Food webs

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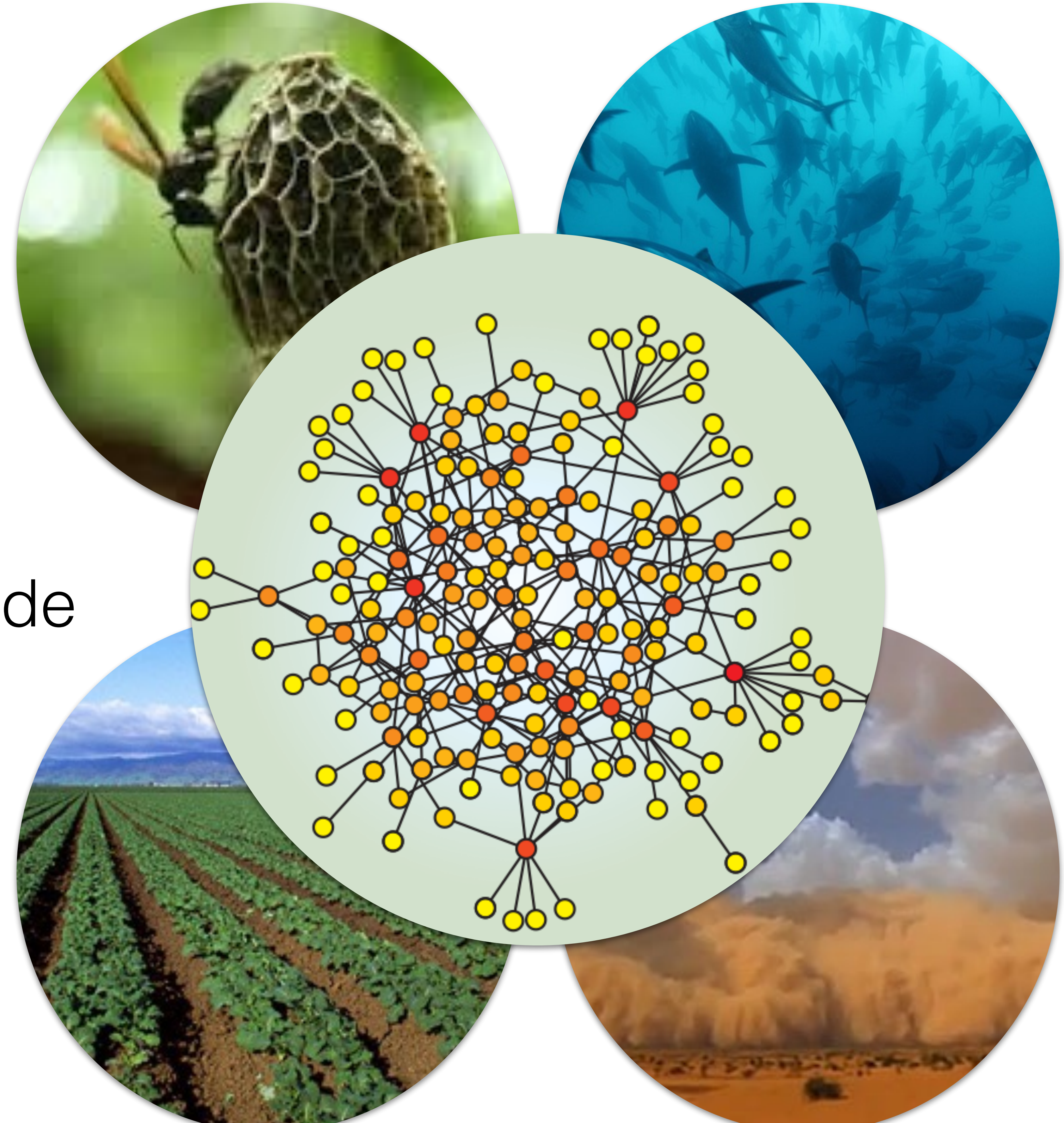
http://jdyeakel.github.io

Biological diversity

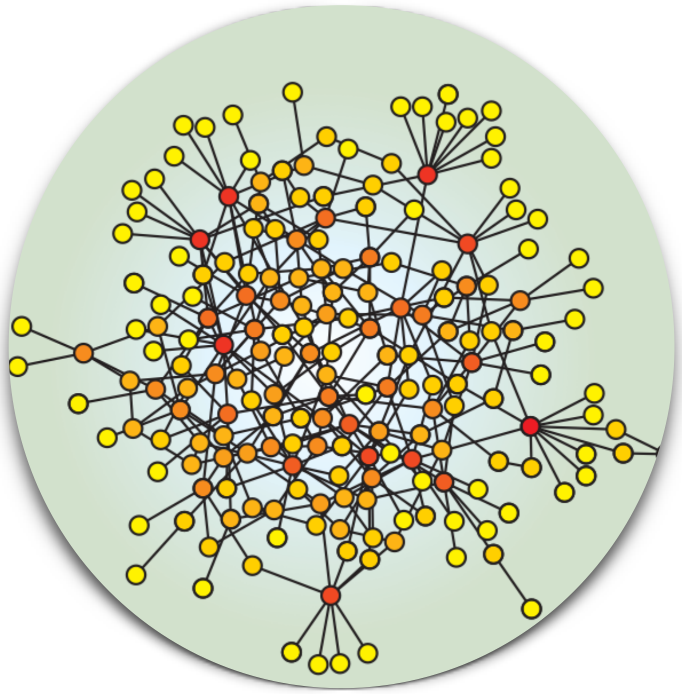
- populations
- species
- communities
- ecosystems

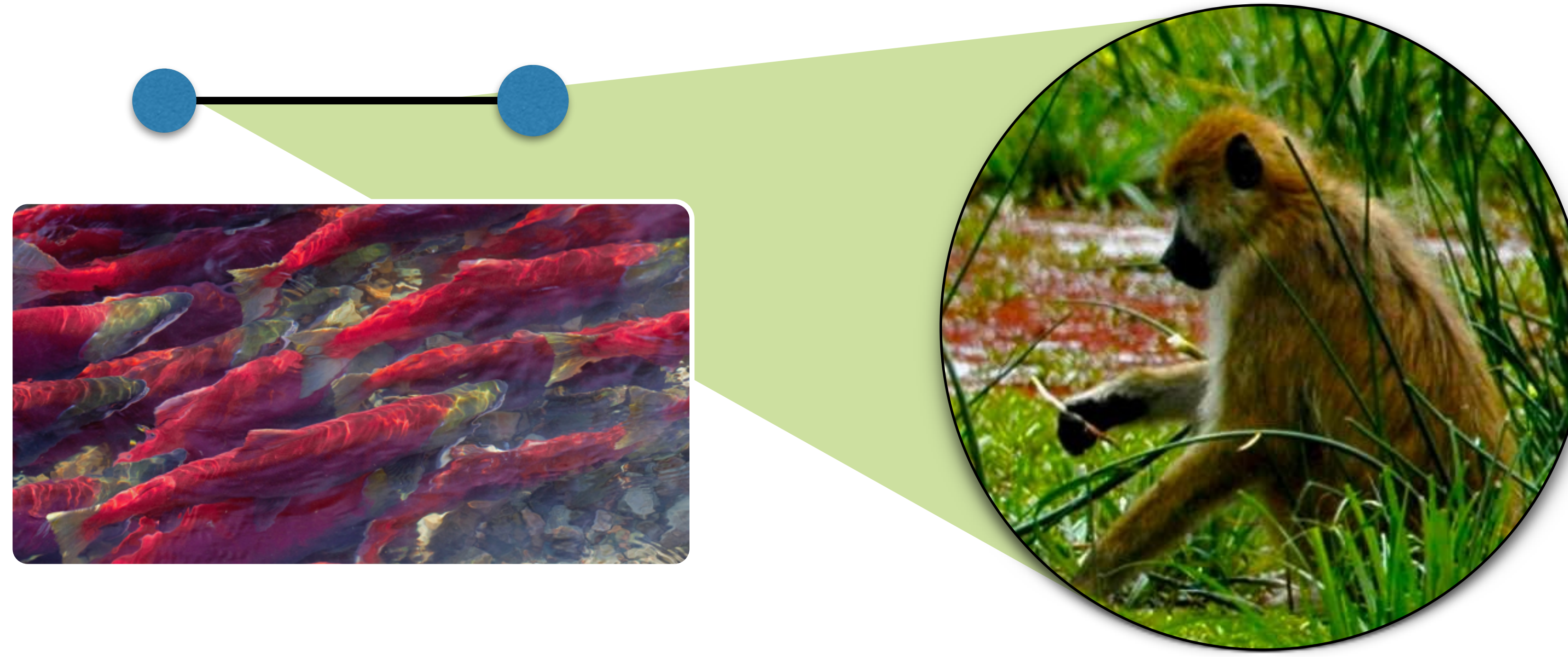
Diverse ecosystems provide

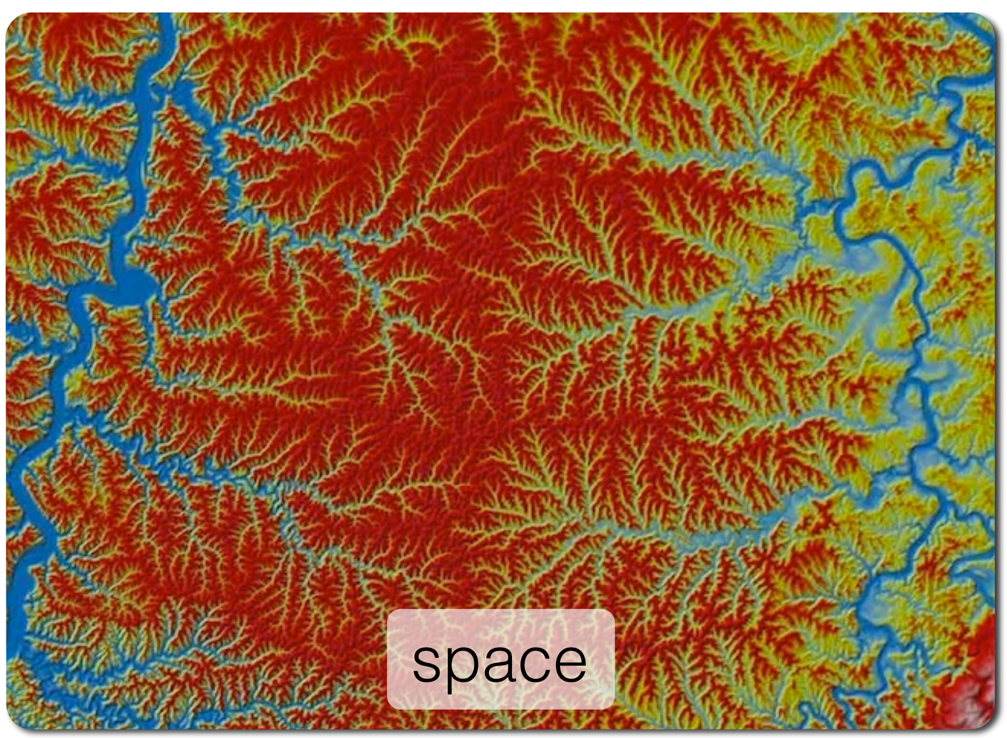
- Food (e.g. fisheries)
- Genetic diversity
- Predictability
- Beauty



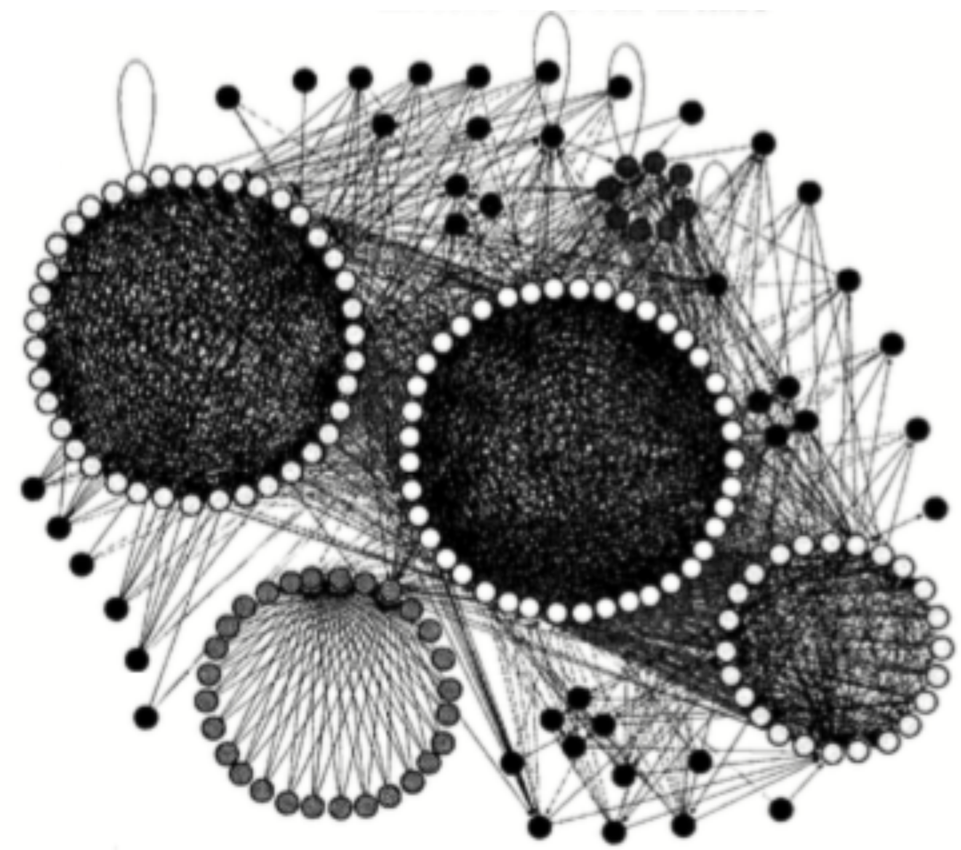
Food webs ⟷ Interactions ⟷ Behavior







Structure of this talk:



Empirical food web networks
  Statistical properties

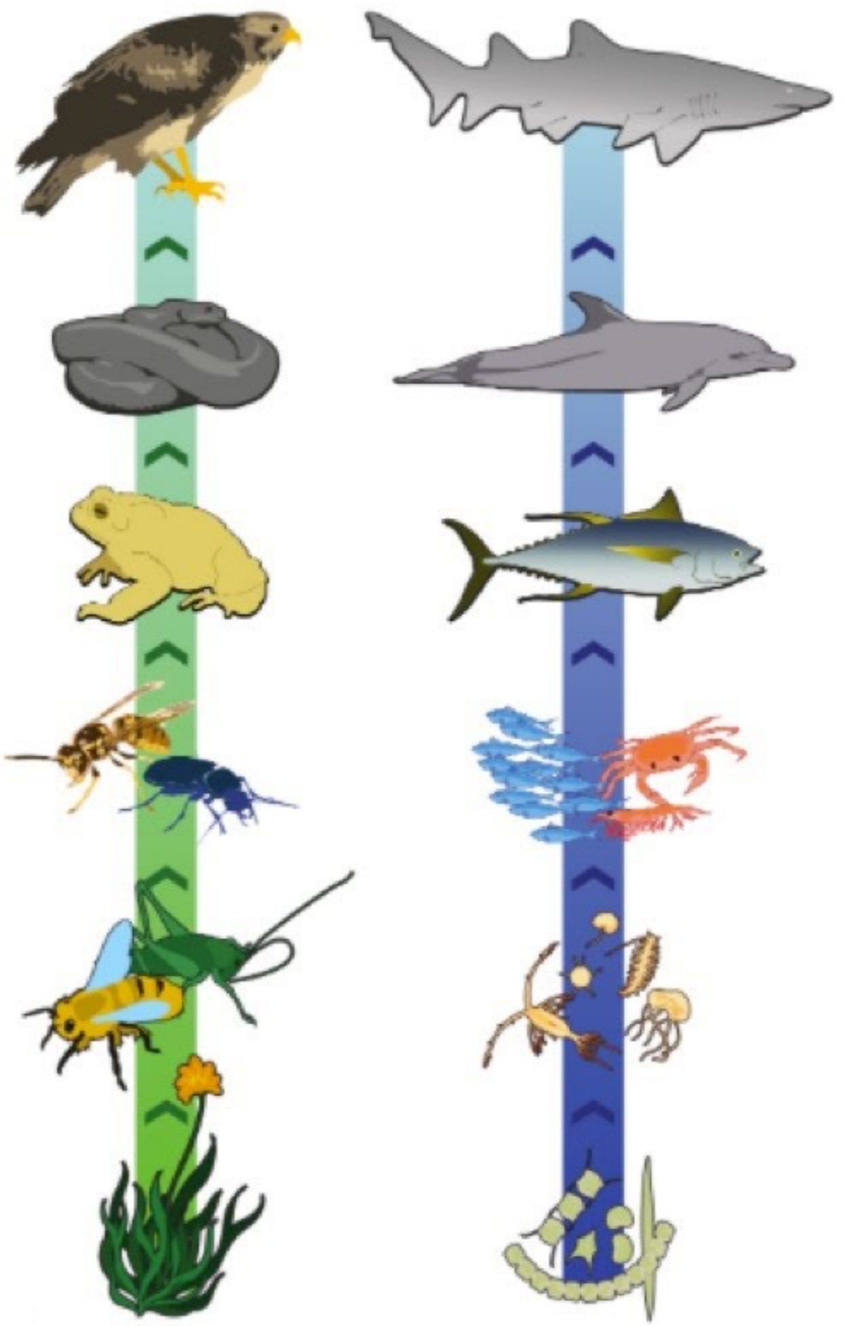
Model food web networks
  Structure
  Parameterizing models from data
  Incorporating additional biological constraints

