independently

→ huge parameter space to be explored;

→ theoretically possible dynamics



# Complex ecological networks



## Allometric scaling

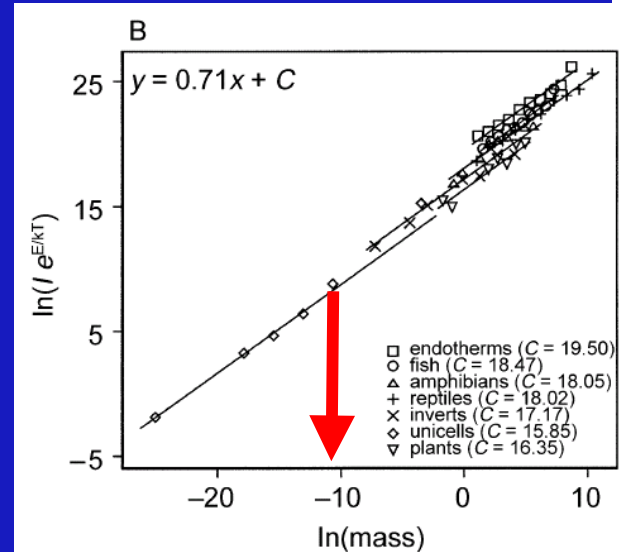
Randomly sampling a respiration rate implies a first body mass

Randomly sampling a production rates implies a second body mass

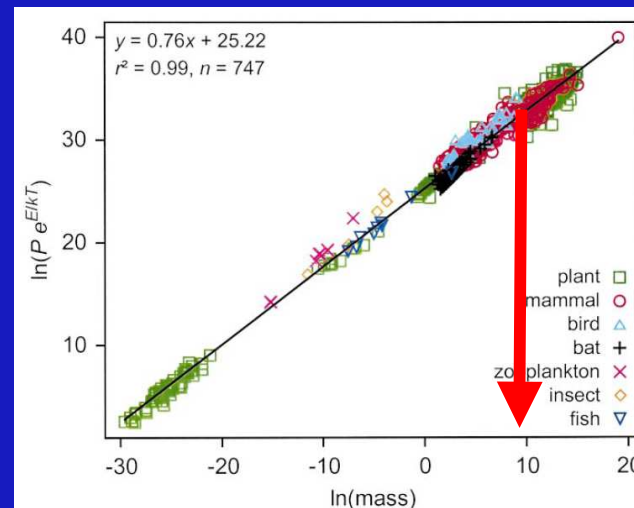
A population cannot have several body masses!

→ Independent random samples are nonsense

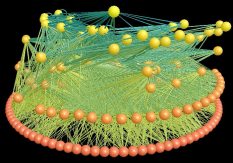
ln respiration rate



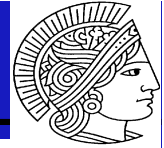
ln production rate



ln body mass



# Complex ecological networks

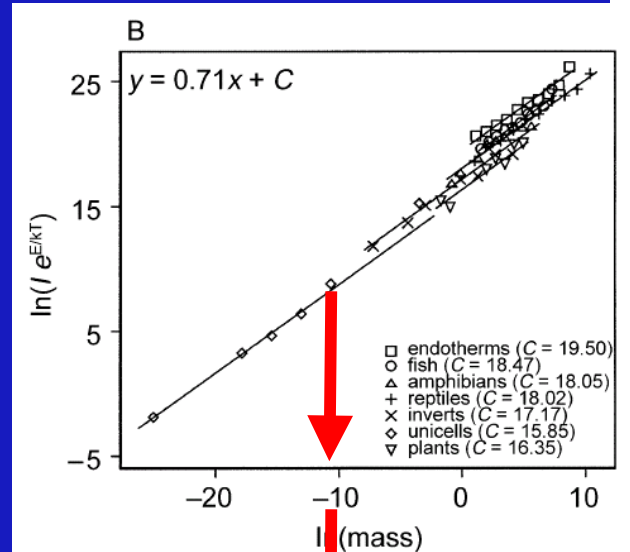


## Allometric scaling

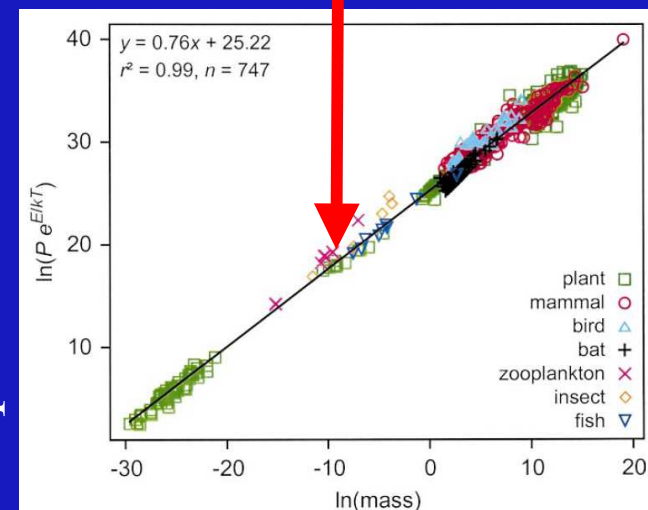
Assigning a respiration rate implies

- 1) a body mass
  - 2) a production rate
  - 3) a consumption rate
- parameters are not independent

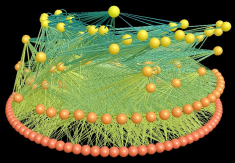
ln respiration rate



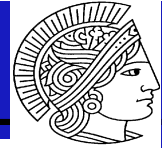
ln production rate



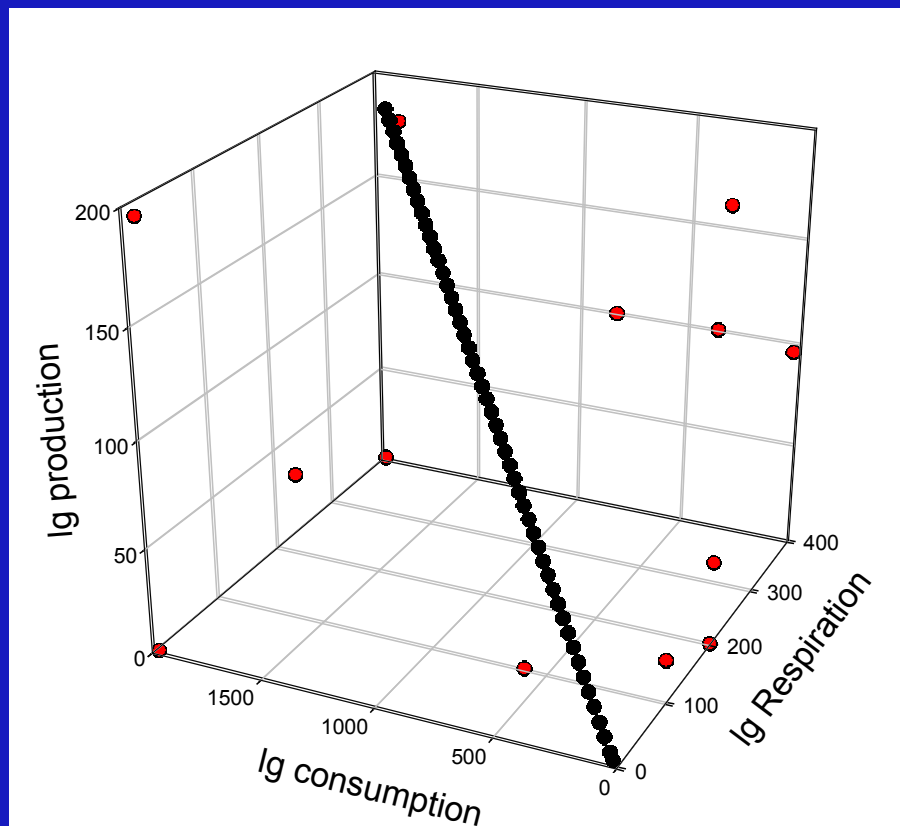
ln body mass



# Complex ecological networks

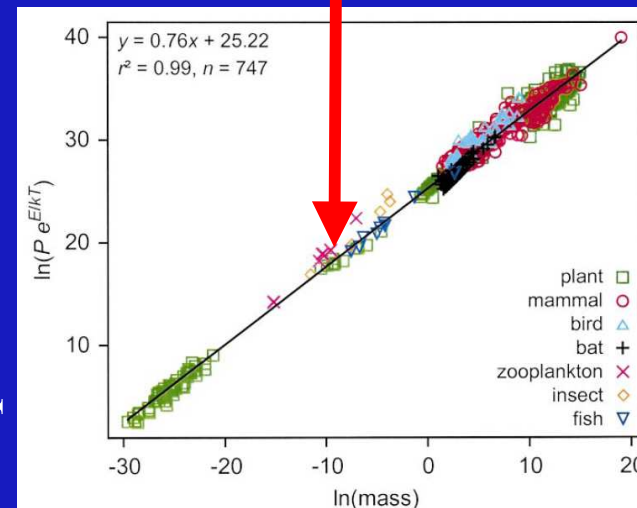
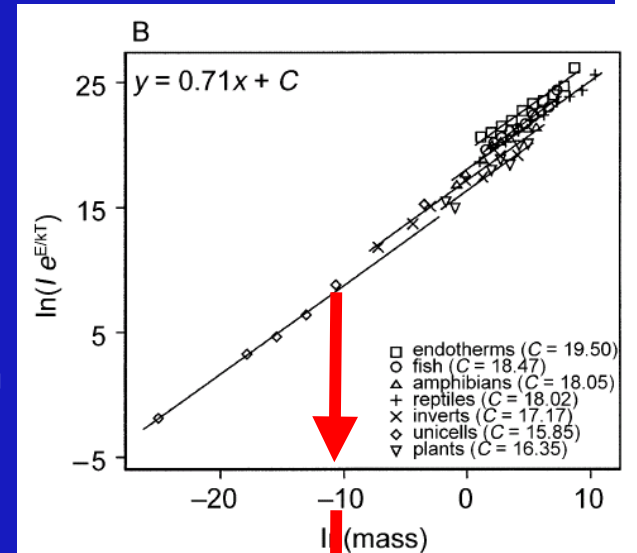