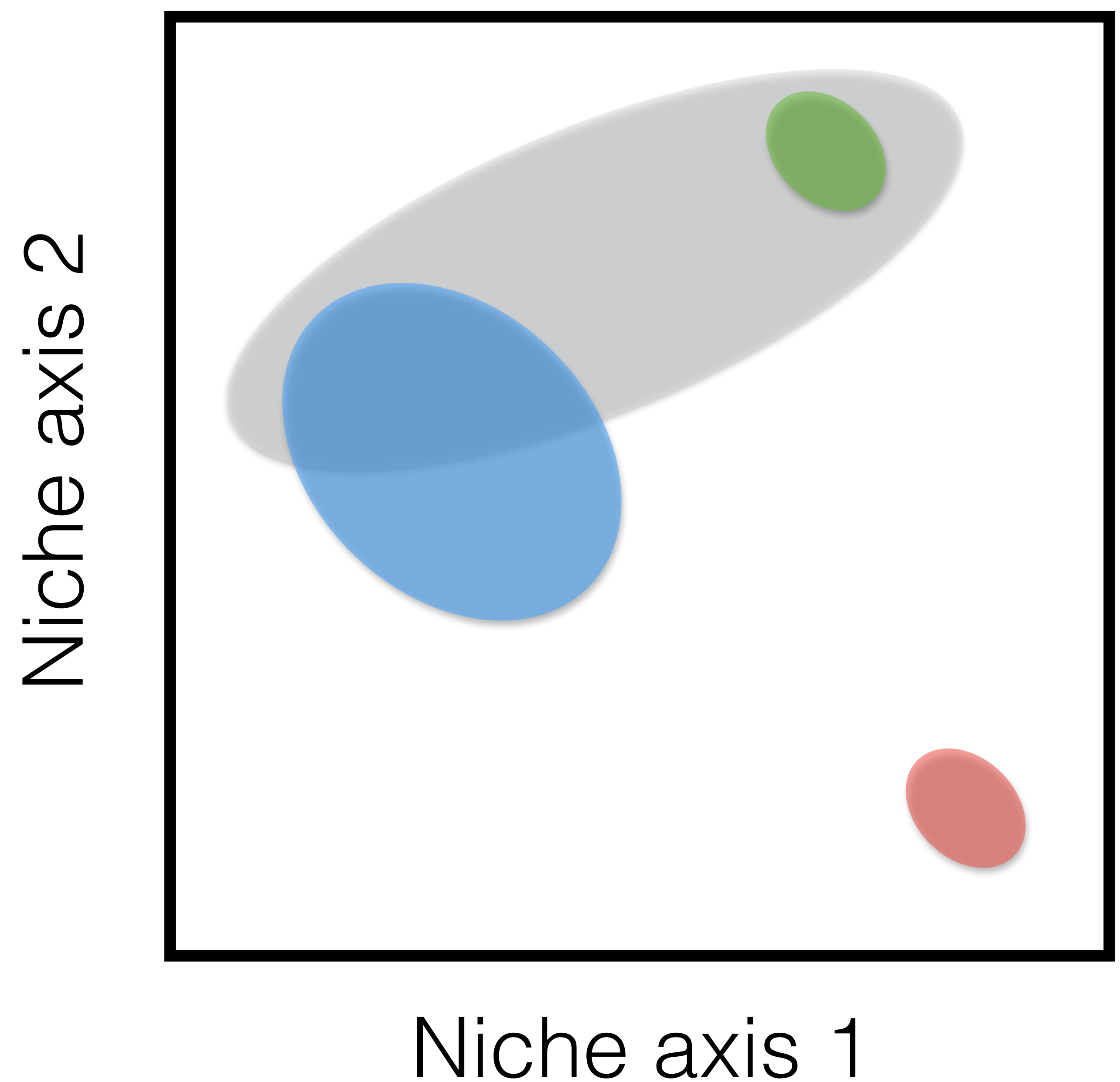
Food web dynamics
  Matrix models
  Generalized models

Food webs over time

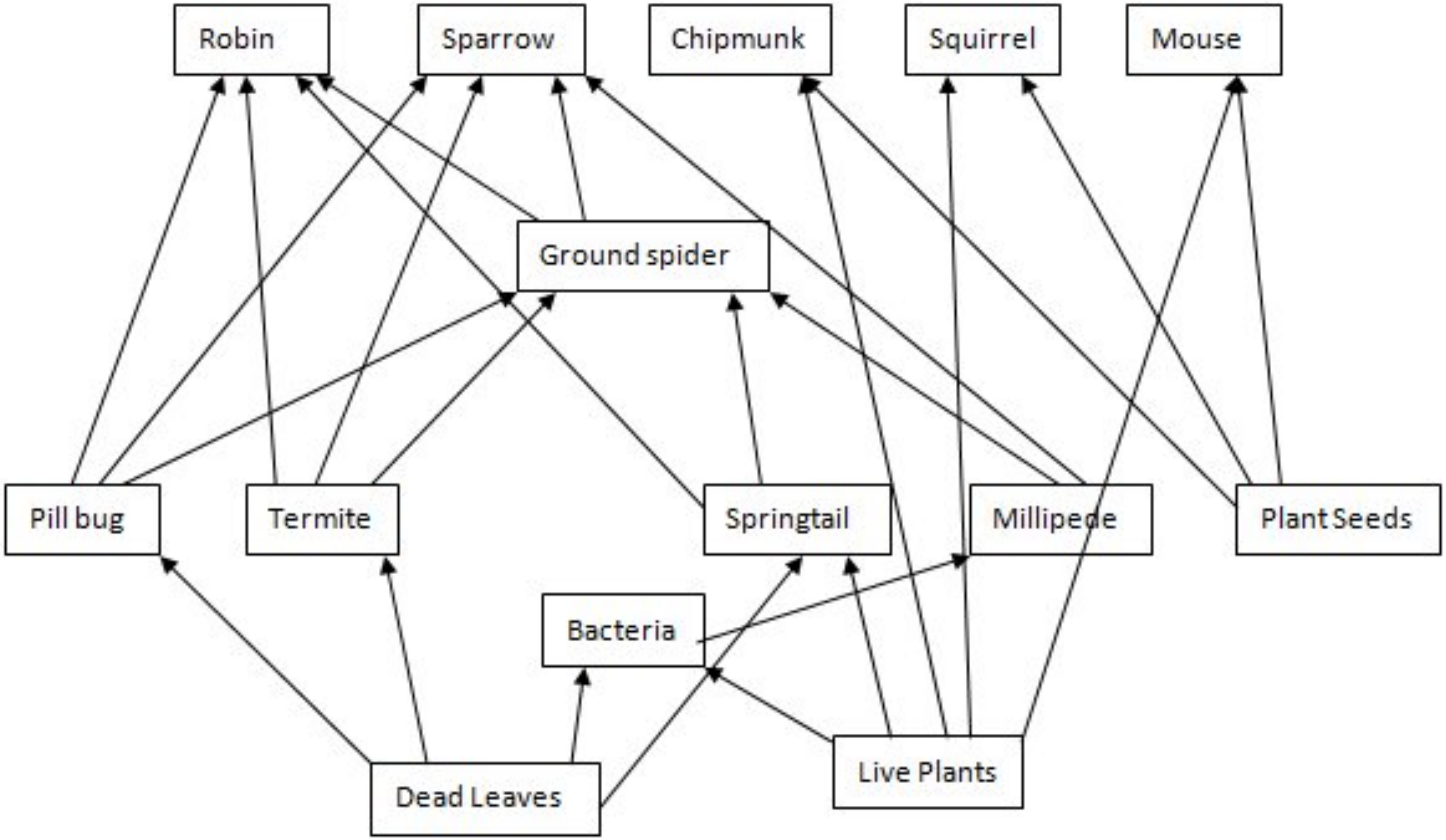
The dietary niche

The food chain



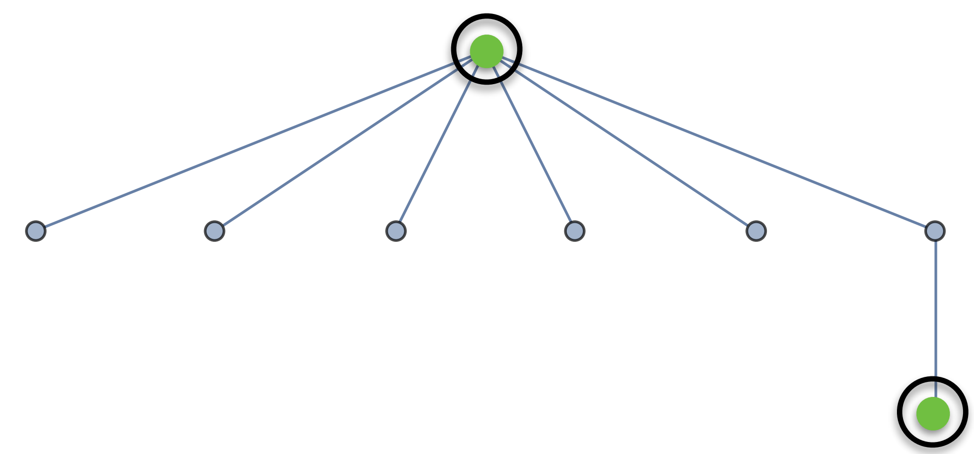


From Forbes 1876



Predation: a +/- interaction

Specialists vs. Generalists

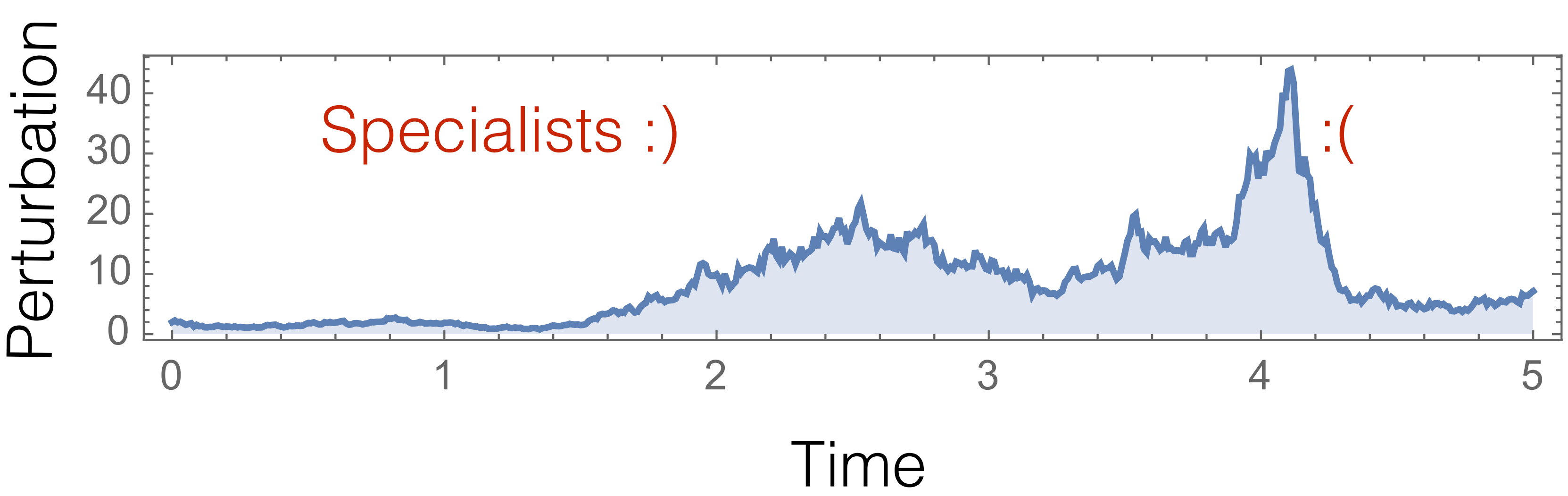


Jack of all trades

Master of one

low “asset diversity”

Ecological rate (ecological timescales)
Evolutionary rate (evolutionary timescales)

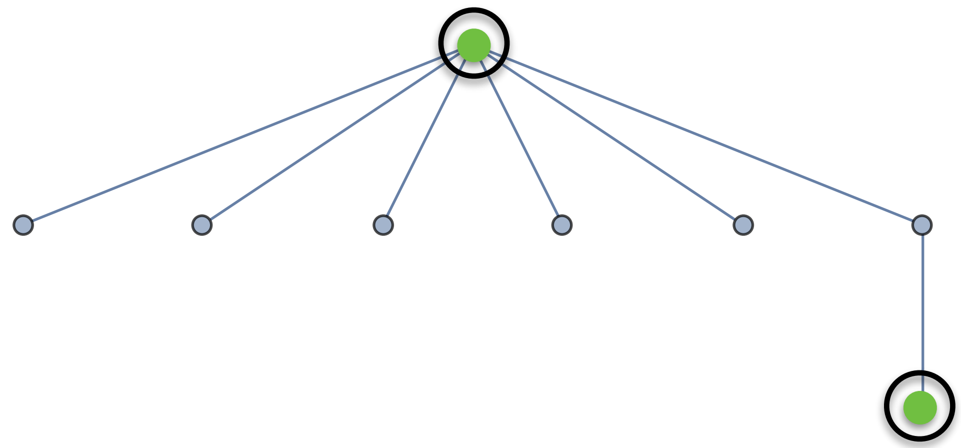


Specialists can outcompete generalists within shorter timescales

Specialists tend to lose in the long run (more sensitive to large perturbations)

Not this simple… eco-evo dynamics

Specialists vs. Generalists



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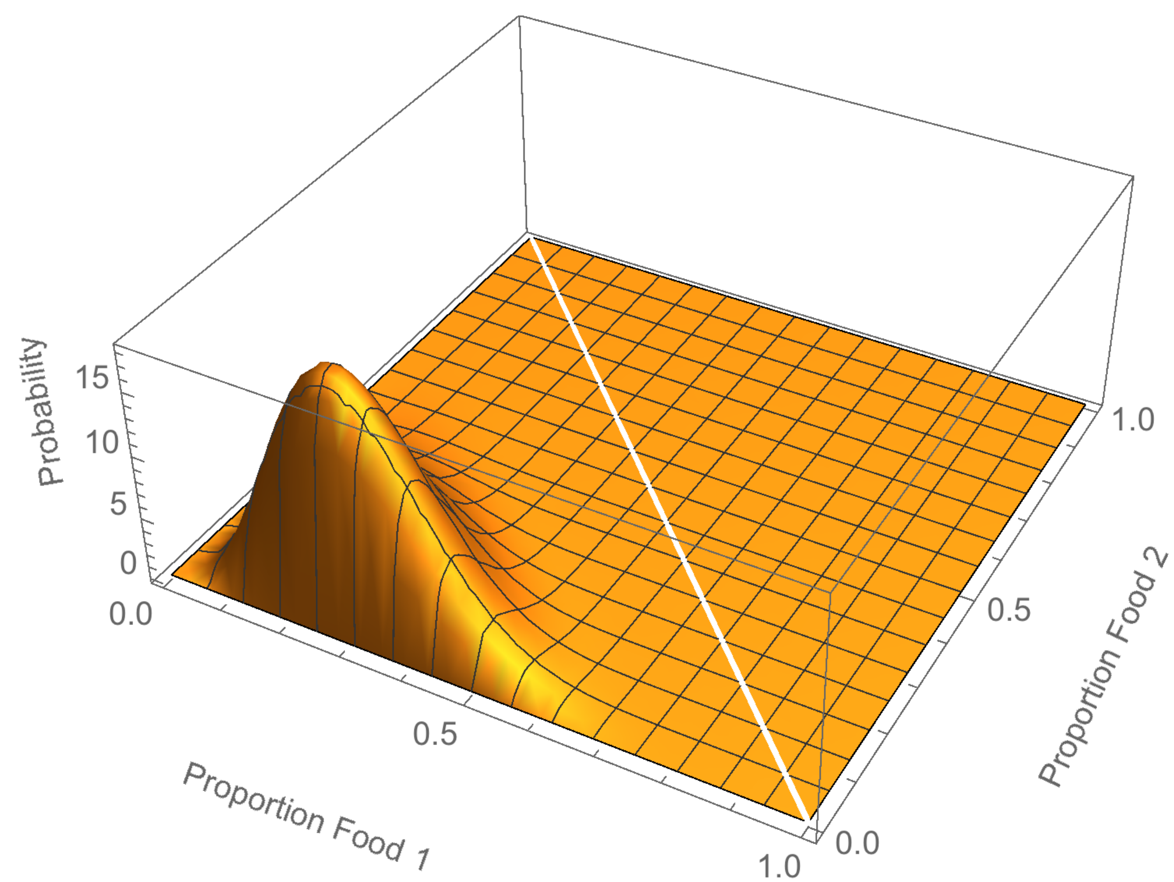
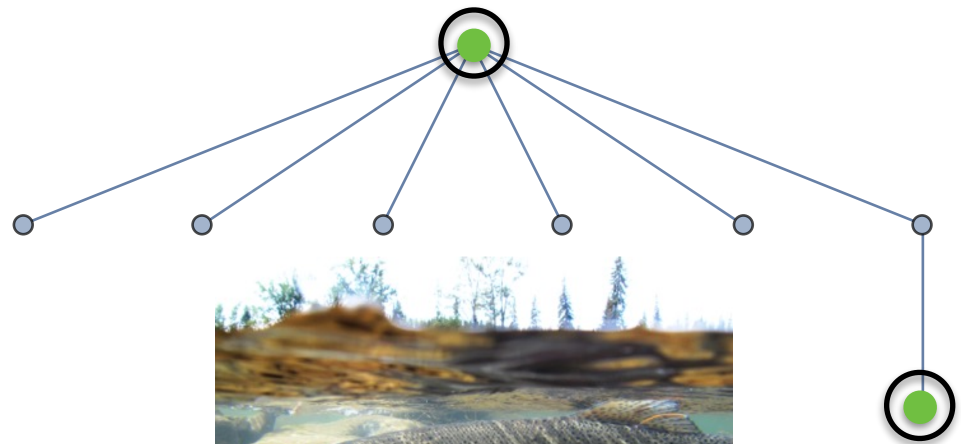
More complicated:
individuality
life-history

Links have probabilistic weights



Specialists vs. Generalists

Jack of all trades



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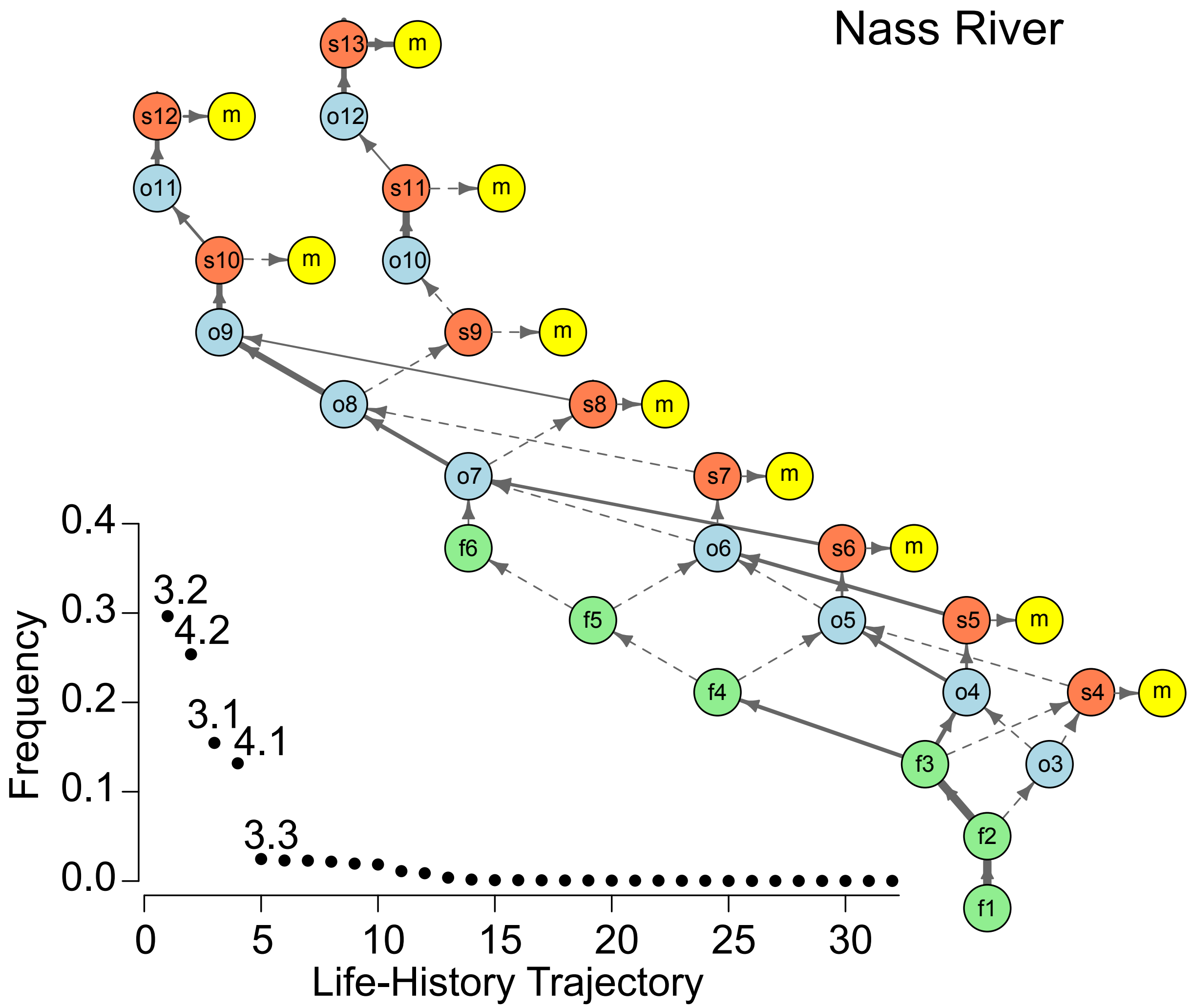
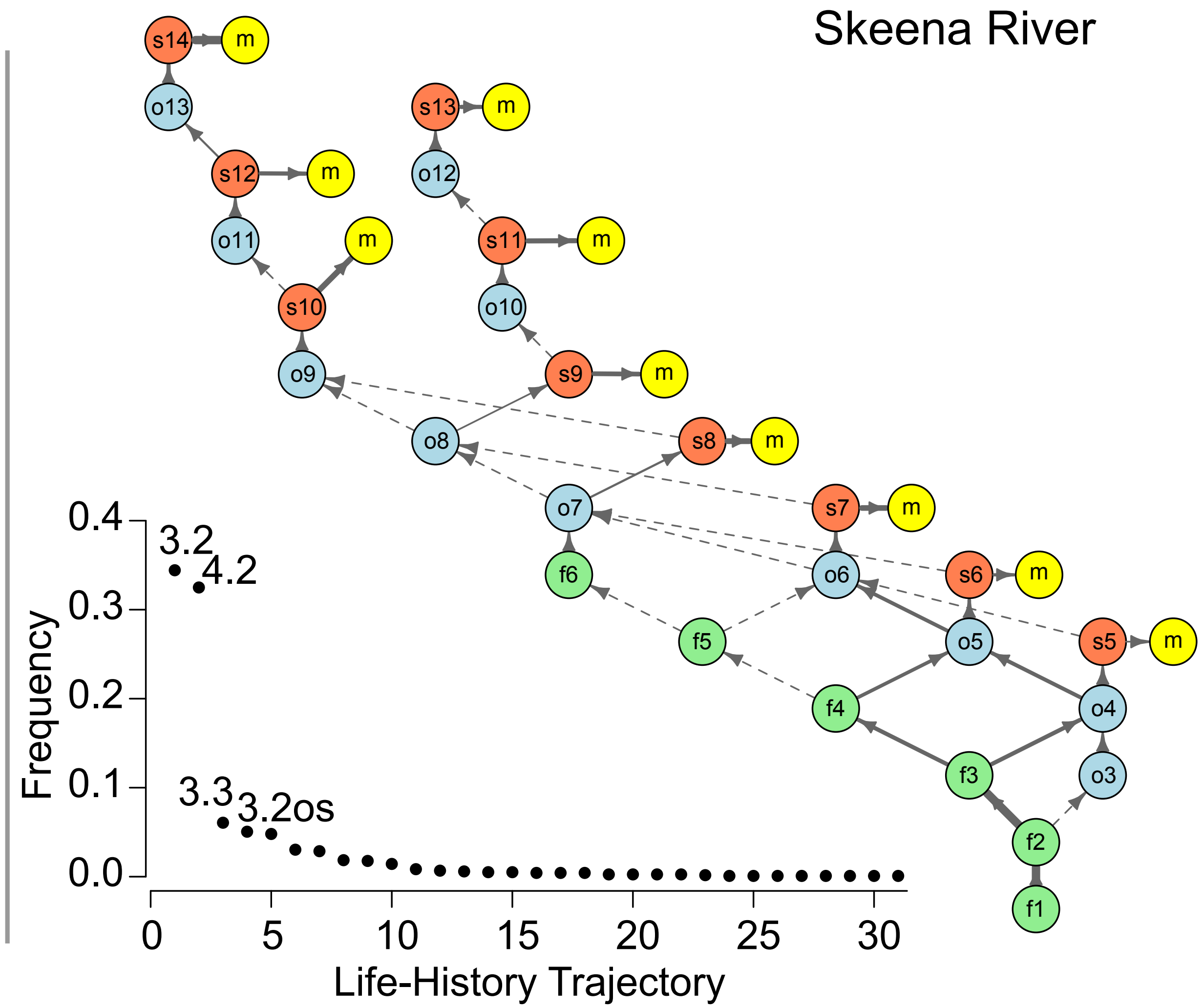
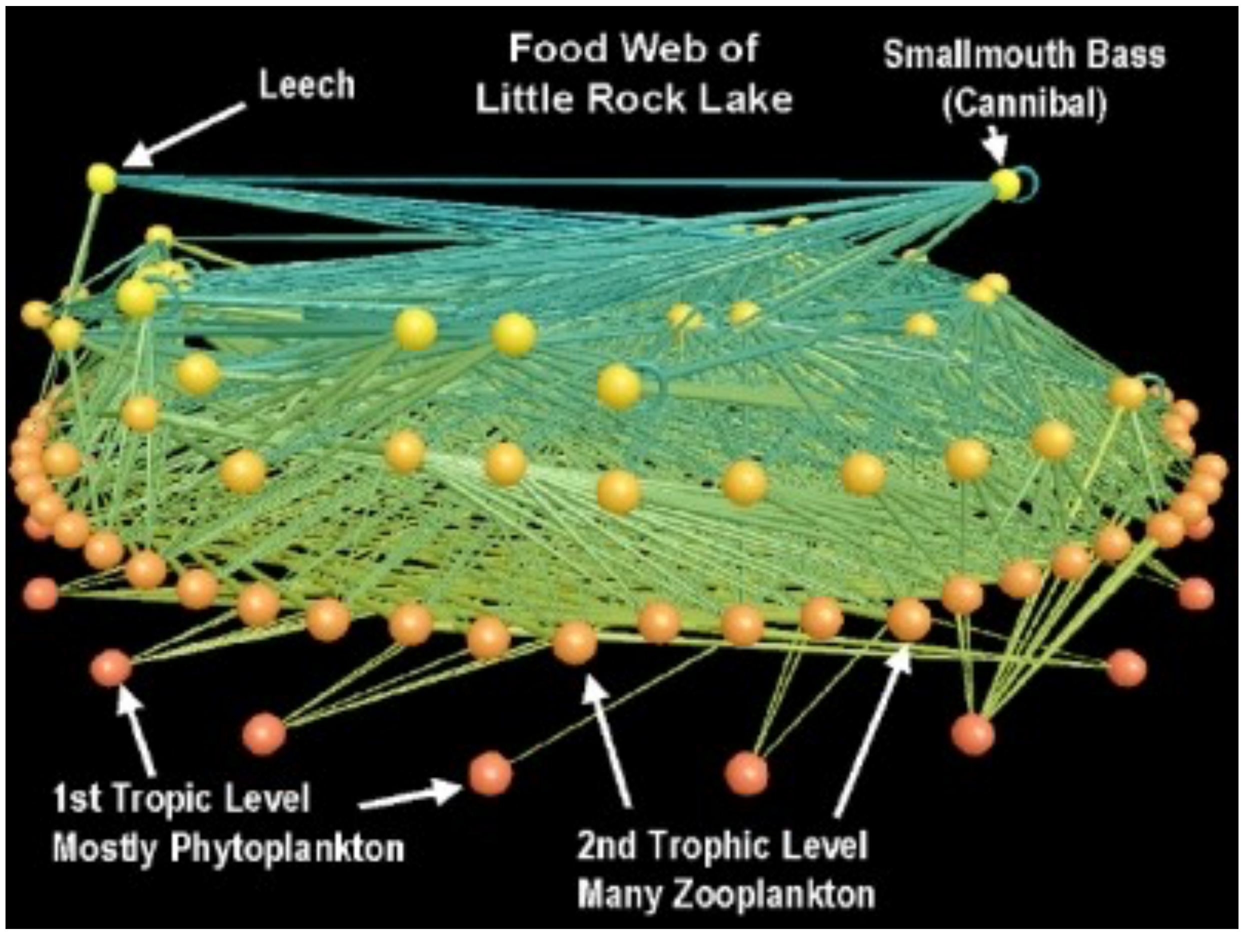




The structure of trophic interactions within communities (Dunne, Stouffer)



Some

S	# species
L	# Links
$C = L/S^2$	Directed connectance
$SC=L/S$	Links per species (Avg generality)

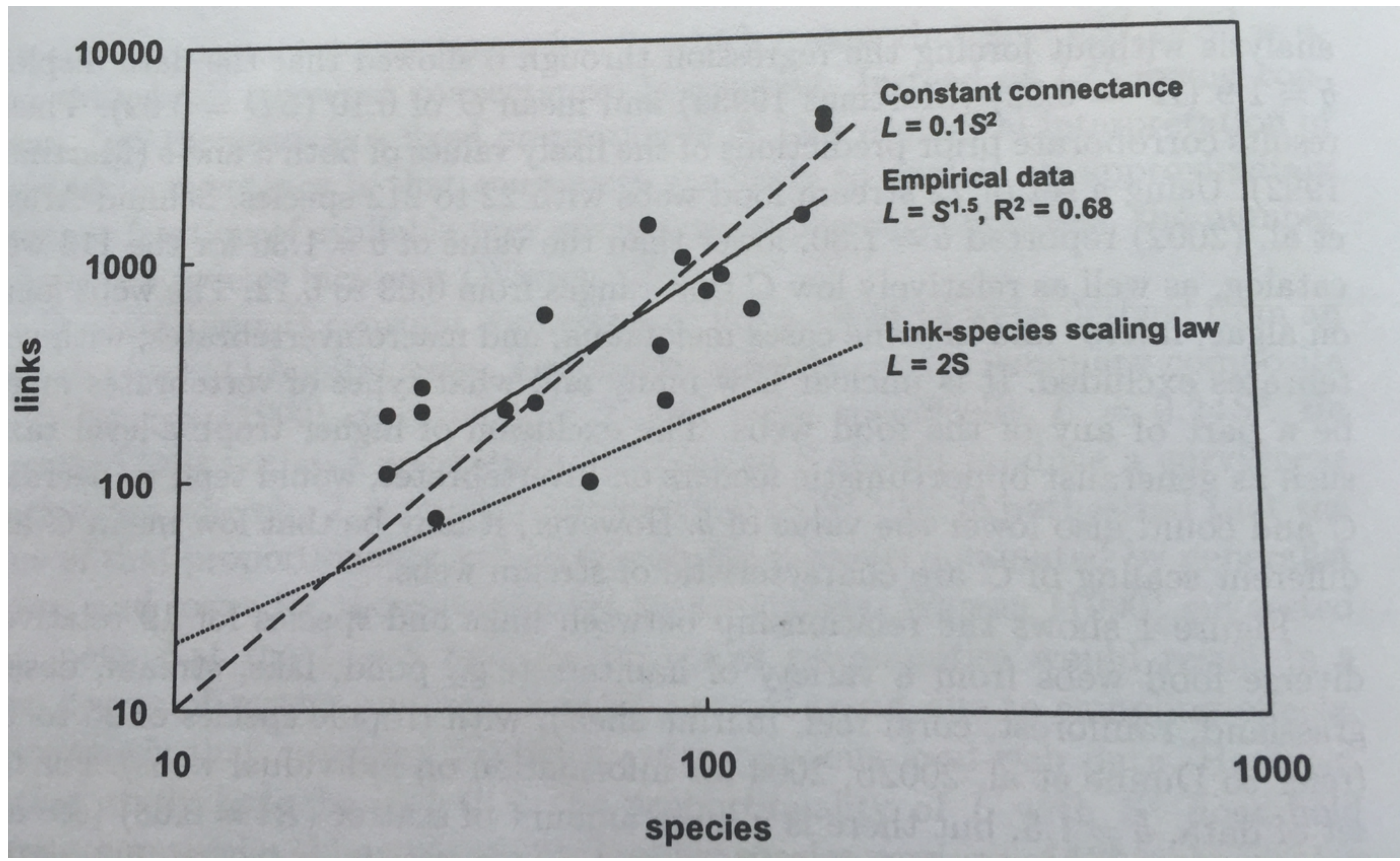
Scale-invariant or Scale-dependent?

Scale-invariant:

Constant link density (L/S) or pred/prey ratios, etc, as the number of species increase
i.e. increasing #links with increasing numbers of species

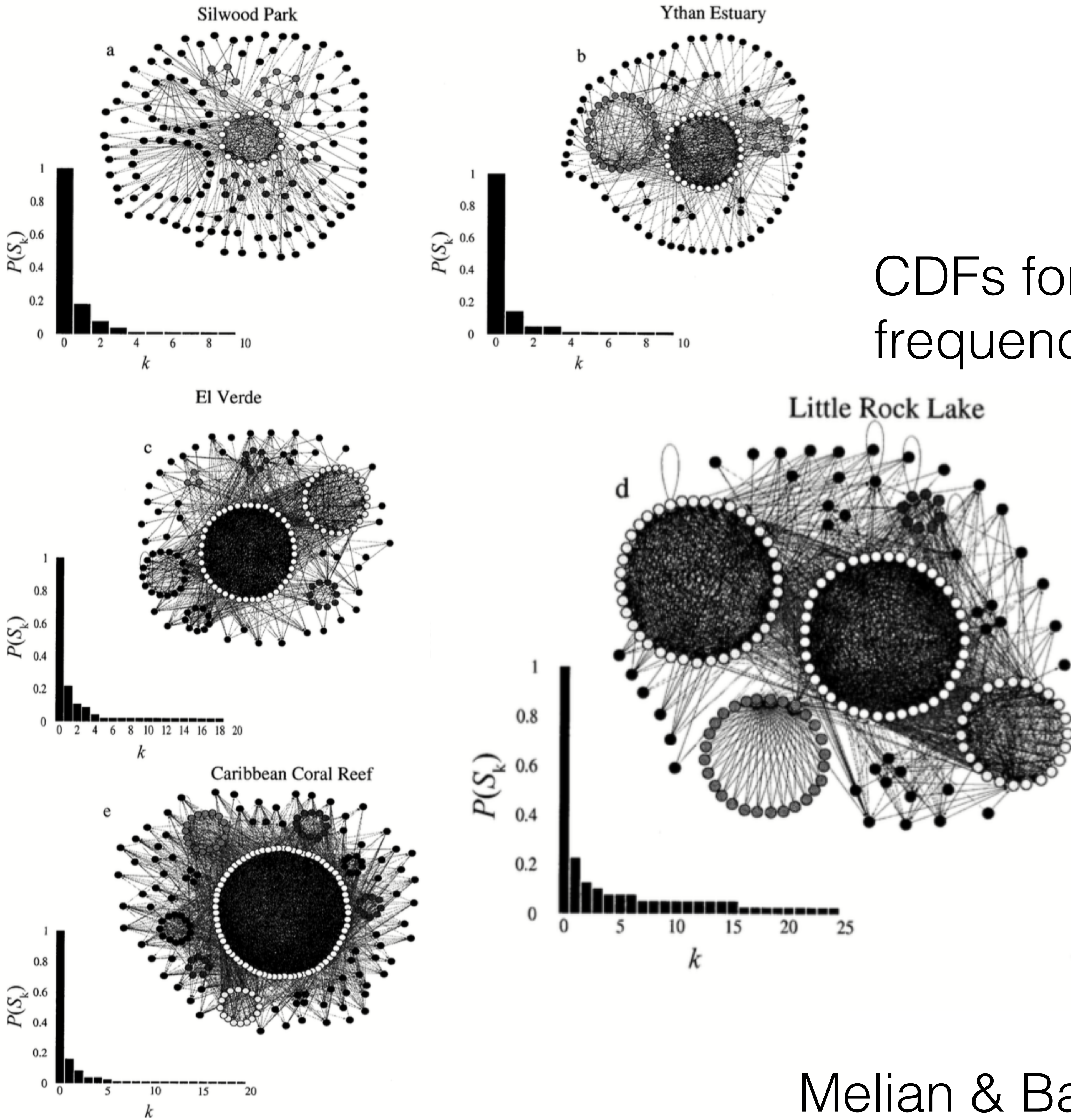
Scale-dependent:

Different link densities (L/S) as well as other structural features for webs of different sizes
There is no universal functional form that describes degree distributions for food web networks