Allometric scaling constraints  
parameters to restricted space

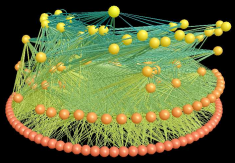


ln respiration rate

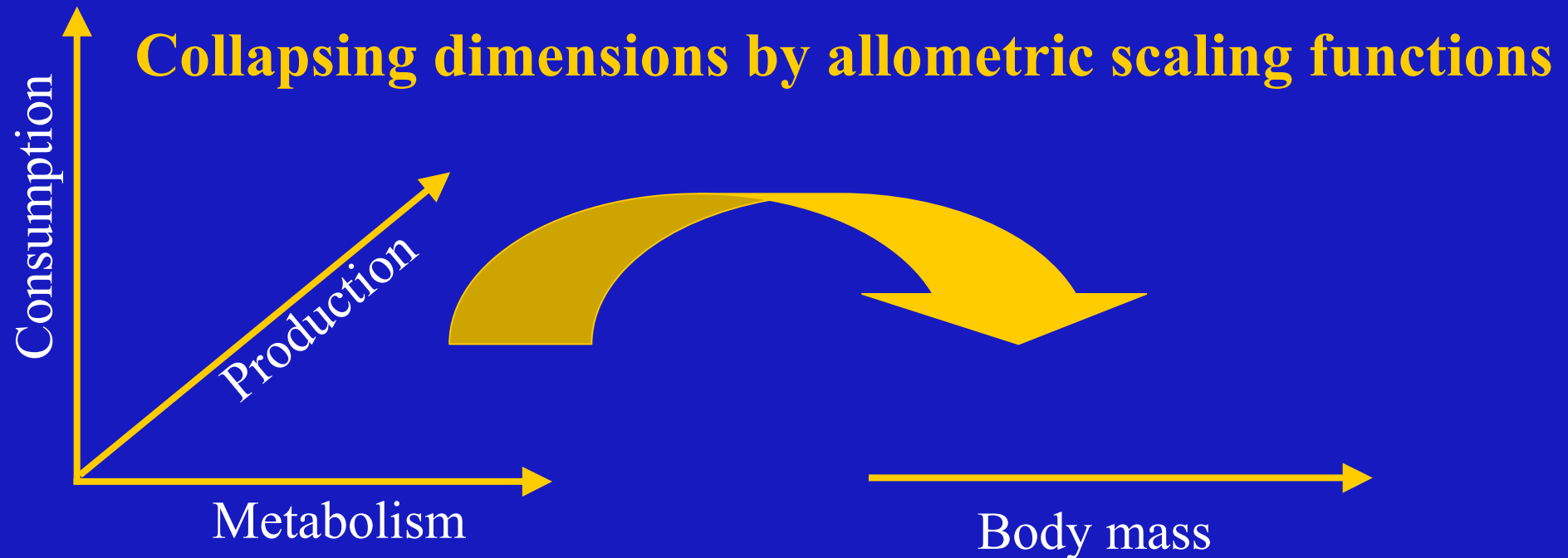
ln production rate



ln body mass



## Complex ecological networks

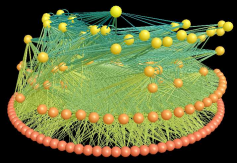


Random parameters:

- huge parameter space to be explored;
- theoretically possible dynamics

Allometric parameters:

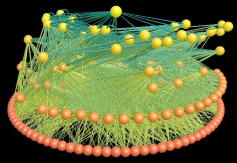
- body masses constrain parameter space;
- empirically possible dynamics



## Complex ecological networks



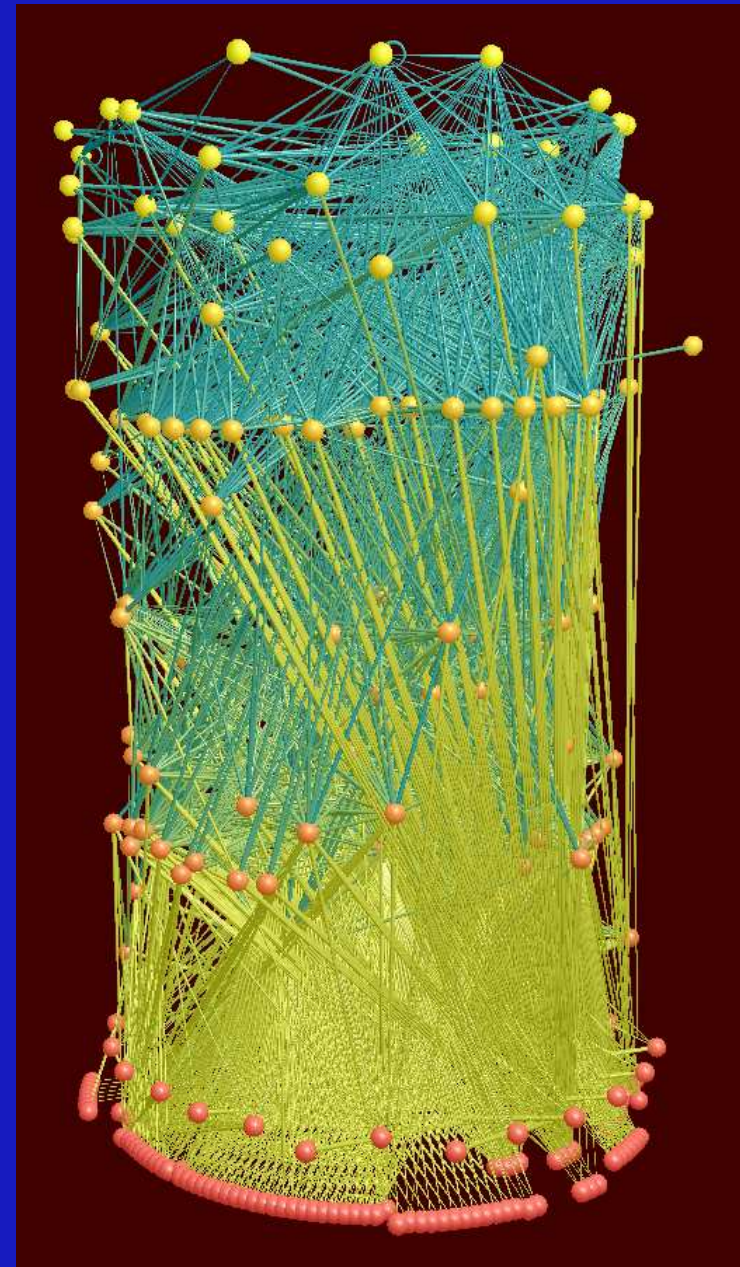
**Allometric scaling: is it important for  
complex food webs?**

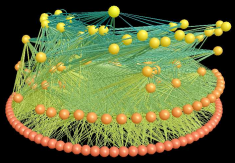


# Complex ecological networks

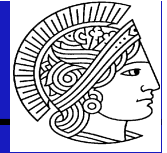


- Dynamic allometric network model
- How do all these species coexist (food-web stability)?
- What are the consequences of species extinctions (interaction strengths)?