Not a scaling law…
but these are also summary statistics

Dunne 2006



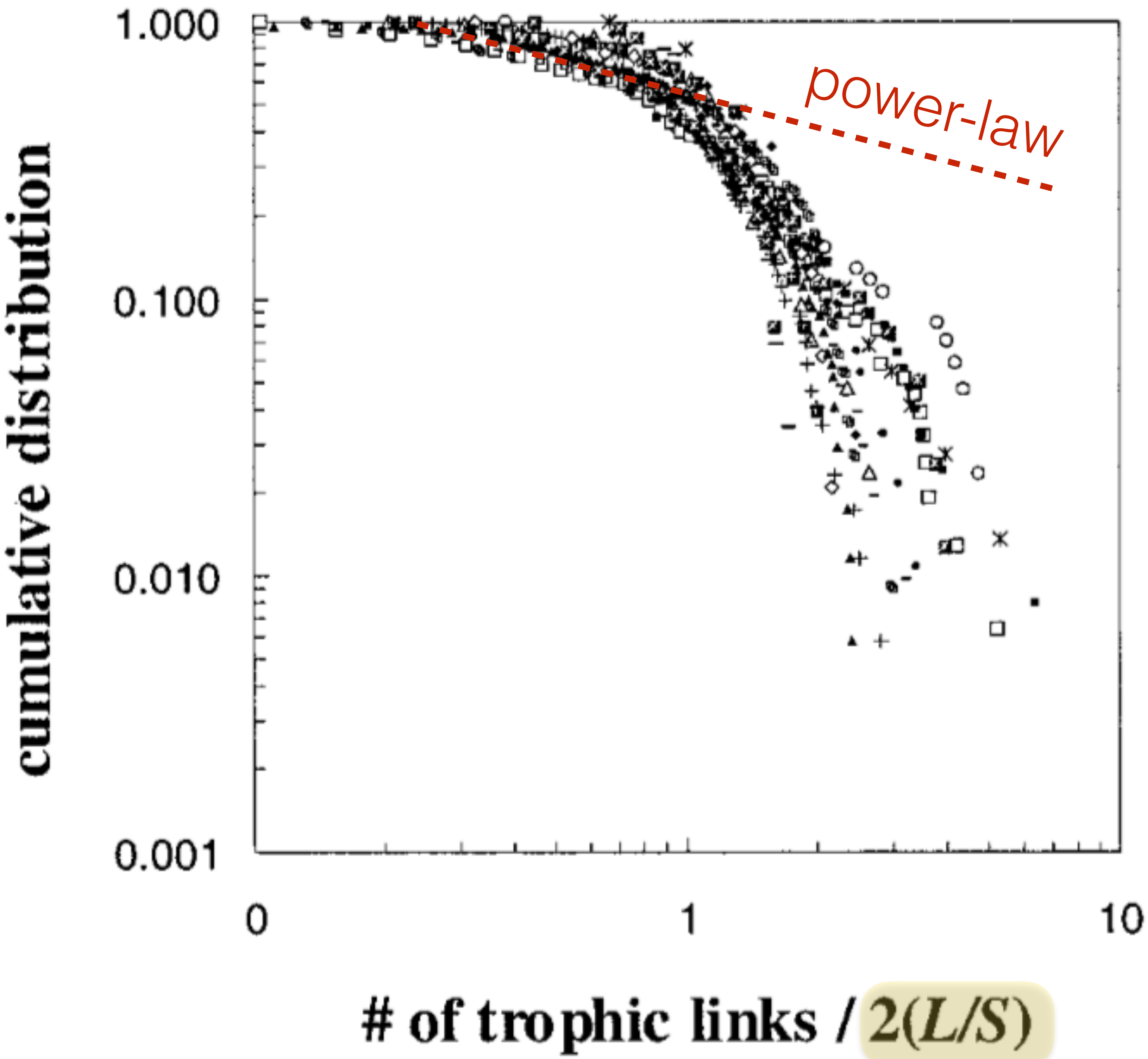
CDFs for k-subweb frequencies

Melian & Bascompte 2004

The structure of trophic interactions within communities

Scaling the CDFs
to 1/2(L/S)…
i.e. controlling for
scale dependence

*Distribution tails fall
off more quickly than
for scale-free nets



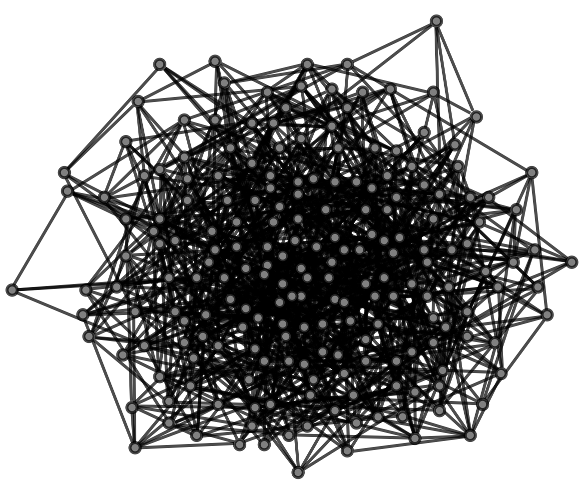
(average degree)

Dunne 2002

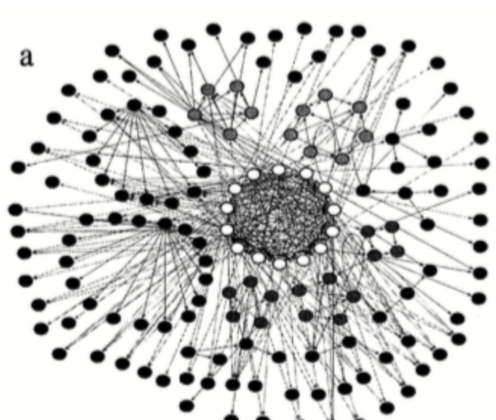
The structure of trophic interactions within communities

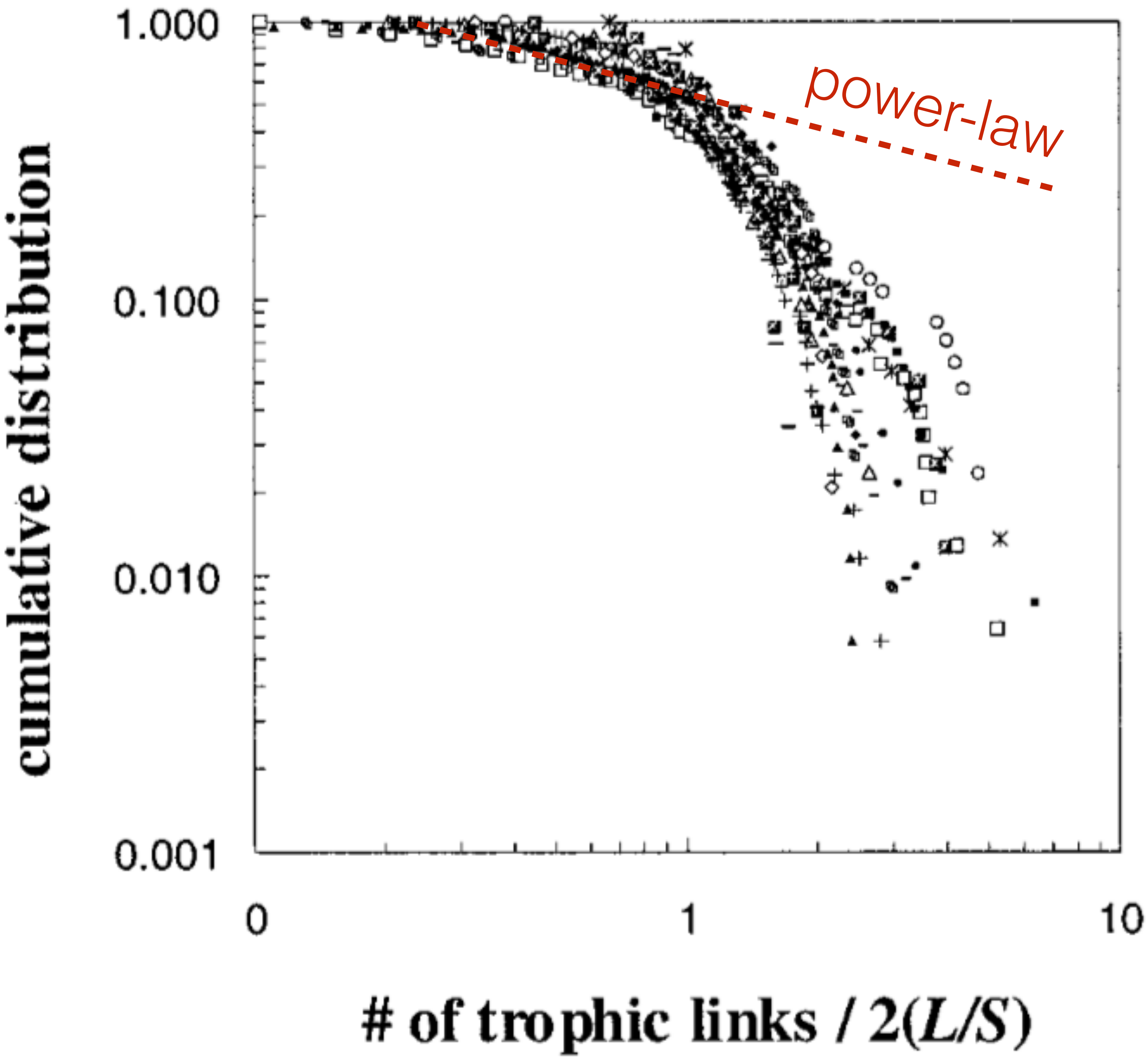
Assembly differences?

preferential attachment
vs.
ecological assembly



vs.

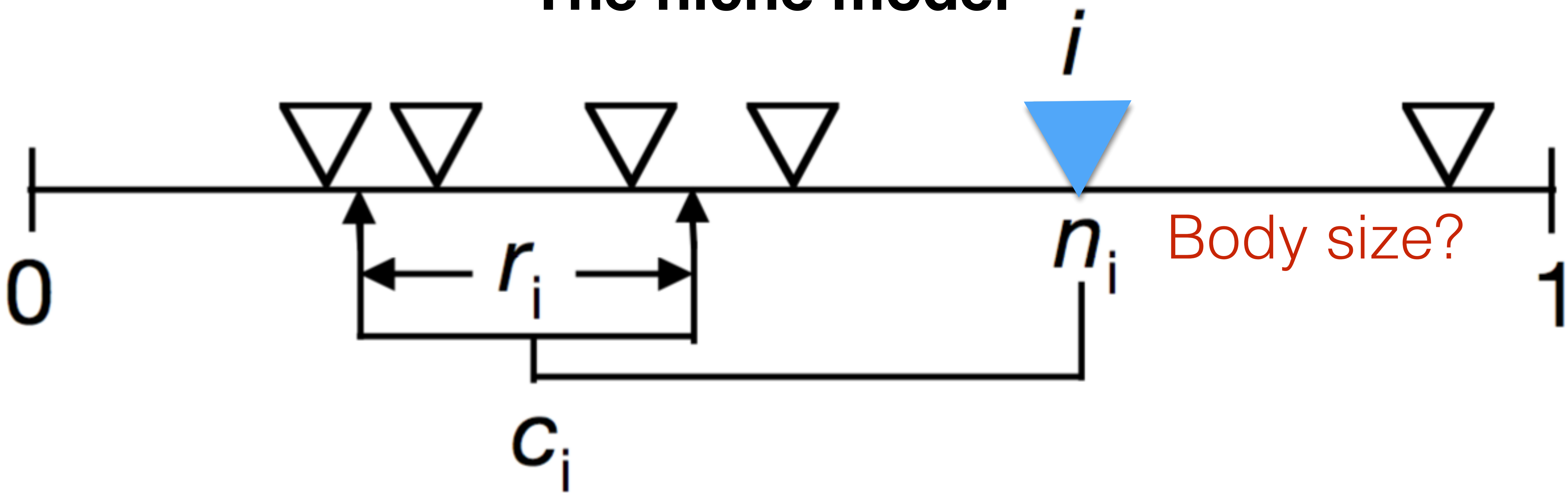




Dunne 2002

A statistical model for food web structure

"The niche model"

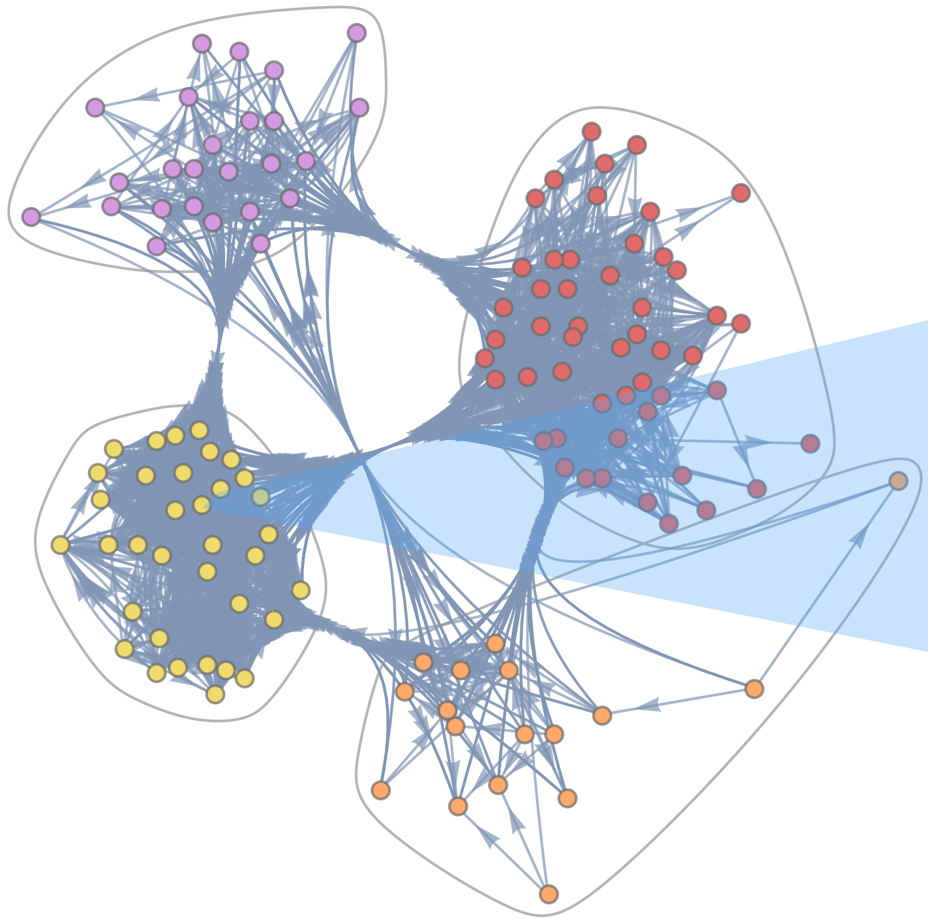


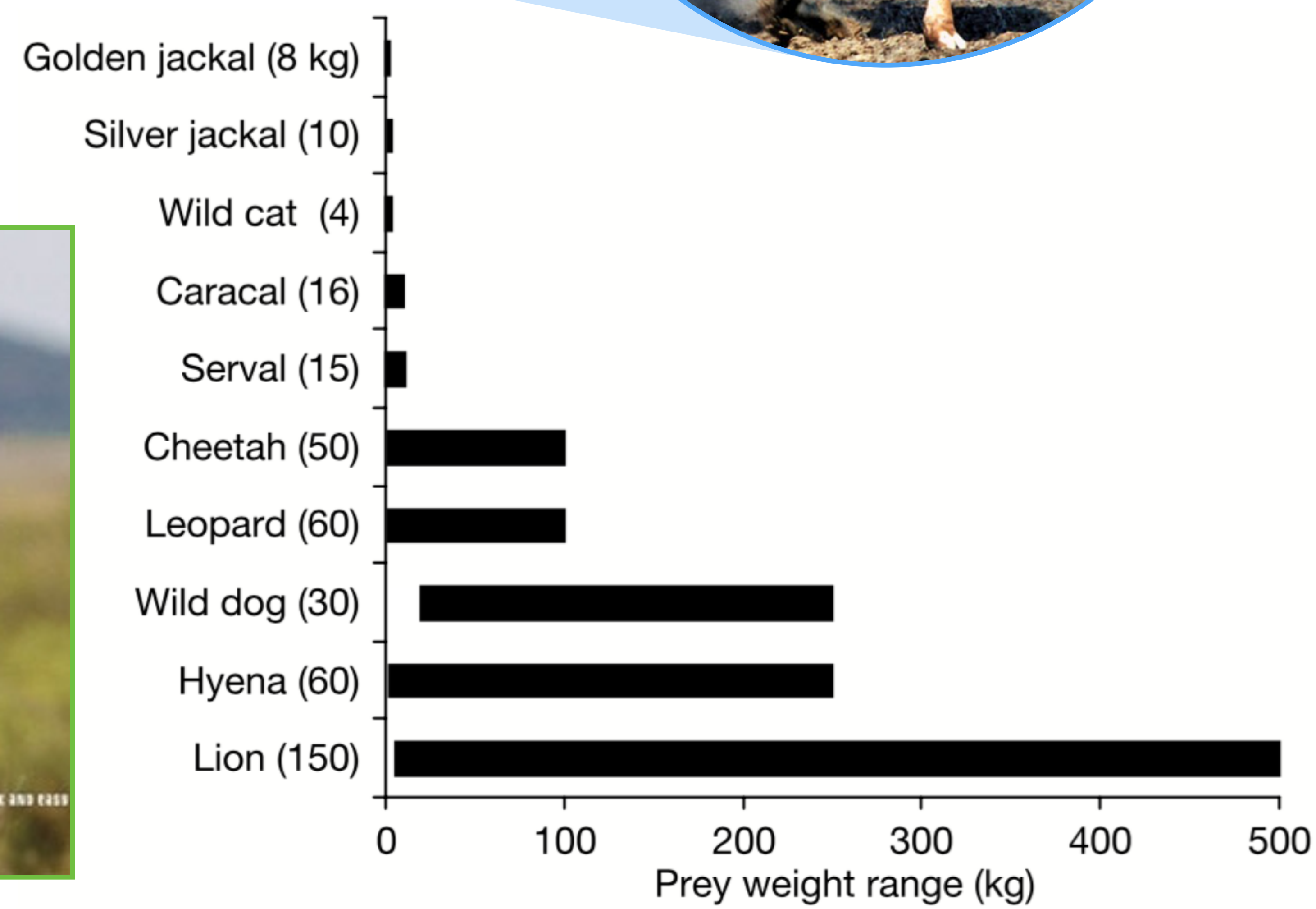
1) Feeding interaction distributed across a niche axis
2) Dietary generality/specialization determined by range
   $r_i = n_i * x_i$ where $x_i \sim \text{Beta}(a=1,b)$ where b is chosen such that system matches observed connectance
3) $c_i \sim \text{Uniform}(r_i/2, n_i)$

Generality increases with n_i!

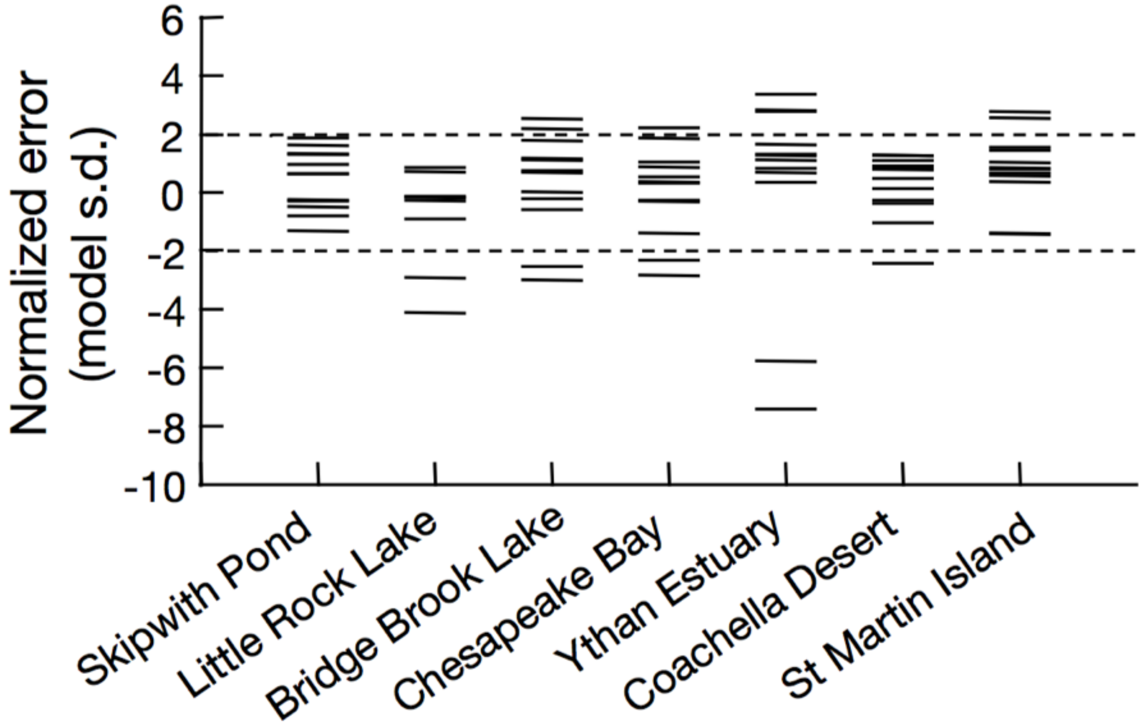
Williams and Martinez 2000

Generality increases with n_i!



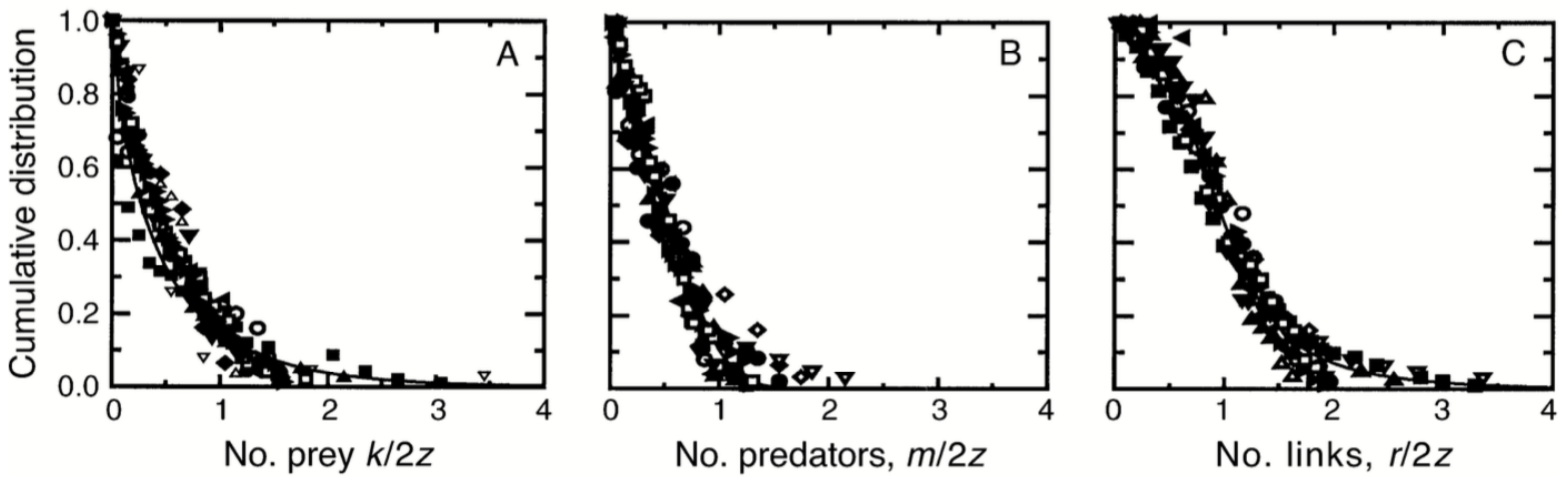


Sinclair et al. 2010



Testing the niche model's ability to replicate various food web properties

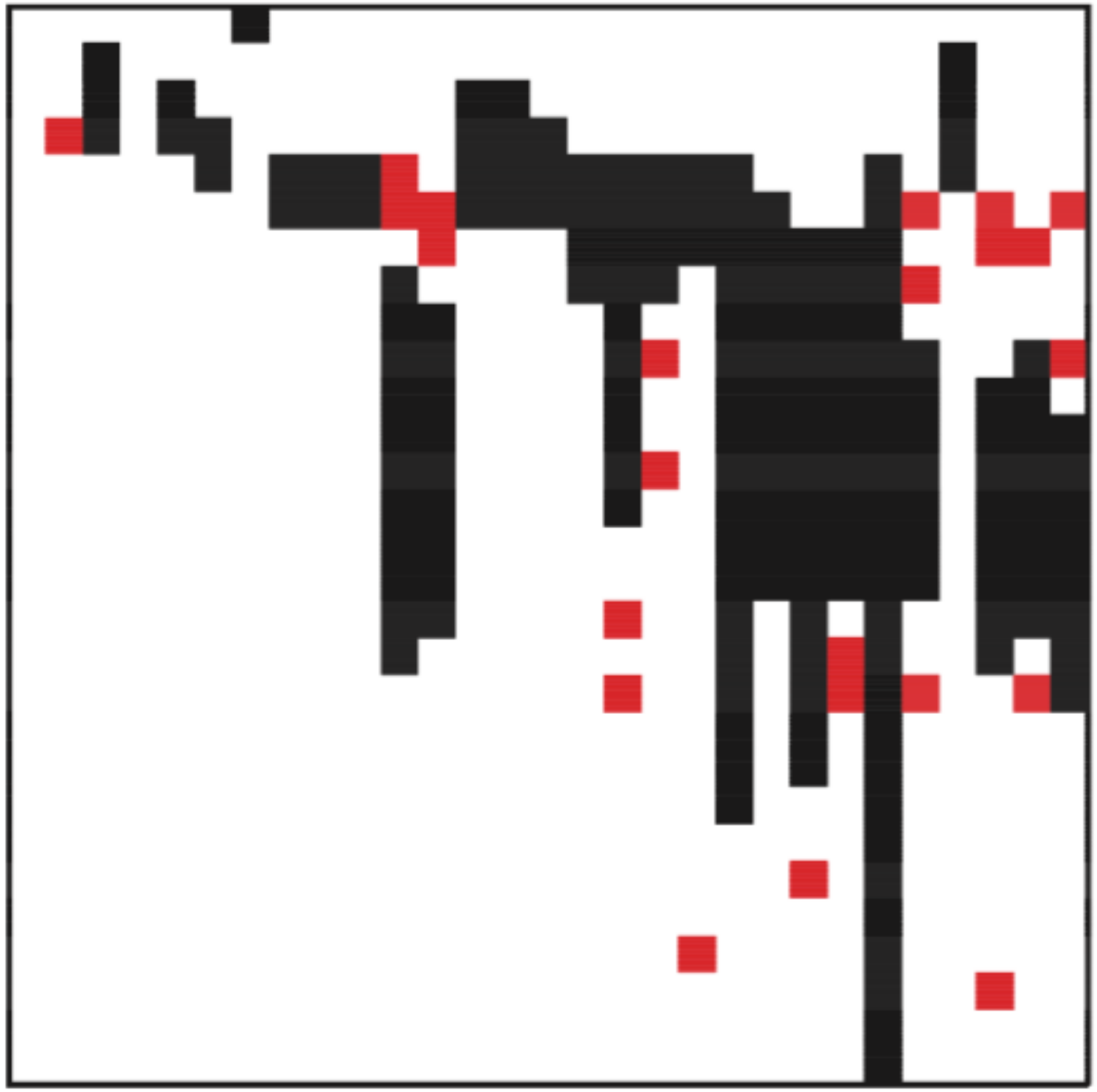
Analytical predictions of the niche model vs. data



Stouffer 2005

here, z=L/S

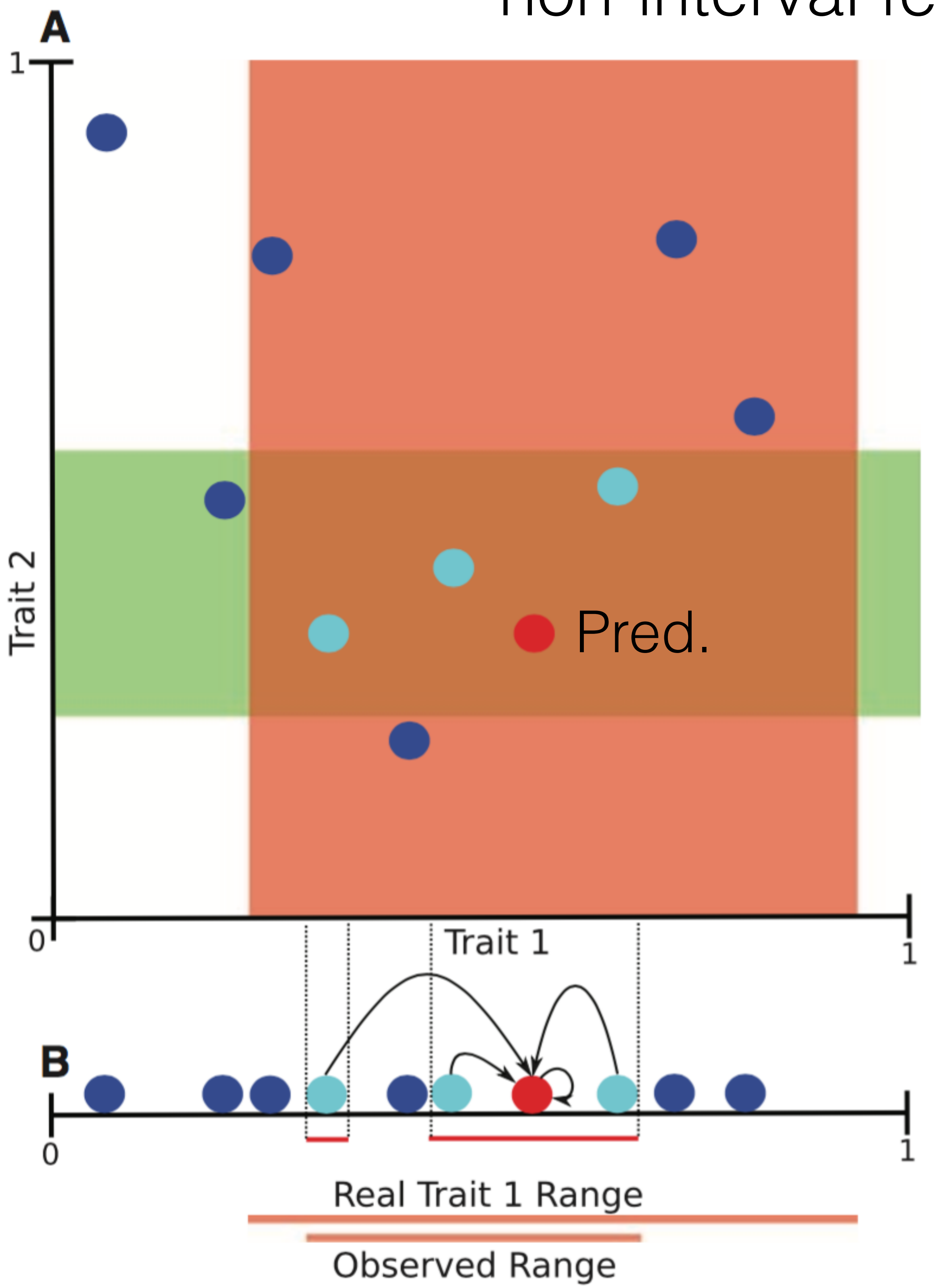
The problem with interval assumptions



Red = interactions incompatible with niche-type models

Allesina 2008

What do we gain from multiple niche dimensions?
non-interval feedings ranges

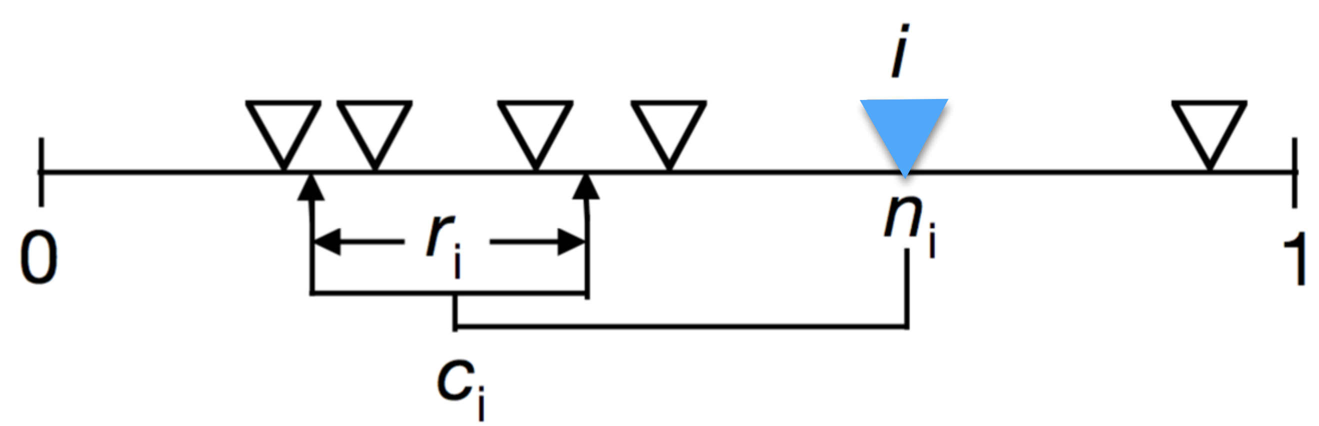


Allesina 2008

Fitting models to data…
The probabilistic niche model (PNM)

Release assumptions about:

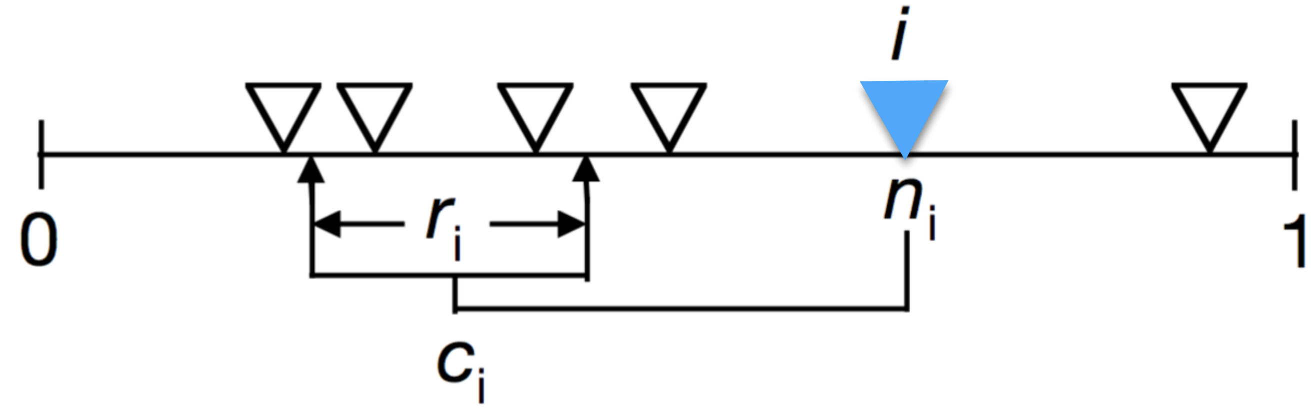
1) distribution of species across n
2) dimensionality of n
3) c_i the center of the dietary range for each species
4) r_i the dietary generalization of each species



Randomly assign $\theta = \{n_{d,i}\ c_{d,i}\ r_{d,i}\} \sim \text{Uniform}(0,1)$

Williams et al. 2009

Fitting models to data…
The probabilistic niche model (PNM)



Randomly assign $\theta = \{n_{d,i}\ c_{d,i}\ r_{d,i}\} \sim$ Uniform(0,1)