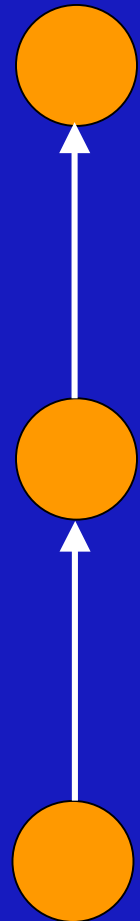




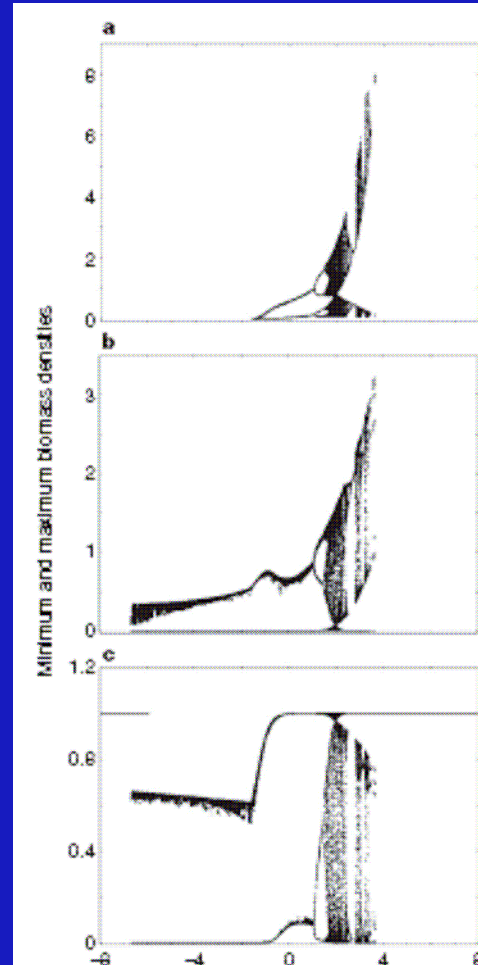
# Complex ecological networks



## Food-chain simulations



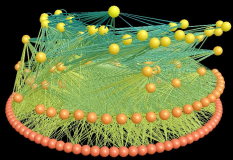
Population minima and maxima



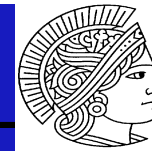
Predator-prey body-mass ratio



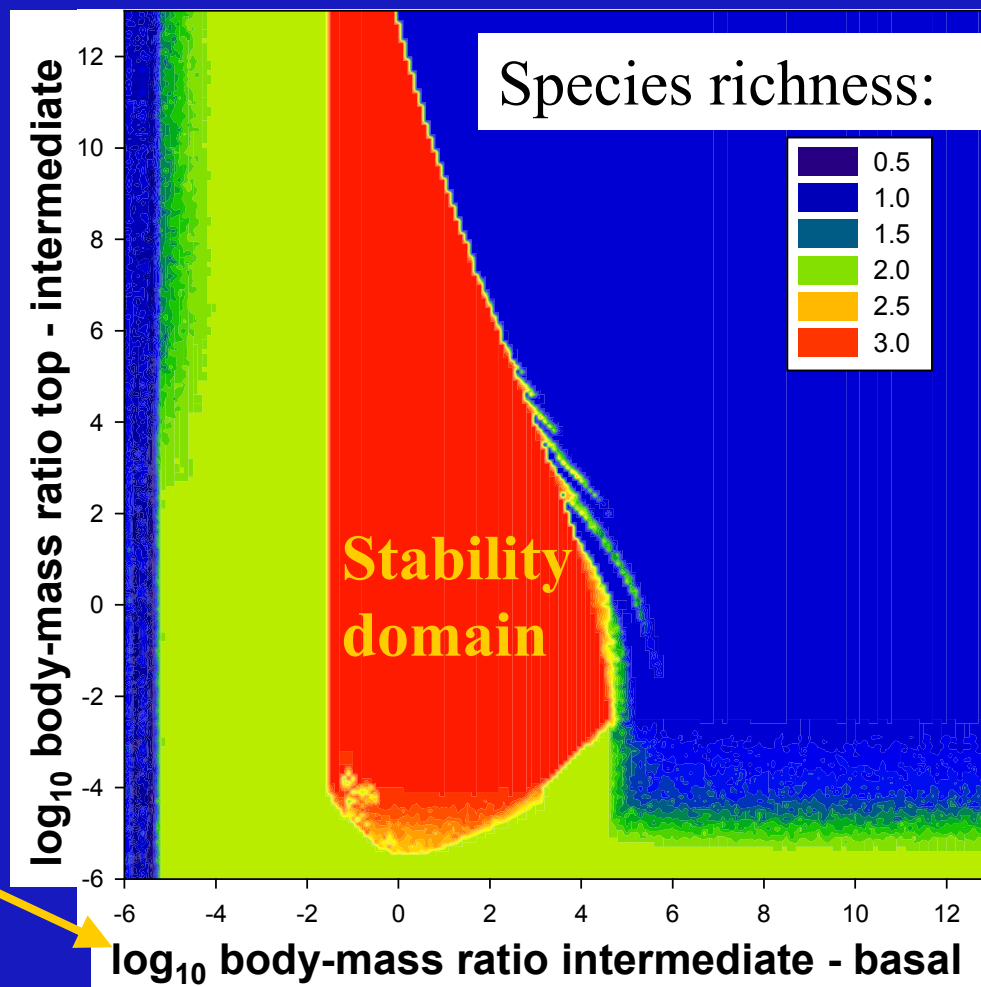
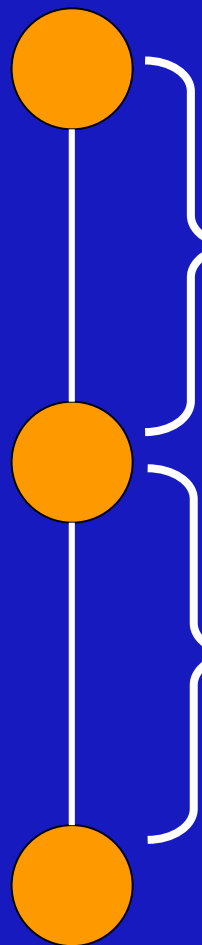
- 1) Body masses affect population dynamics;
- 2) Coexistence only in a limited domain of body masses.

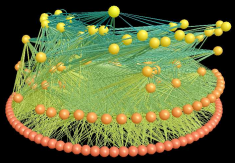


# Complex ecological networks



## Food-web stability





# Complex ecological networks

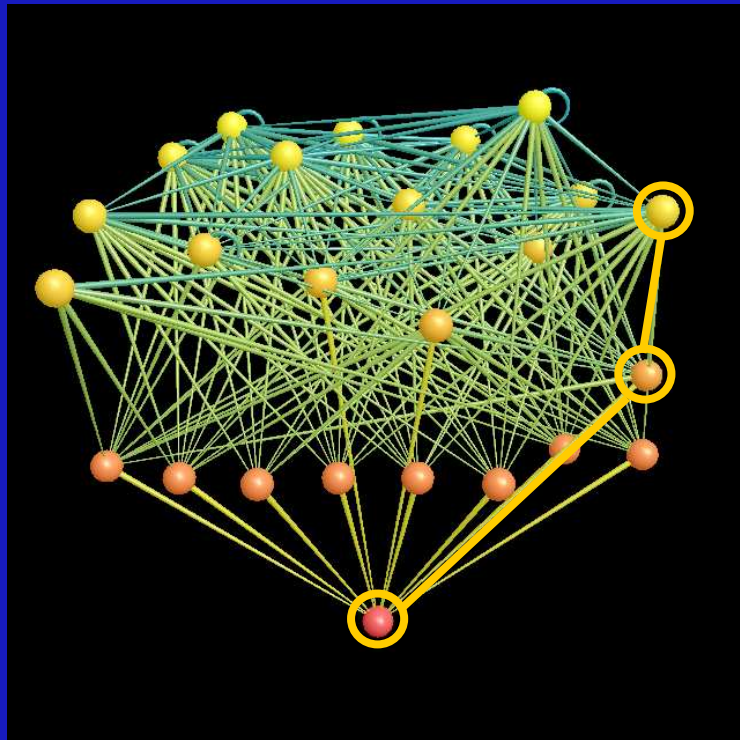


## Food-web stability

Empirical food web

isolate food chains

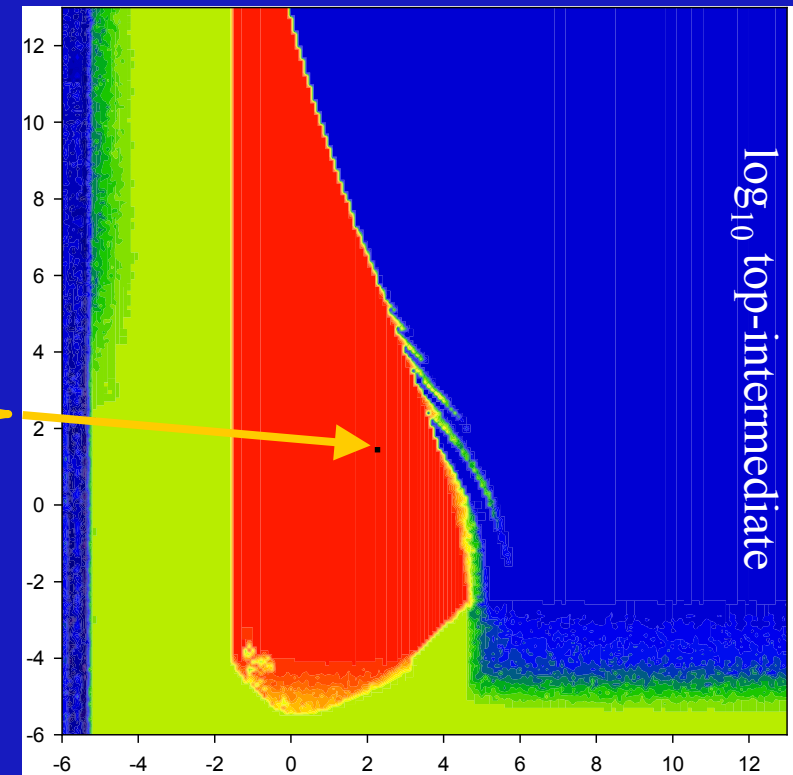
Compare to model predictions



Calculate body-mass ratios

top-inter

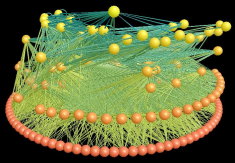
inter-basal



e.g. Skipwith Pond  
*Warren 1989, Oikos*

$\log_{10}$  intermediate-basal

*Otto et al. 2007 Nature*

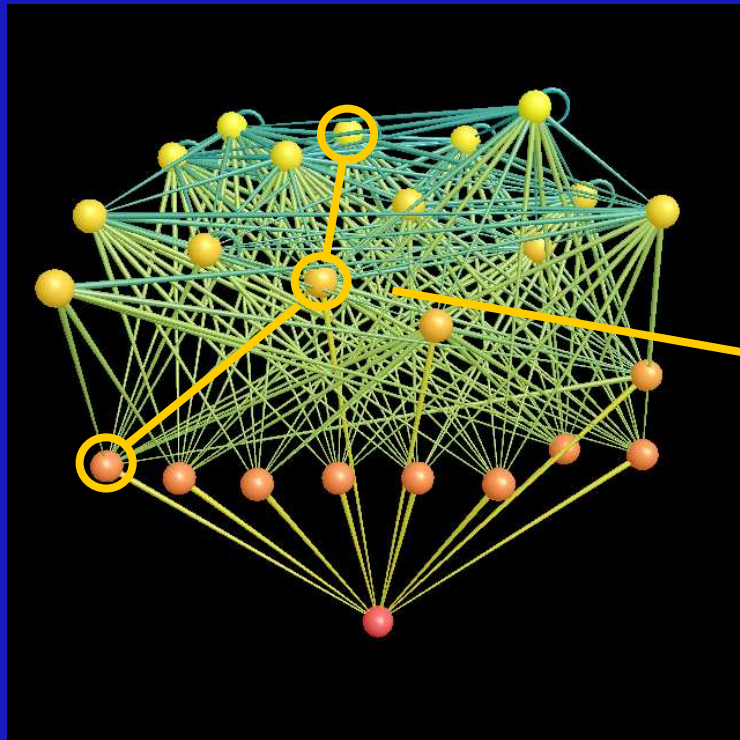


# Complex ecological networks



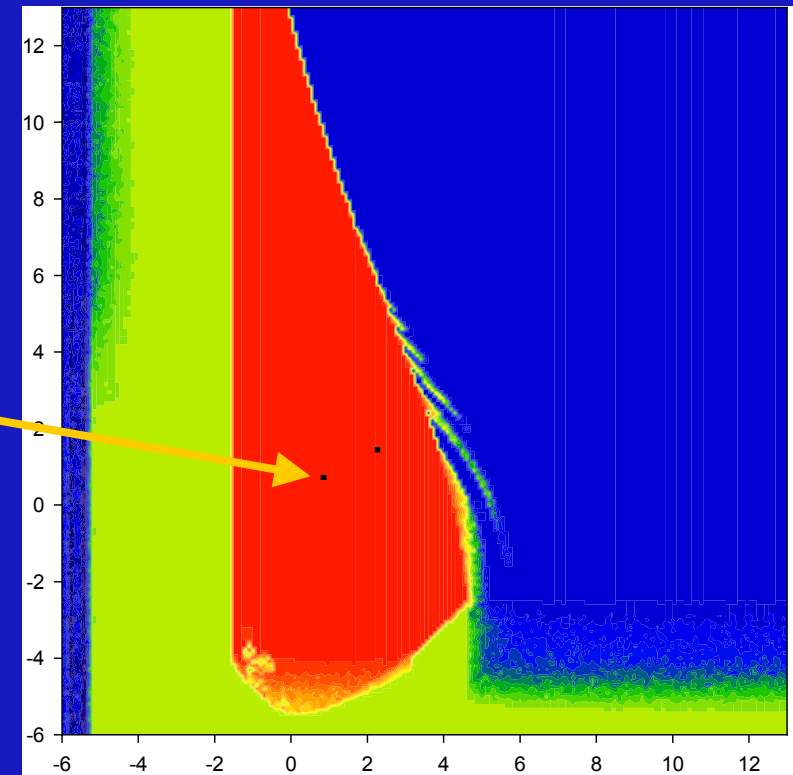
## Food-web stability

Empirical food web

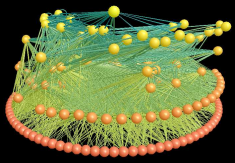


e.g. Skipwith Pond  
*Warren 1989, Oikos*

Compare to model predictions



*Otto et al. 2007 Nature*

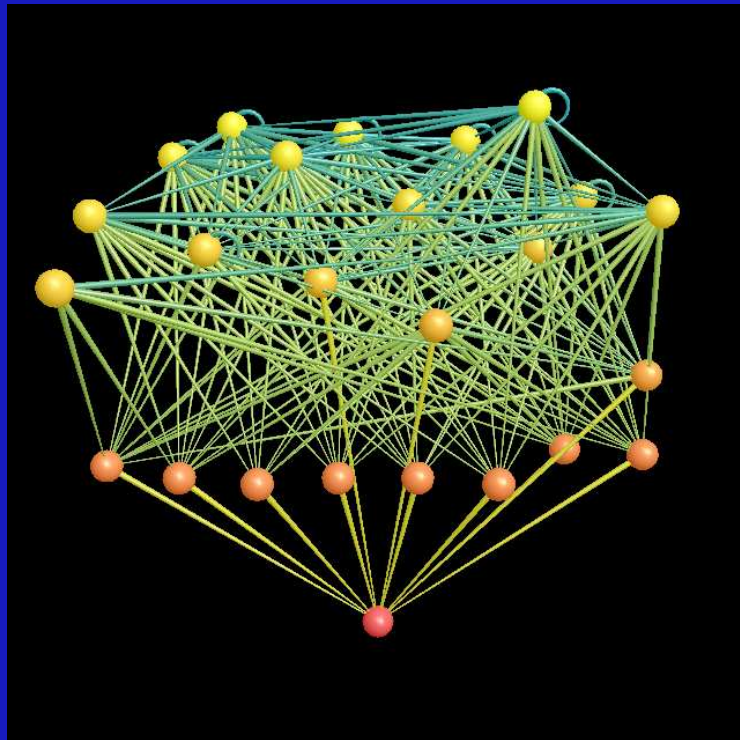


# Complex ecological networks



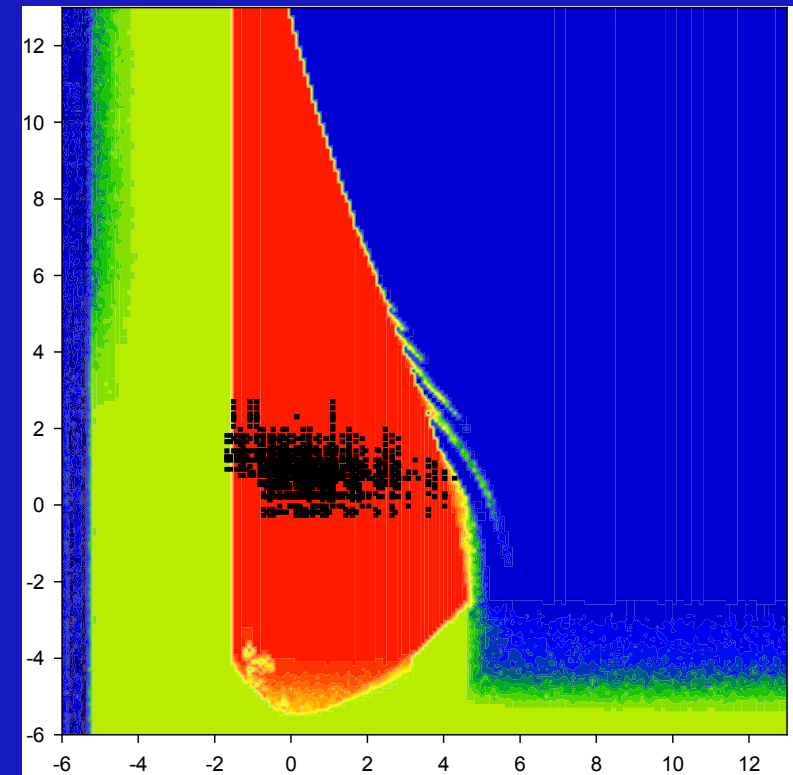
## Food-web stability

Empirical food web

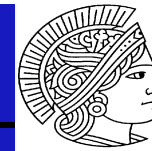
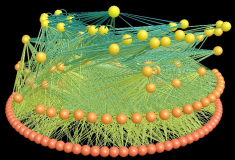