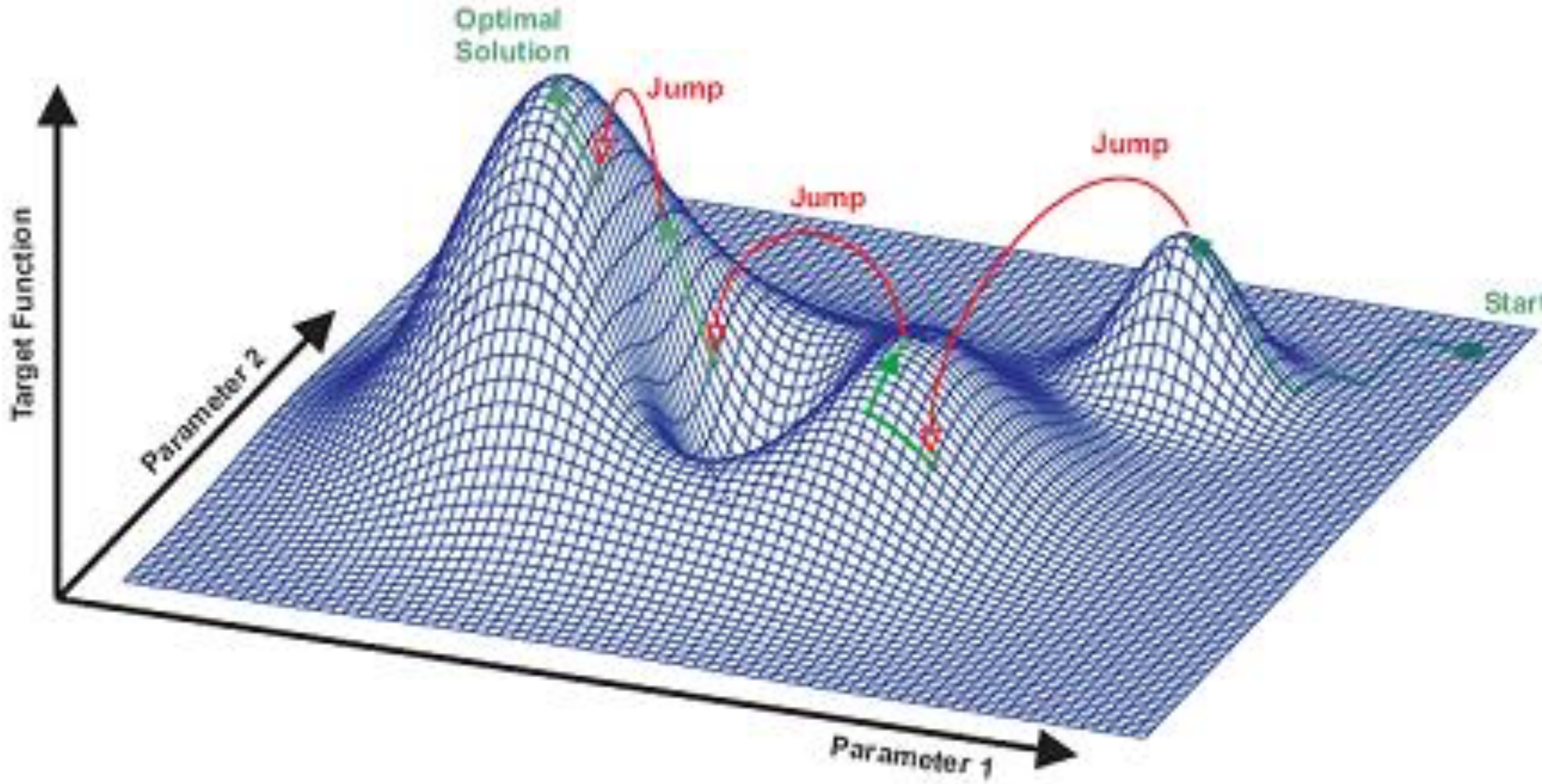
Use simulated annealing algorithm to find Maximum Likelihood Estimate *given* observed set of feeding relationships **A**

$$L(\theta|\mathbf{A}) = \sum_i \sum_j \ln \left\{ \begin{array}{ll} P(i,j|\theta) & \text{if } a_{ij} = 1 \\ 1 - P(i,j|\theta) & \text{if } a_{ij} = 0 \end{array} \right\}.$$

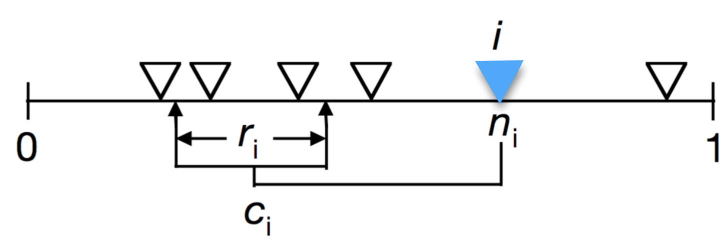
given $$P(i,j\,|\,\theta) = \alpha \prod_{d=1}^{D} \exp\left(- \left| \frac{n_{d,j} - c_{d,i}}{r_{d,i}/2} \right|^e \right)$$

Williams et al. 2009

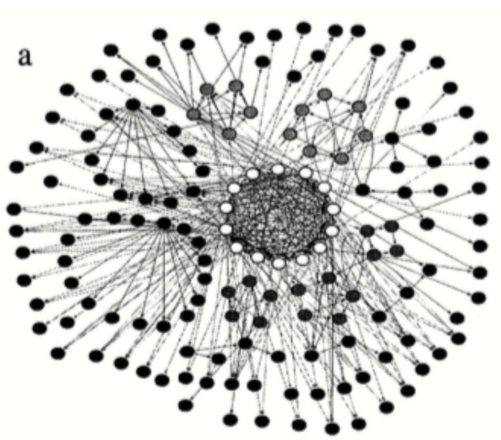
Simulated Annealing



Fitting models to data…
The probabilistic niche model



+



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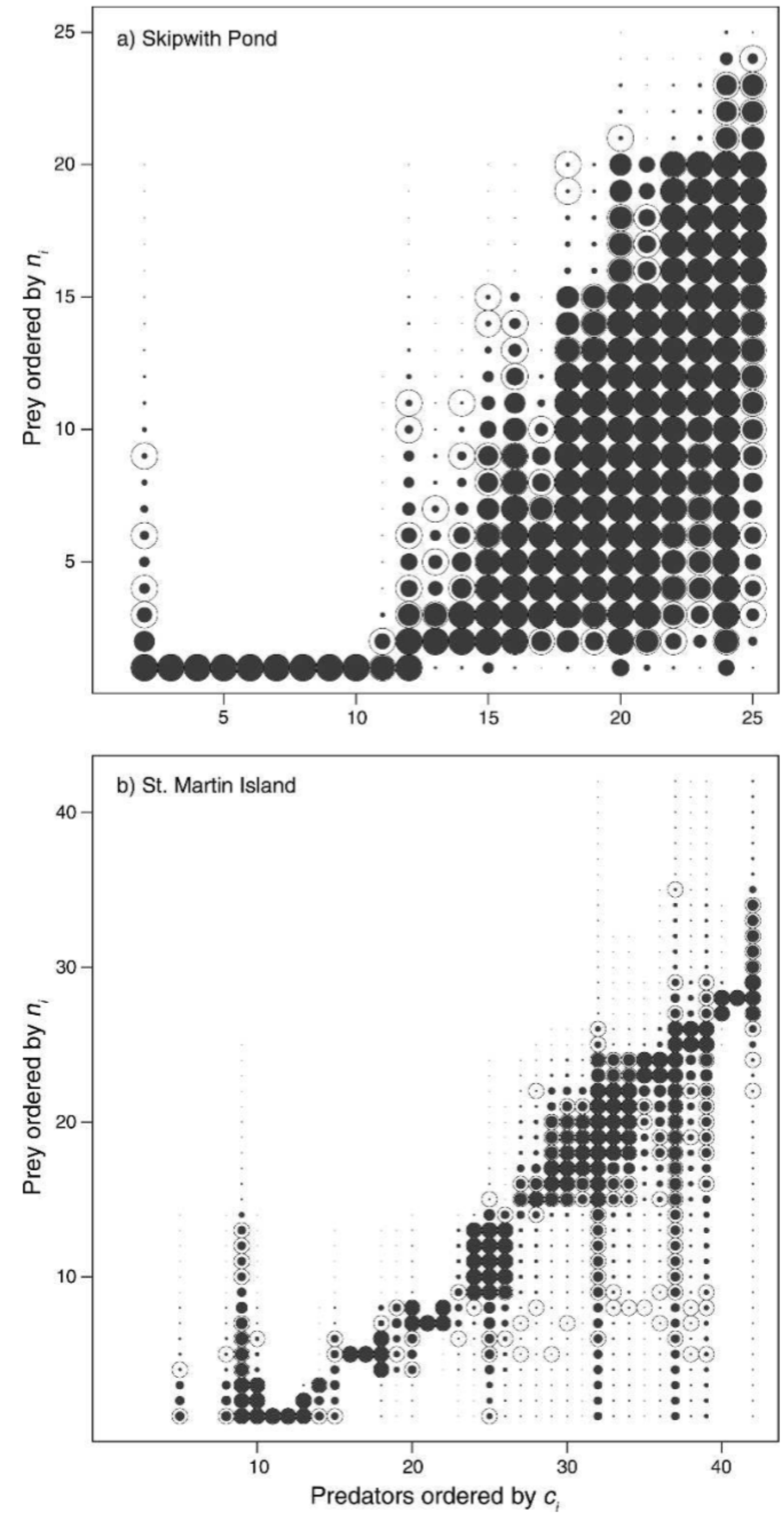
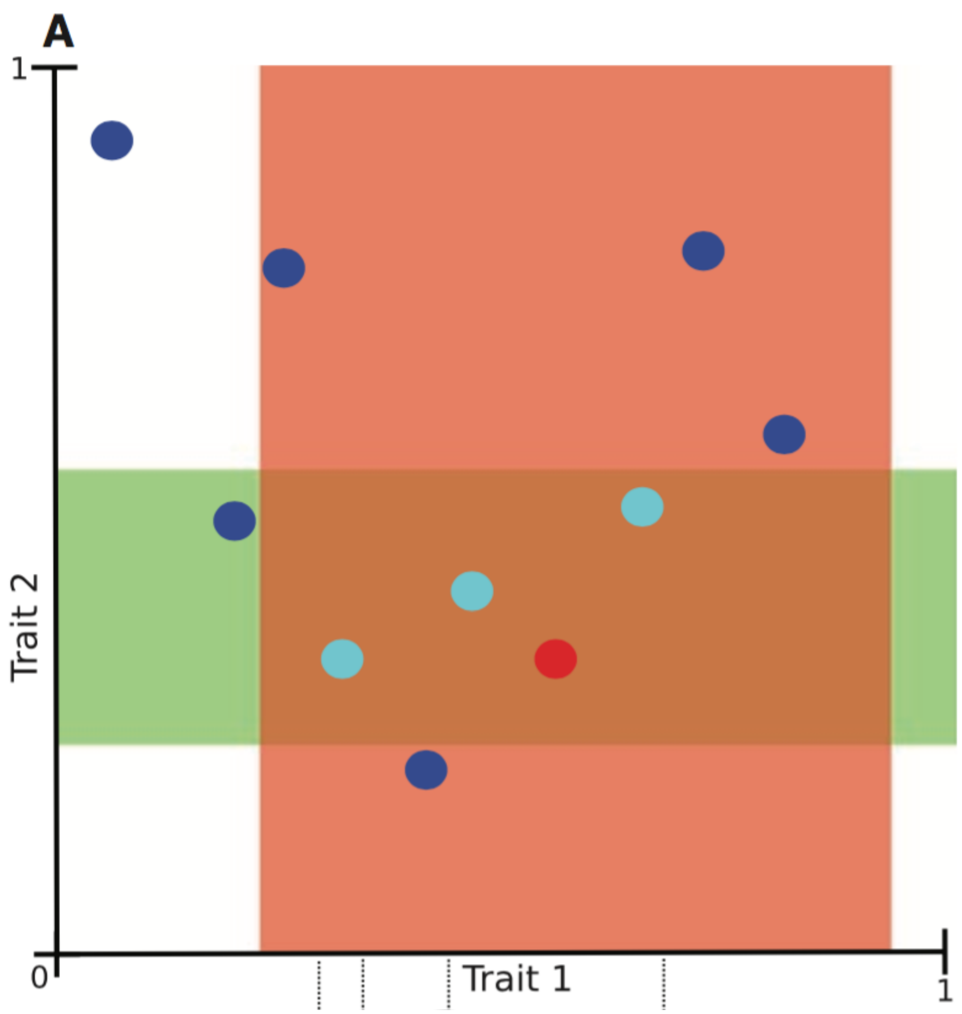


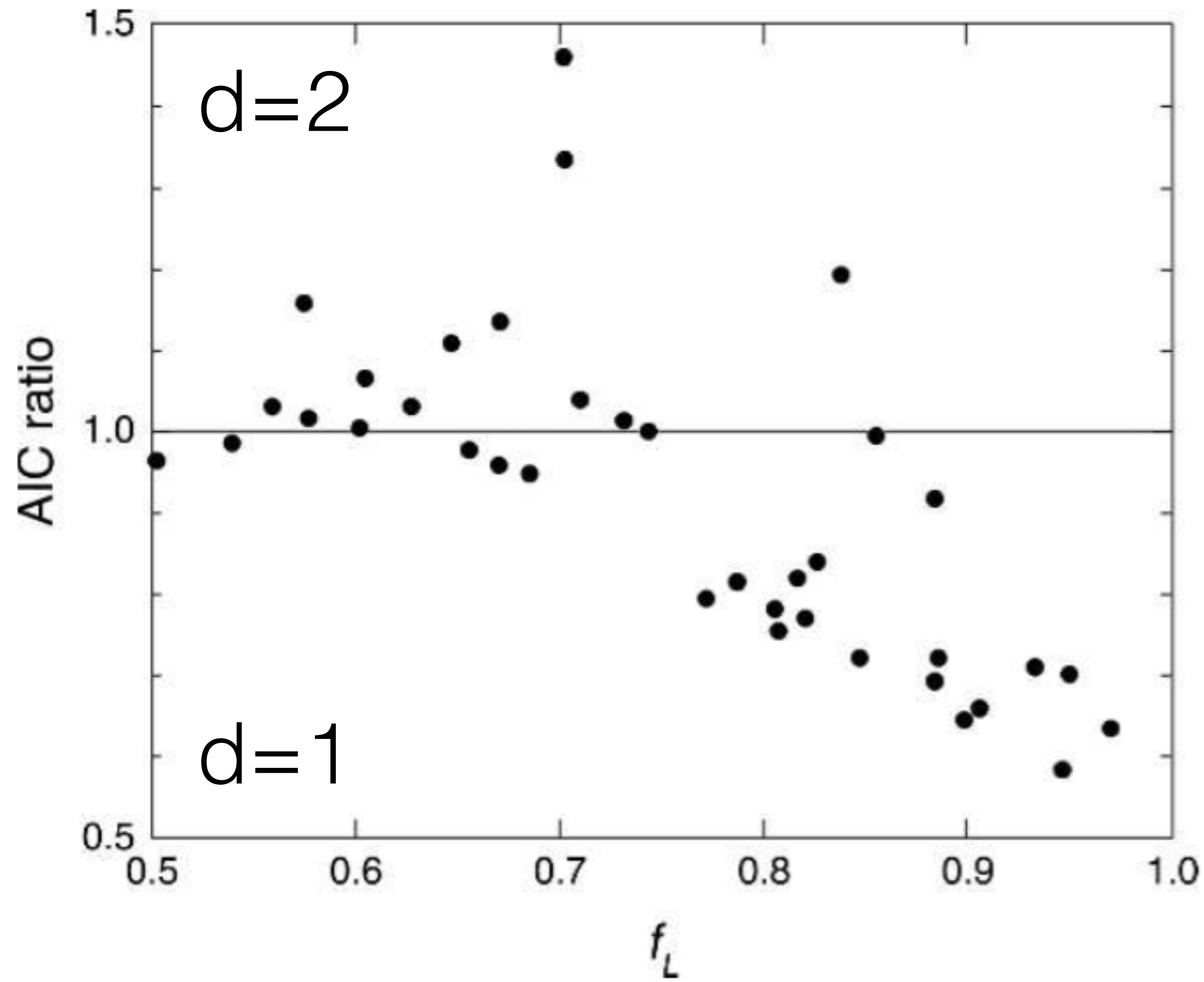
Estimated link probability ●

Measured interaction ○

Williams et al. 2009

How many dimensions are required?





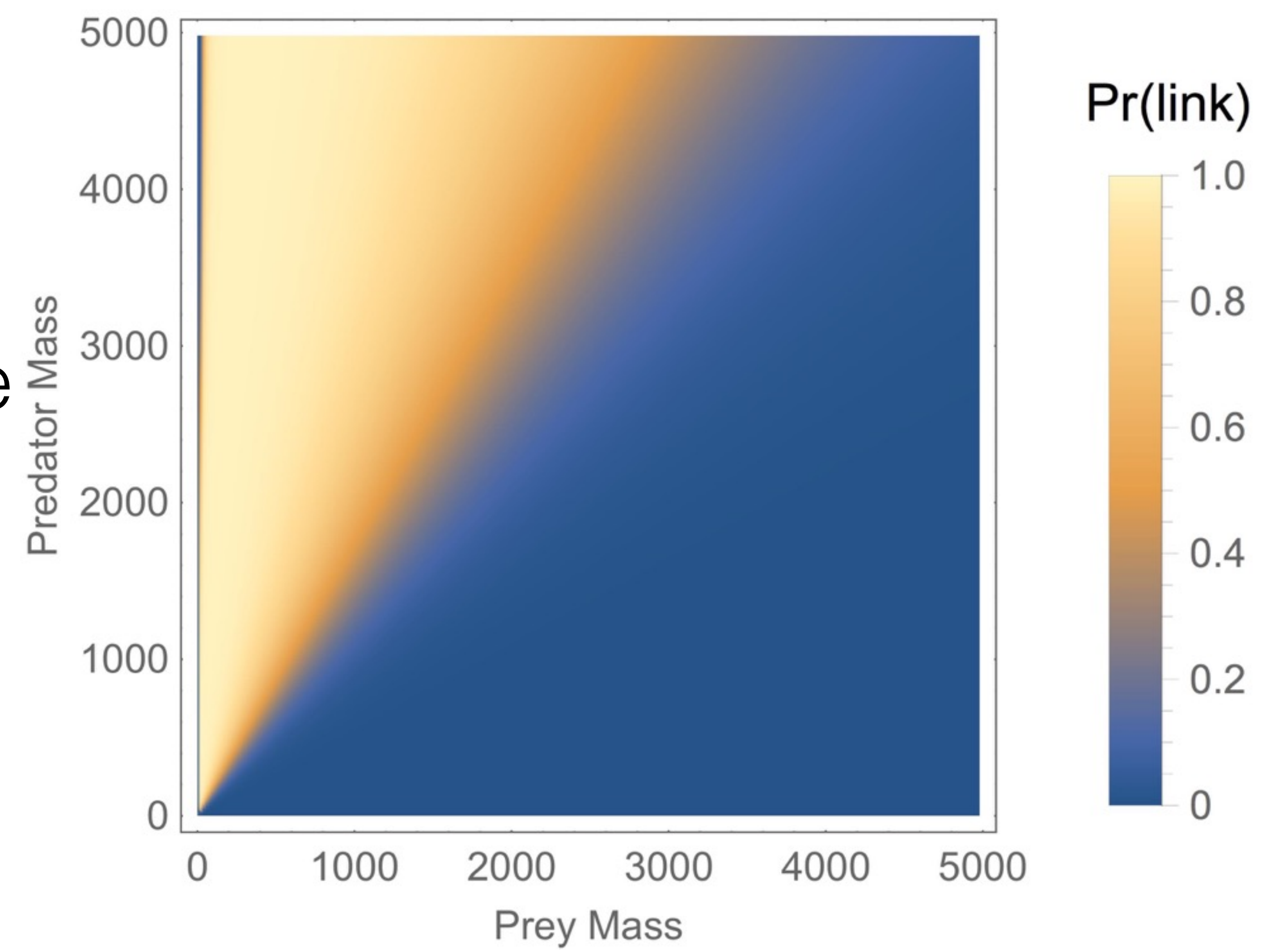
Fraction of links correctly predicted

tend to be
larger webs

tend to be
smaller webs

Fitting models to data…
The Log-Ratio Model (LRM)