e.g. Skipwith Pond  
*Warren 1989, Oikos*

Compare to model predictions



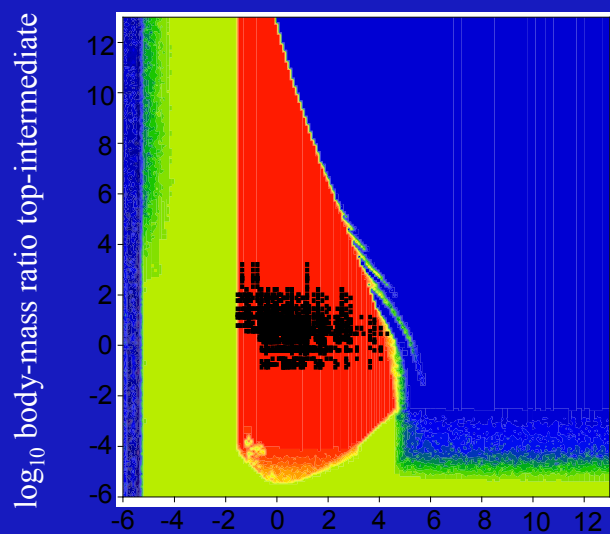
*Otto et al. 2007 Nature*



# Complex ecological networks

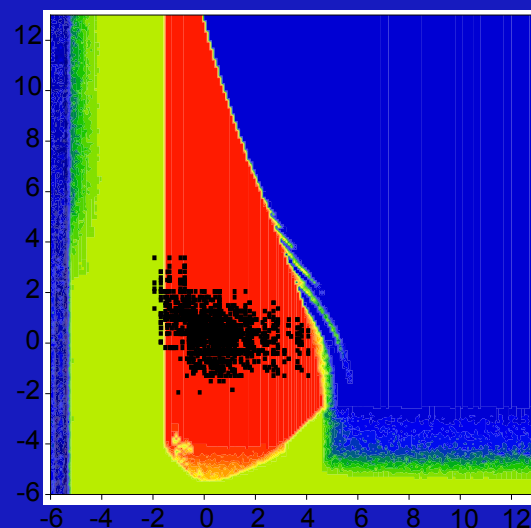
## Food-web stability

empirical



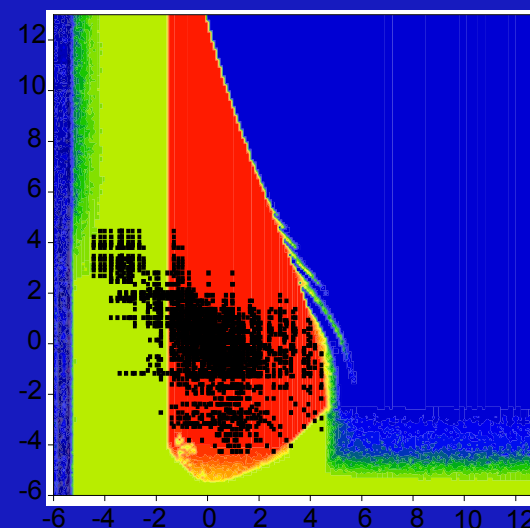
97.5%

restricted



94.7%

random

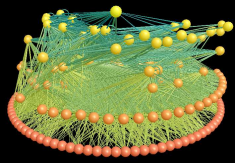


81%

$p = 0.17$

$p = 0.05$

*Otto et al. 2007 Nature*



# Complex ecological networks



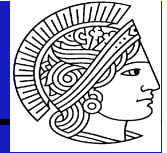
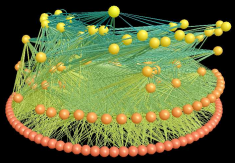
## Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems

Peter C. de Ruiter,\* Anje-Margriet Neutel, John C. Moore

Ecologists have long been studying stability in ecosystems by looking at the structuring and the strengths of trophic interactions in community food webs. In a series of real food webs from native and agricultural soils, the strengths of the interactions were found to be patterned in a way that is important to ecosystem stability. The patterning consisted of the simultaneous occurrence of strong “top down” effects at lower trophic levels and strong “bottom up” effects at higher trophic levels. As the patterning resulted directly from the energetic organization of the food webs, the results show that energetics and community structure govern ecosystem stability by imposing stabilizing patterns of interaction strengths.

Body-mass structures of food webs might drive  
interaction strength patterns

*De Ruiter et al. 1995, Science*



# Complex ecological networks

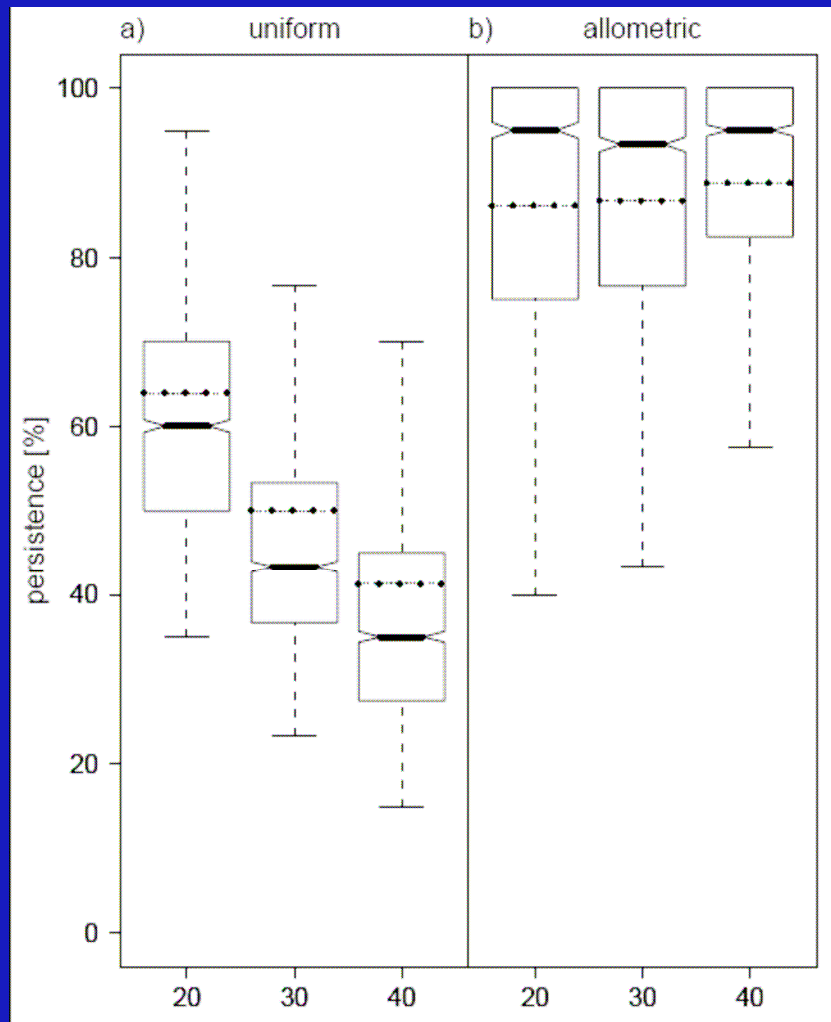
## Simulations of complex food webs

Body-mass structure:

Without

With

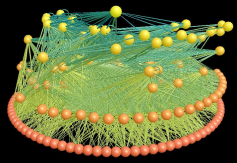
% persistent populations



Body-mass structure

- stabilizes food webs;
- converts negative into neutral diversity-stability relationships.

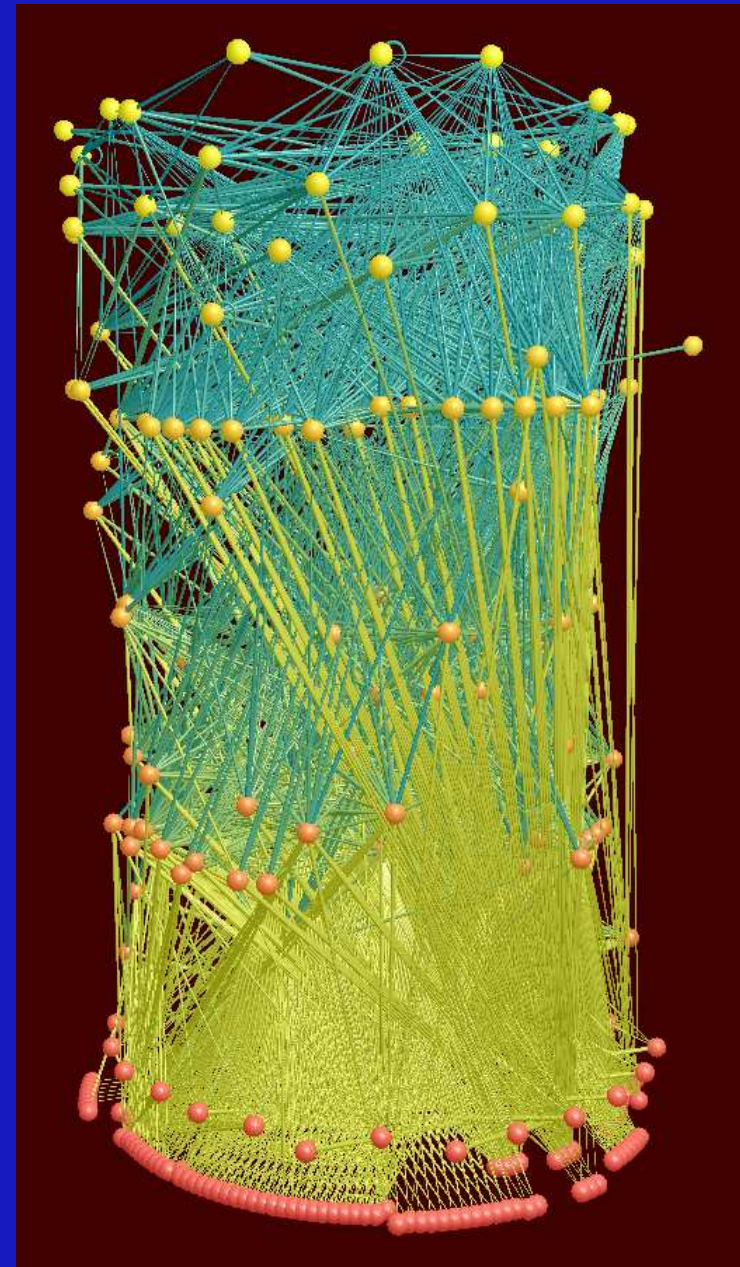
*Brose et al. 2006, Ecology Letters*

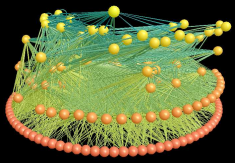


# Complex ecological networks



- Dynamic allometric network model
- How do all these species coexist?
- What are the consequences of species extinctions?





# Complex ecological networks



Intact community

Manipulated community

Removed Species

R

T

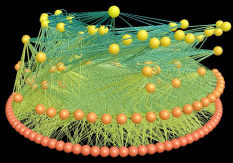
Target Species



T

T biomass increases  
after removal of R  
→ negative effect  
of R on T (in intact  
community)

$$\text{per capita } I = (B_{T+} - B_{T-}) / N_R$$



# Complex ecological networks



Intact community

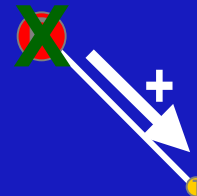
Manipulated community

Removed Species

R

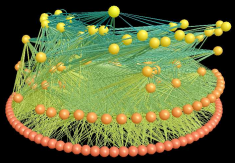
T

Target Species



T biomass decreases  
after removal of R  
→ positive effect of  
R on T (in intact  
community)

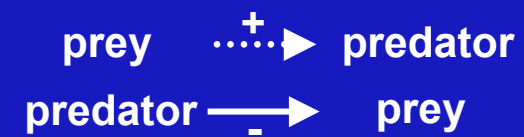
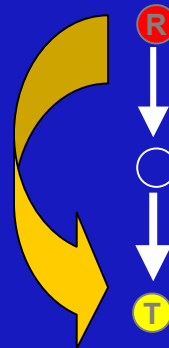
$$\text{per capita } I = (B_{T+} - B_{T-}) / N_R$$

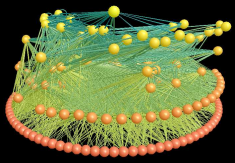


# Complex ecological networks



Positive effect

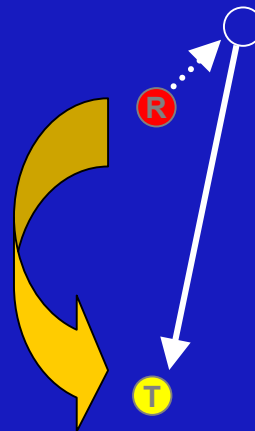




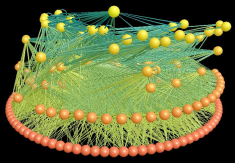
# Complex ecological networks



Negative effect



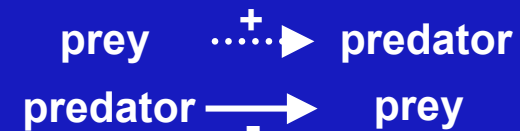
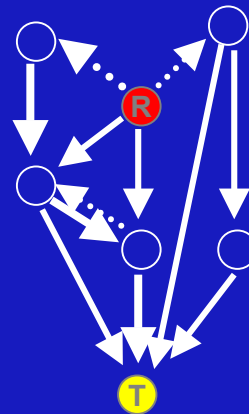
prey  $\xrightarrow{+}$  predator  
predator  $\xrightarrow{-}$  prey



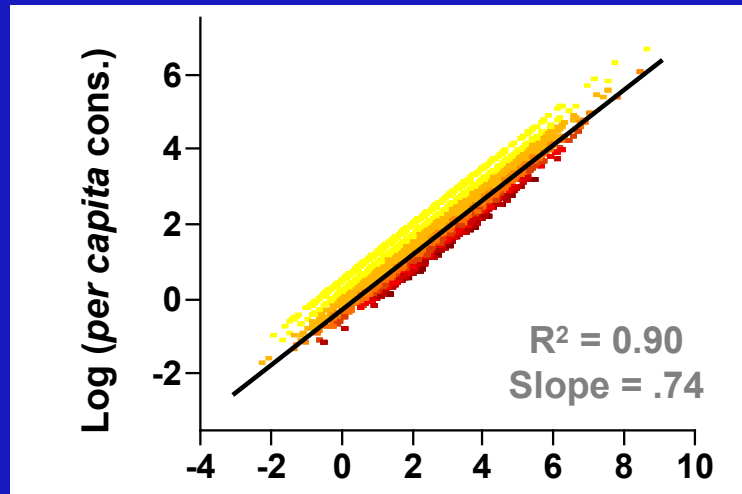
# Complex ecological networks



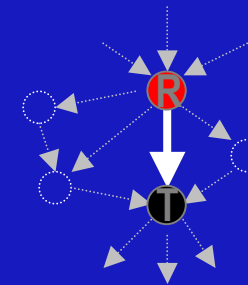
Negative or  
positive effect?

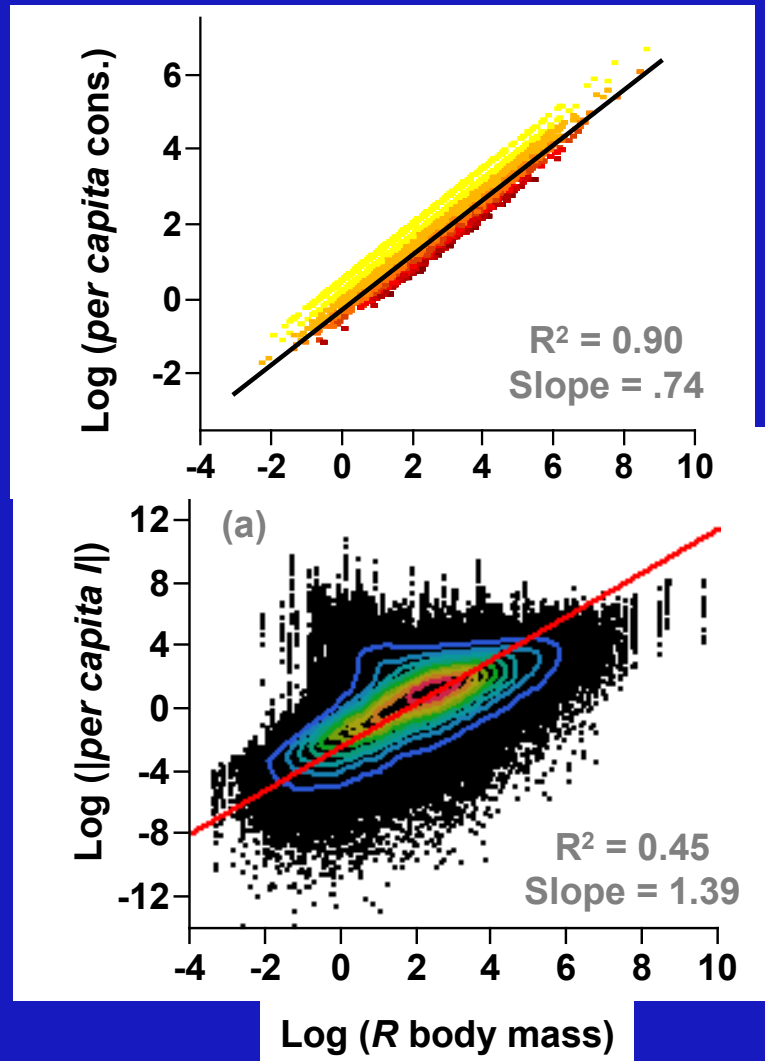


Predicting the consequences of species loss in complex networks  
is intractable (Yodzis 1988, Ecology)

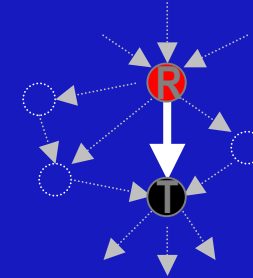


Input parameter: each feeding interaction scales with  $(\text{body size})^{0.75}$