Better results, particularly for systems with strong body size constraints (large mammal communities, marine food webs)



m_i = predator mass

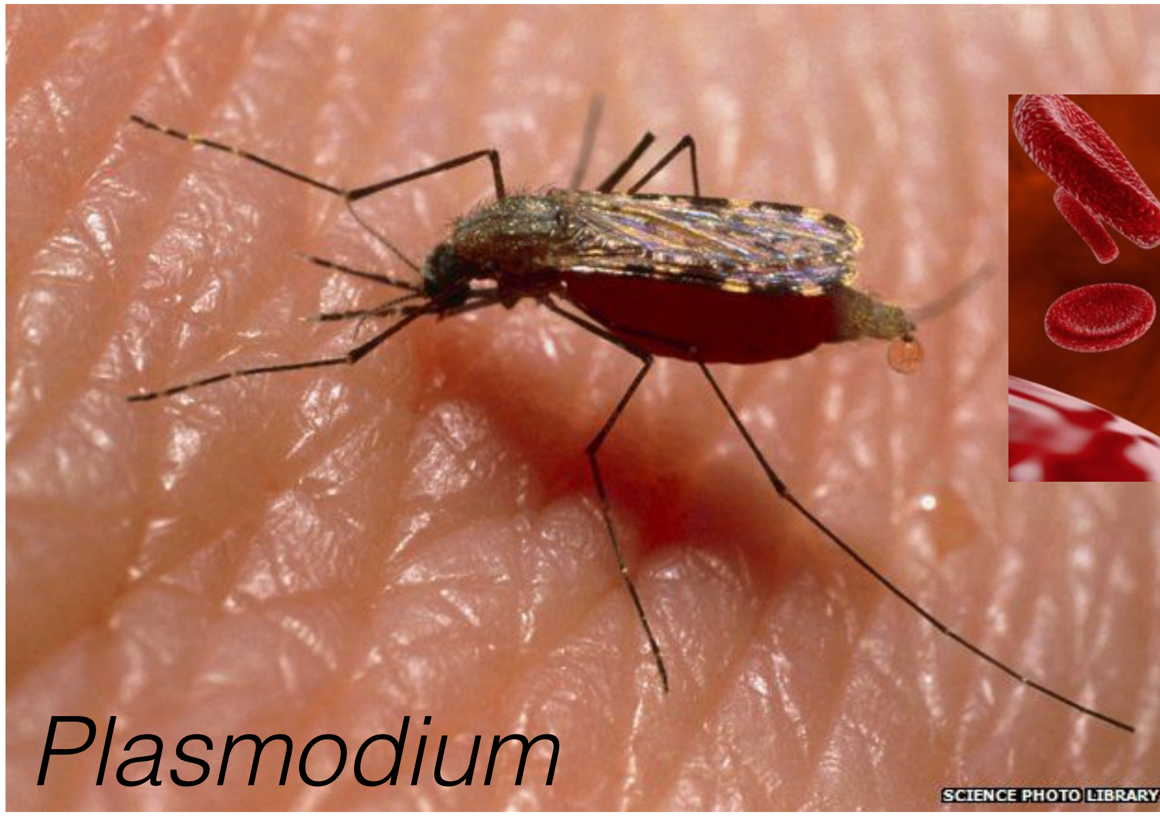
m_j = prey mass

$$\log\left[\frac{P(a_{ij}=1)}{P(a_{ij}=0)}\right] = \alpha + \beta\log\left(\frac{m_i}{m_j}\right) + \gamma\log^2\left(\frac{m_i}{m_j}\right),$$

Interaction probabilities modeled as a Logit regression

Quadratic term allows interaction probabilities to have a Gaussian-like shape

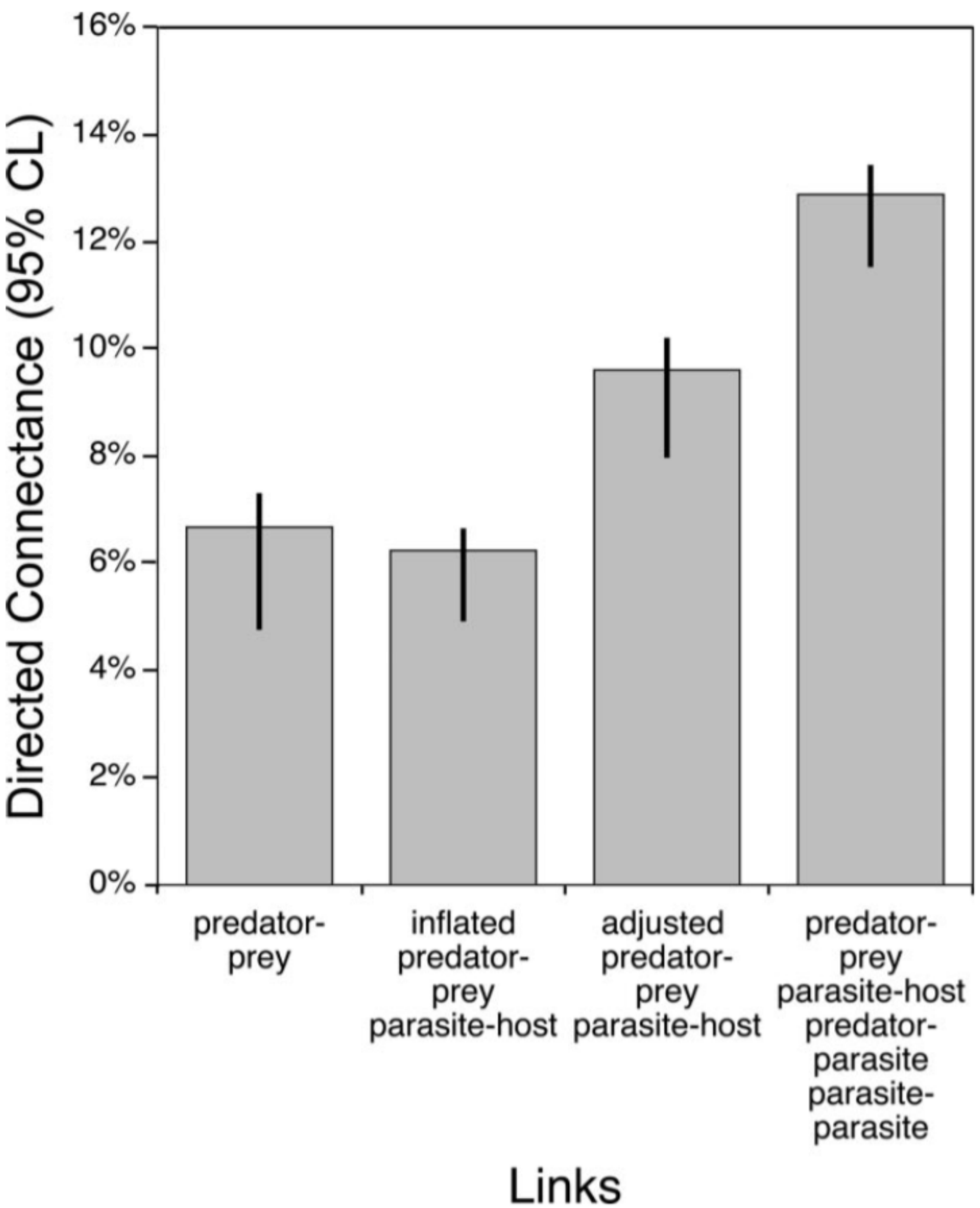
What about the parasites???

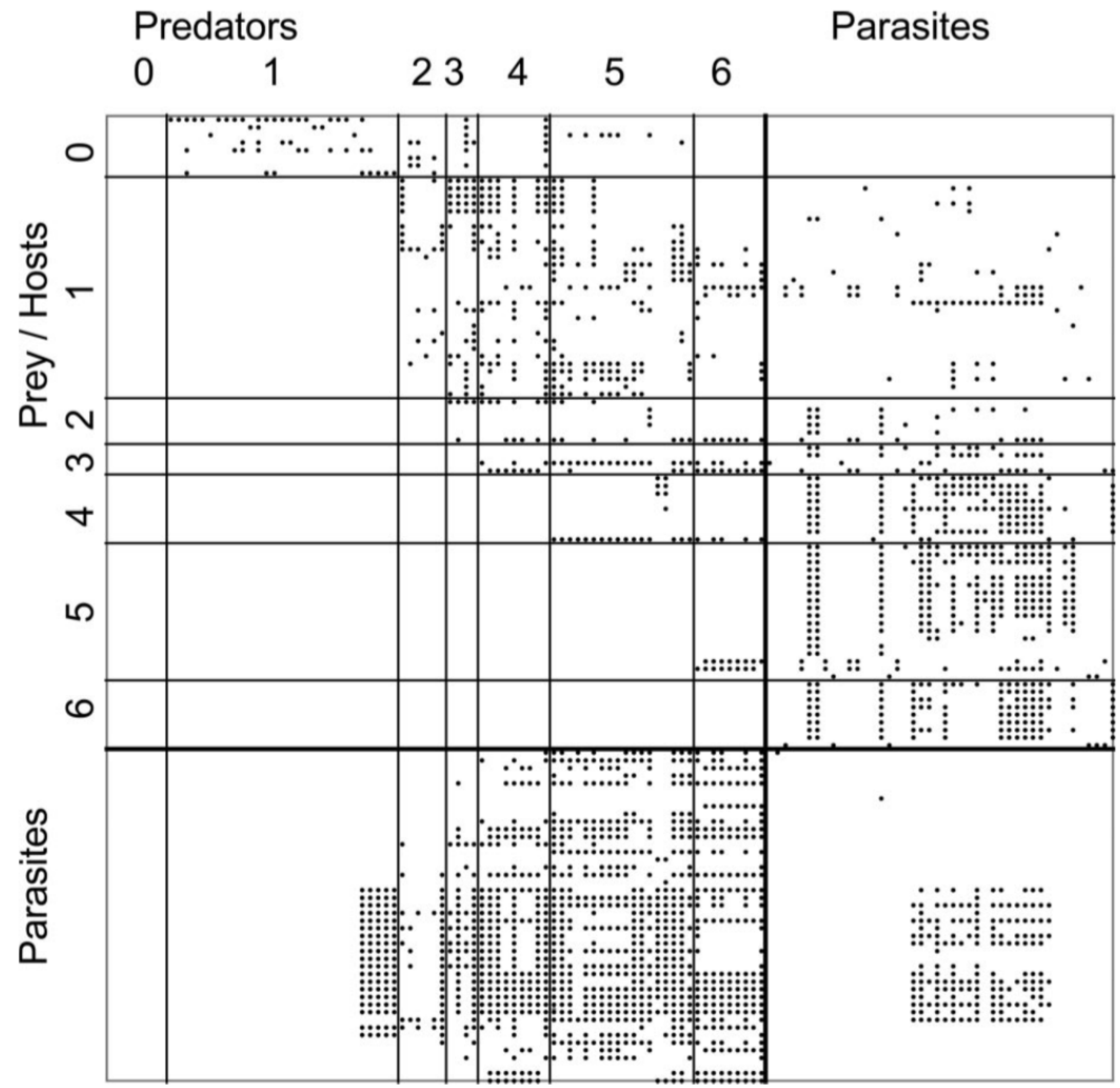


A qualitatively different (+/-) interaction

What about the parasites???

Parasites may dominate food web links





Lafferty et al. 2006

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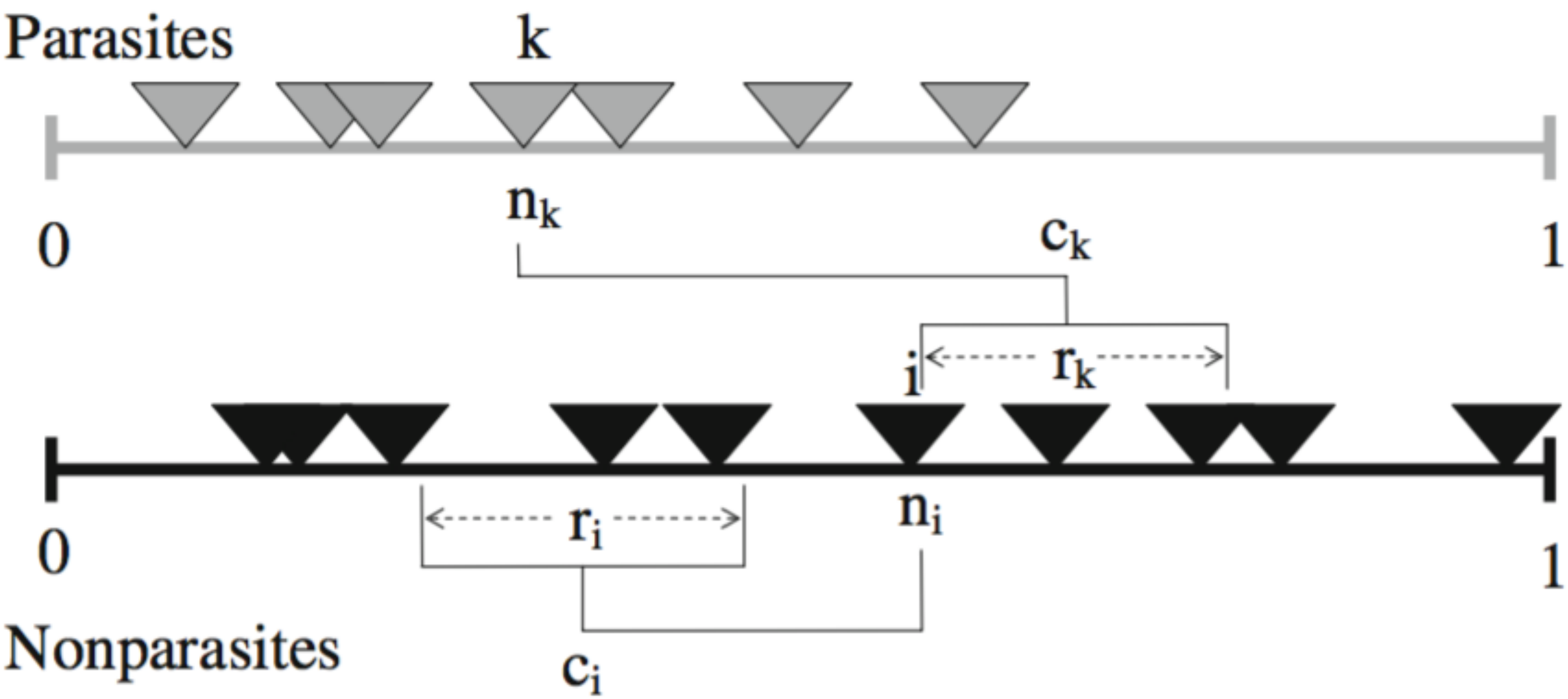

Higher trophic level parasites have **greater** specialization

"…the inclusion of parasites pushes the overall food web structure away from the niche model's expectation."

Warren et al. 2010

Dynamics on food webs

Linear Stability

$$\frac{\mathrm{d}}{\mathrm{dt}}x = f(x), \quad x^* \text{ is fixed point}$$

$$x(t) = x^* + \eta(t)$$

$$\eta(t) = x(t) - x^*$$

$$\frac{\mathrm{d}}{\mathrm{dt}}\eta(t) = \frac{\mathrm{d}}{\mathrm{dt}}(x(t) - x^*) = \frac{\mathrm{d}}{\mathrm{dt}}x(t)$$

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$$f(x^* + \eta) = f(x^*) + \eta f'(x^*) + \text{h.o.t.}$$

$$\frac{\mathrm{d}}{\mathrm{dt}}\eta = \eta \left.\frac{\partial f}{\partial x}\right|_{x^*}$$

$$\eta = \exp\left(\left.\frac{\partial f}{\partial x}\right|_{x^*} t\right)$$

$$\lambda = \left.\frac{\partial f}{\partial x}\right|_{x^*}$$

→ >0 unstable

→ <0 stable

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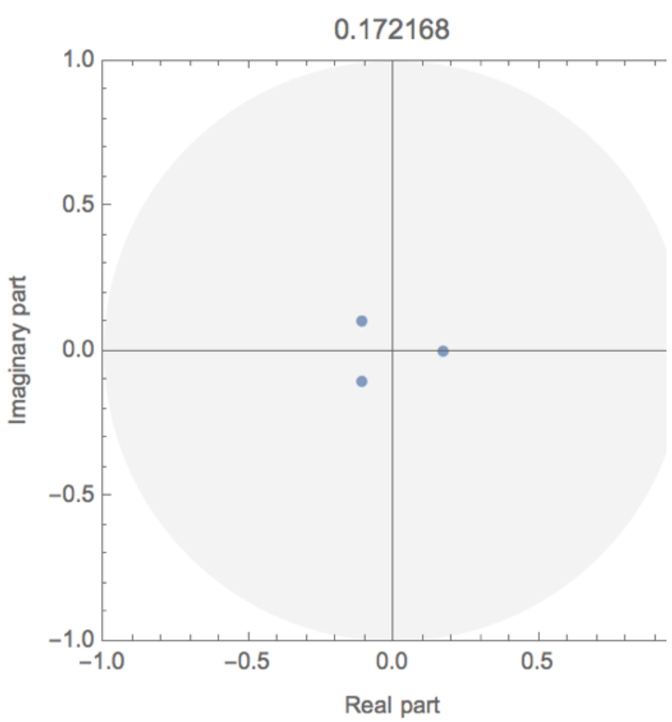
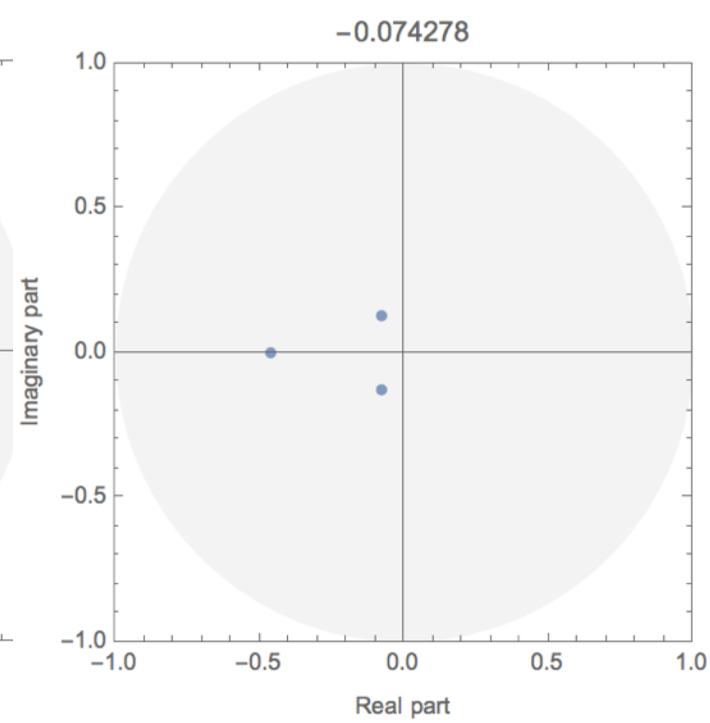
Multi-dimensional Systems