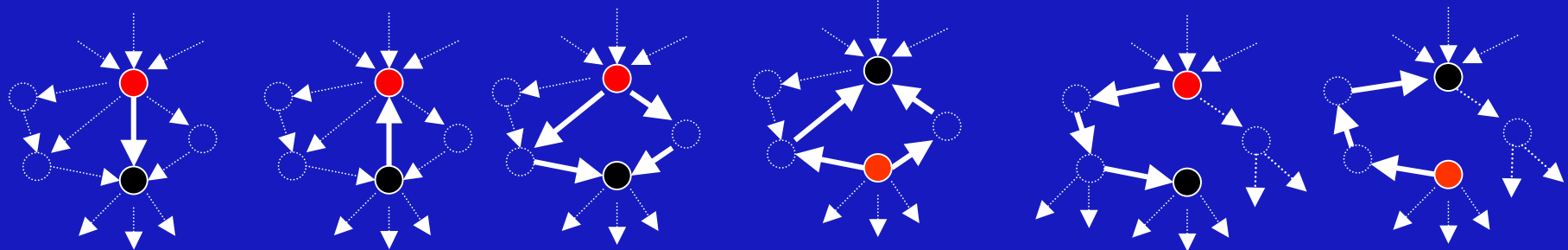


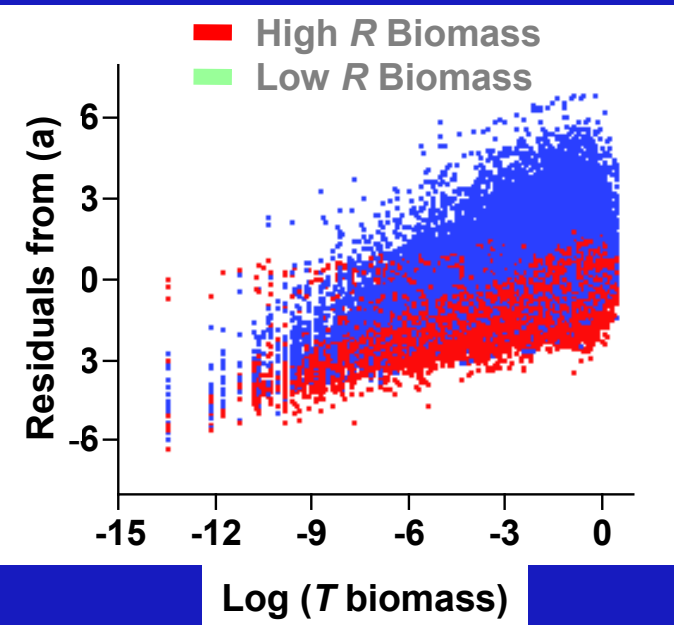
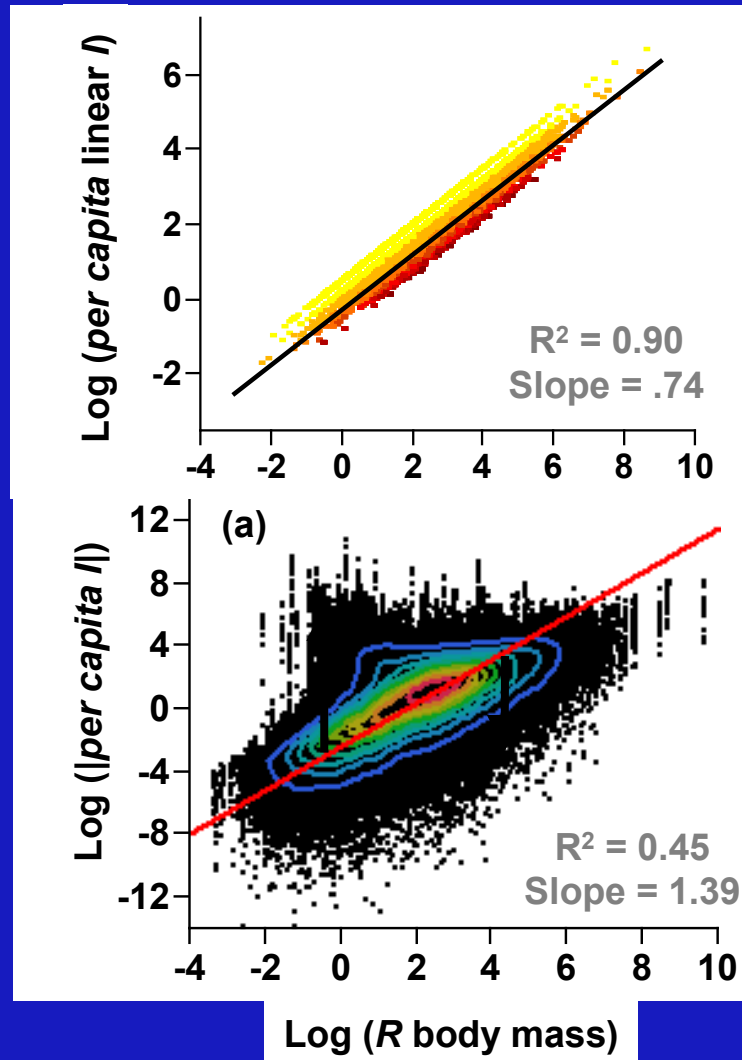


Input parameter: each feeding interaction scales with  $(\text{body size})^{0.75}$



Result: interaction strength scale with  $(\text{body size})^{1.39}$

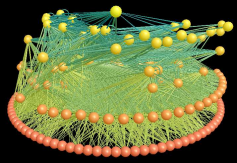




## Summary:

- (1) 3/4 scaling disappears in complex networks,
- (2) strongest per capita I: large bodied, low biomass R effects on high biomass T,  $R^2 = 0.88$

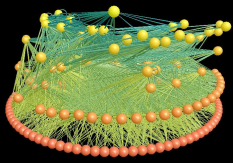
*Berlow et al. submitted*



# Complex ecological networks



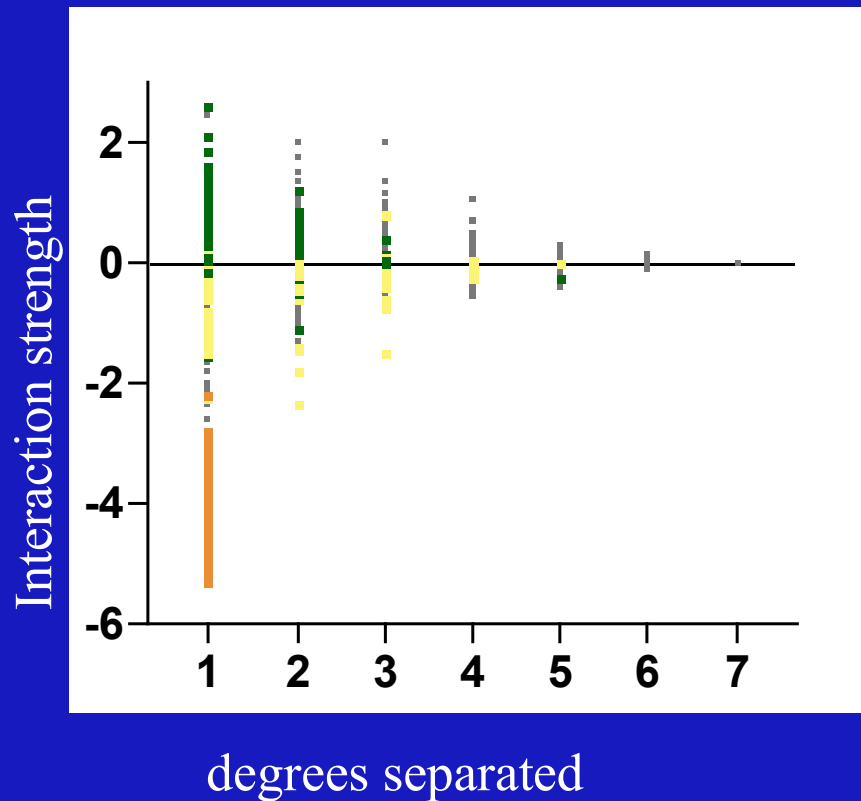
**How can it be so simple?**



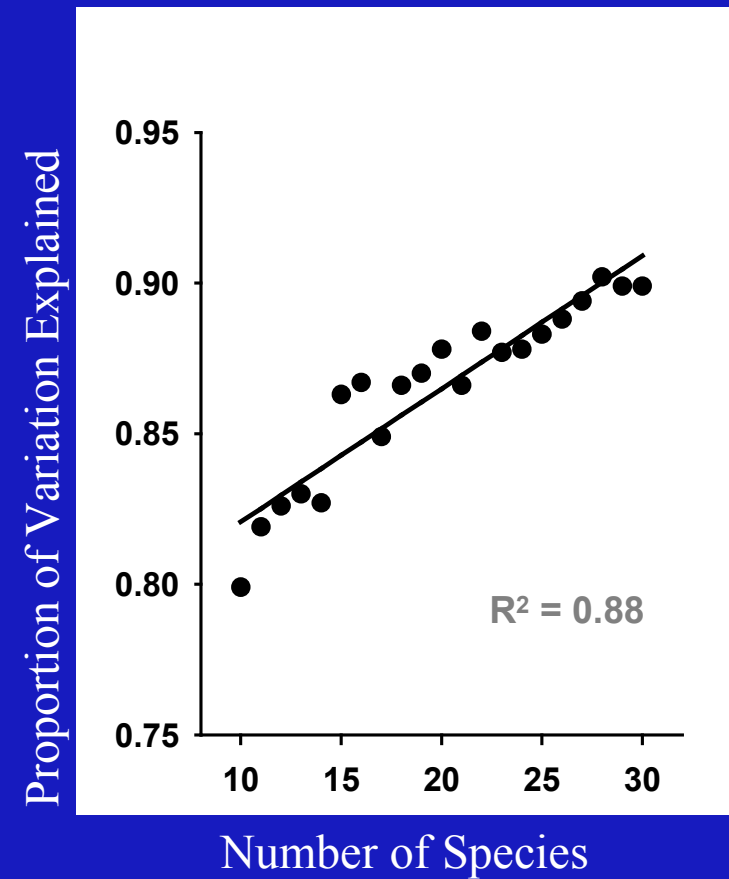
# Complex ecological networks



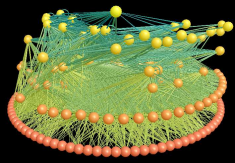
**Multiple pathways cancel out**



**More Complex is More Simple**



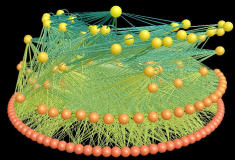
*Berlow et al. submitted*



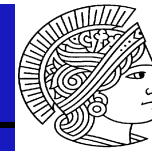
## Complex ecological networks



**Does it apply to natural ecosystems?**

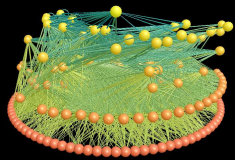


# Complex ecological networks

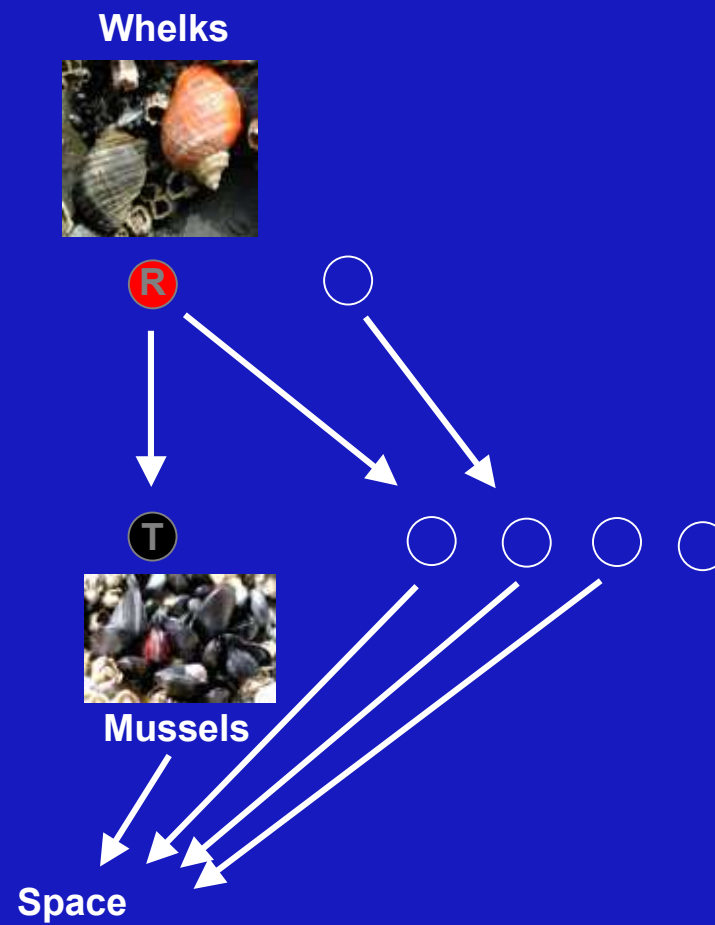
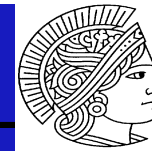


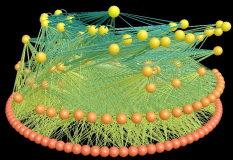
Berlow 1999 *Nature* 398:330



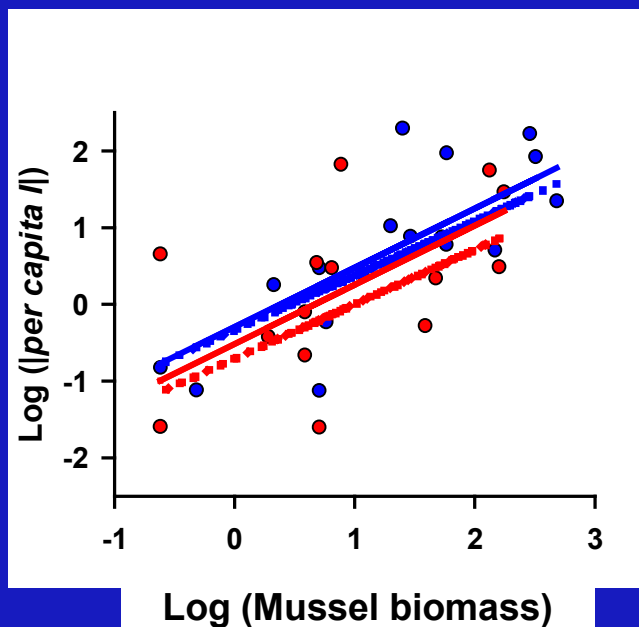
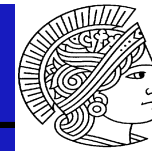


# Complex ecological networks



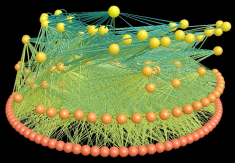


# Complex ecological networks



predicted  
..... High *R* Biomass  
..... Low *R* Biomass

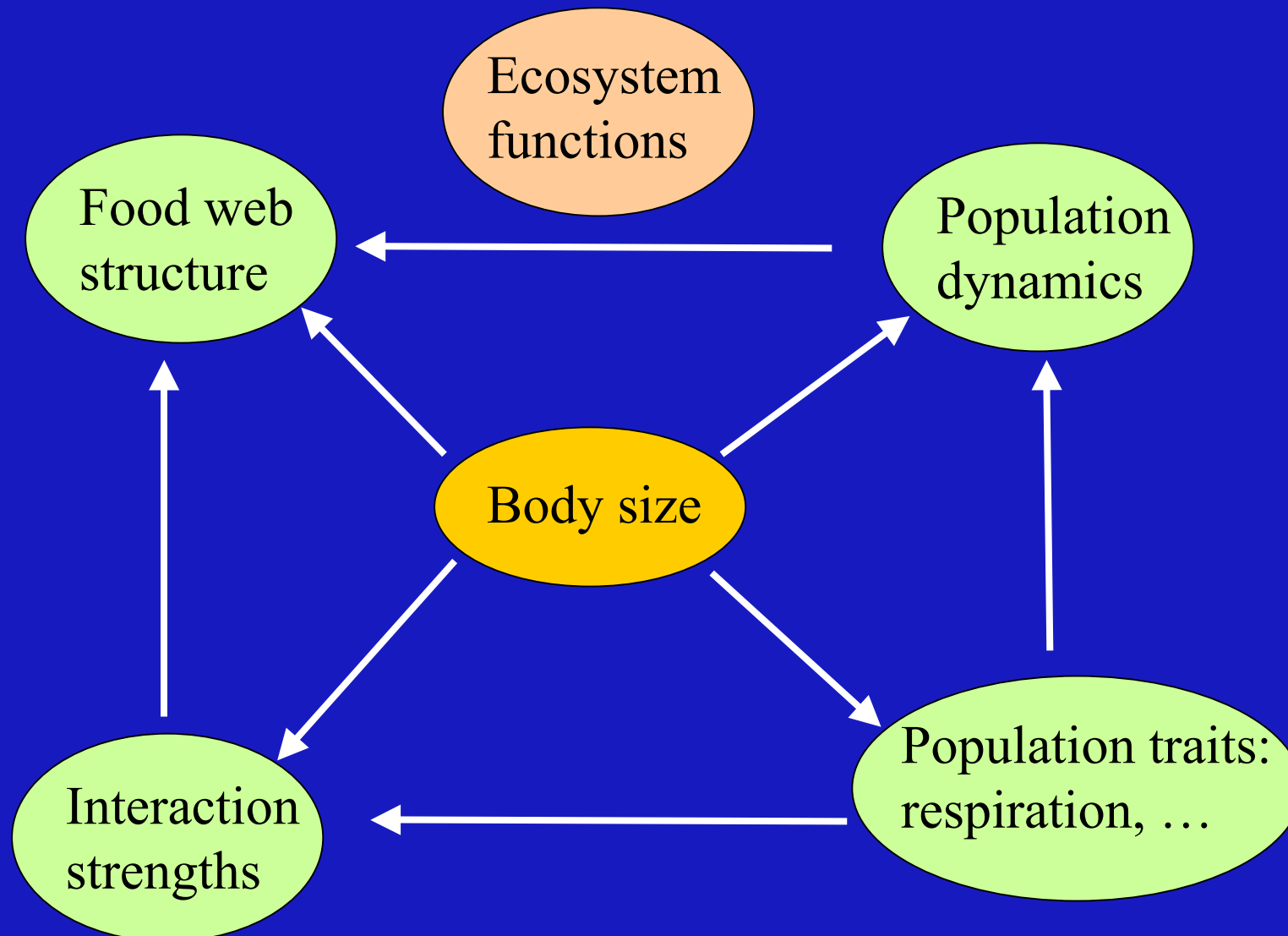
observed  
———— High *R* Biomass  
———— Low *R* Biomass

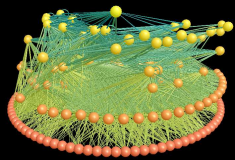


## Complex ecological networks

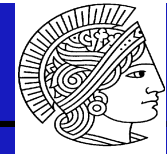


**Where does species identity (size) matter the most?**





# Complex ecological networks



**AG Brose**

**EcoNetLab**

**Eric Berlow**  
(Interaction strengths)



**Björn Rall**  
(Temperature scaling in food webs)



**Jens Riede**  
(Body-size structure of food webs)



**Gregor Kalinkat**  
(multi-species functional responses)



**Roswitha Ehnes**  
(Metabolism / Macroecology)



**Olivera Vucic-Pestic**  
(Functional responses)



**Carolyn Banasek-Richter**  
(Spatial food webs)

**Sonja Otto**  
(Species' extinction / food-web stability)



**Emmy Noether-Programm**

Deutsche  
Forschungsgemeinschaft

**DFG**