$$\mathbf{J}|_* = \begin{pmatrix} \left.\frac{\partial F}{\partial X}\right|_* & \left.\frac{\partial F}{\partial Y}\right|_* & \left.\frac{\partial F}{\partial Z}\right|_* \\ \left.\frac{\partial G}{\partial X}\right|_* & \left.\frac{\partial G}{\partial Y}\right|_* & \left.\frac{\partial G}{\partial Z}\right|_* \\ \left.\frac{\partial H}{\partial X}\right|_* & \left.\frac{\partial H}{\partial Y}\right|_* & \left.\frac{\partial H}{\partial Z}\right|_* \end{pmatrix}$$



unstable



stable

Dynamics on food webs

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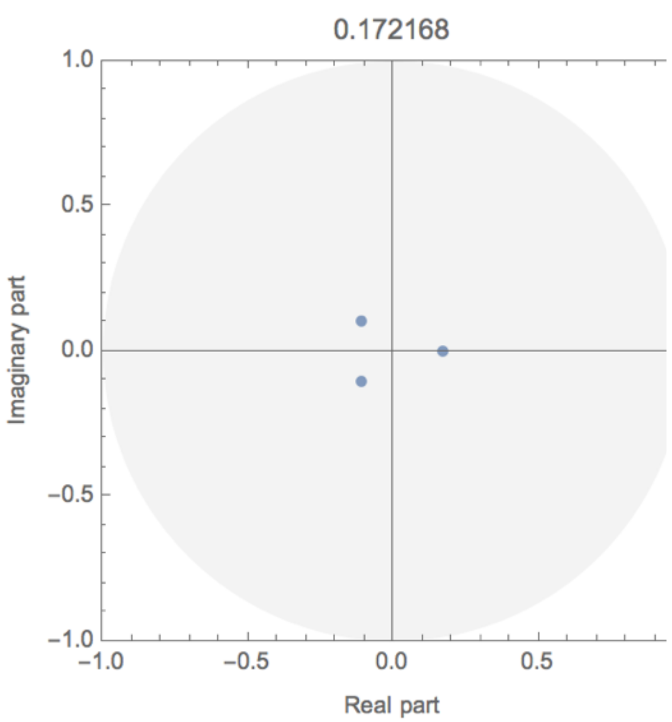
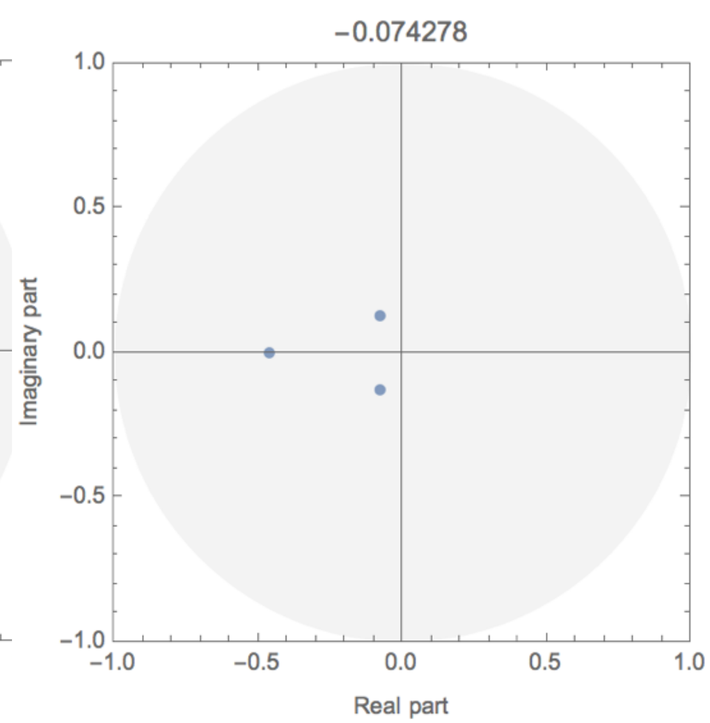


unstable



stable

Trophic interactions on random graphs

'Will a large complex system be stable?'

(May 1972)

M = SxS adjacency matrix

Diag(**M**) = -1

offDiag(**M**) ~ Norm(0,$\boldsymbol{\sigma}^2$) w/ Pr(C)

offDiag(**M**) = 0 w/ Pr(1-C)

Big finding:

Pr(Stability) → 0 when

$$\sigma\sqrt{SC} > 1$$

big, complex ecosystems shouldn't exist

Different types of interactions in the food web

Trophic interactions on random graphs
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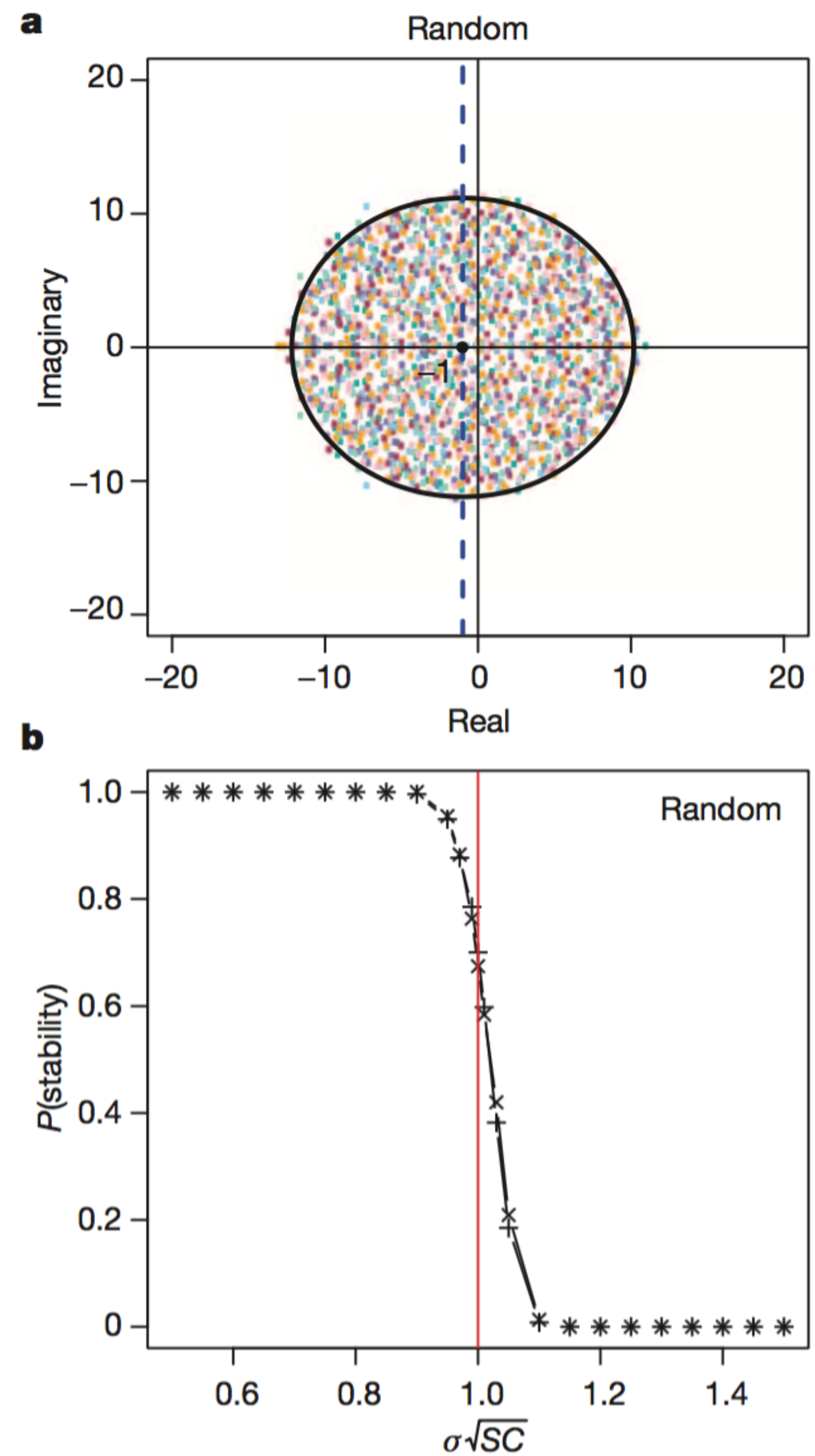
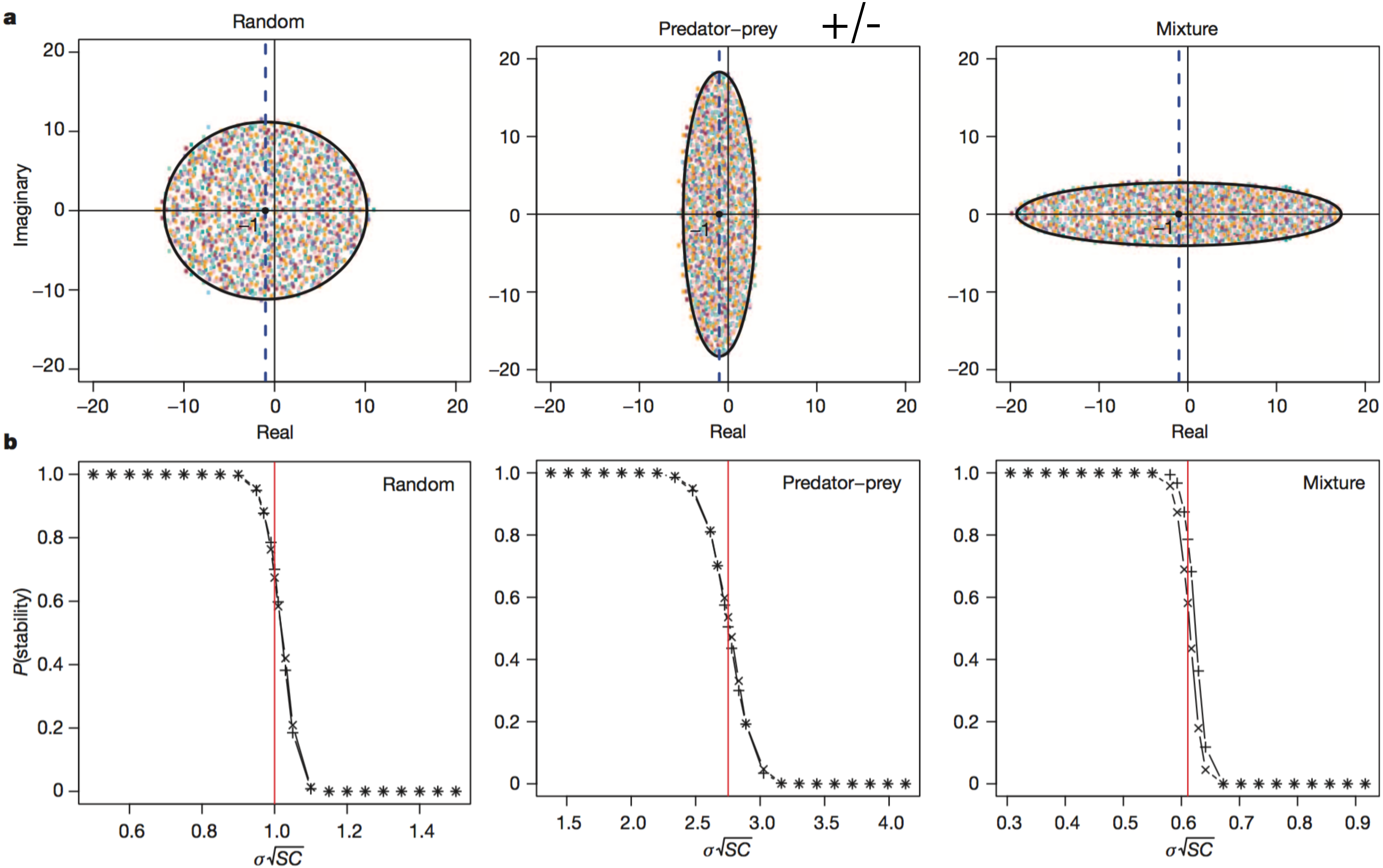


Allesina & Tang 2012

Different types of interactions in the food web

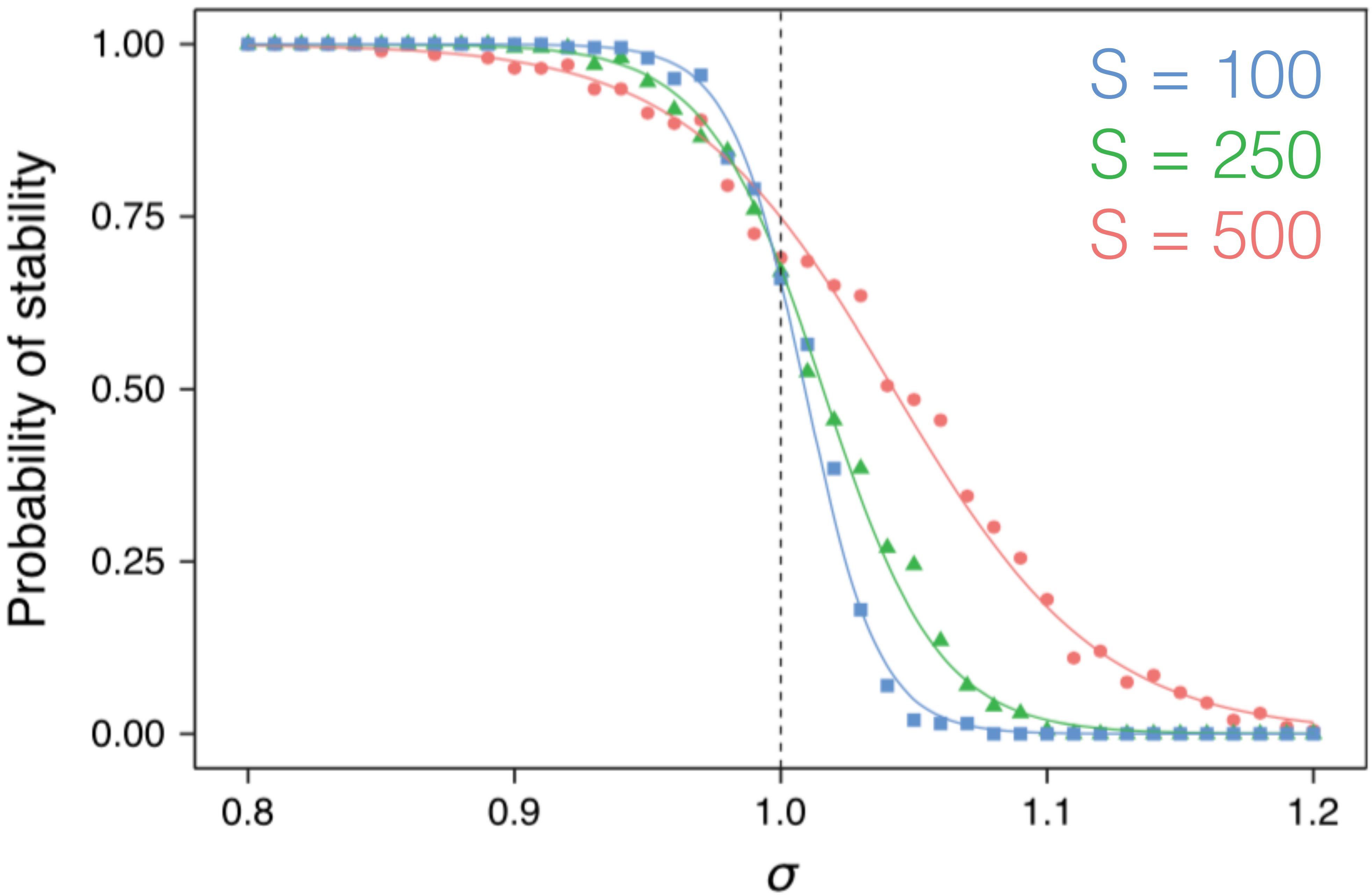
predator/prey: +/-
mutualism: +/+



Allesina & Tang 2012

Across different values of $\boldsymbol{\sigma}$

(interaction strength variability)



Random matrix approaches to food webs
may be missing some important constraints

Dynamic modeling via simulations to
explore things like **adaptive foraging**

Energetics:
Optimal/Adaptive foraging

search

acquire

consume

— gains vs. costs —

Adaptive foraging and food webs

Realism vs. Complexity

$$\frac{\mathrm{d}}{\mathrm{dt}}X_i = X_i\left(r_i - s_iX_i + \sum_{j\in \mathrm{res.}} e_{ij}f_{ij}a_{ij}X_j - \sum_{j\in \mathrm{cons.}} f_{ji}a_{ji}X_j\right)$$

growth rate

self-regulation intensity

met. rate

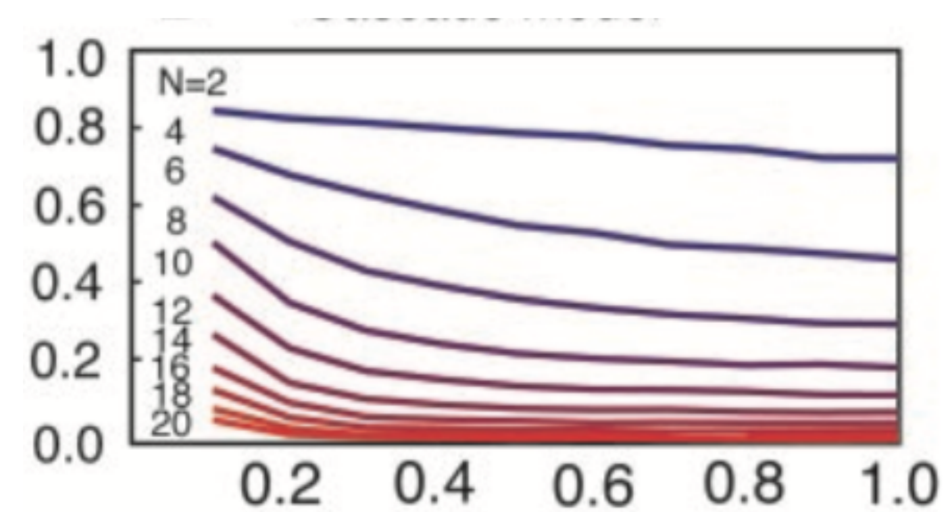
efficiency

foraging effort of consumer j on resource i

The effort is itself dynamic, and changes in response to changing resource densities

If resource profitability (i.e. energy gain per unit effort) is higher than an 'average profitability', the effort increases

w/o a



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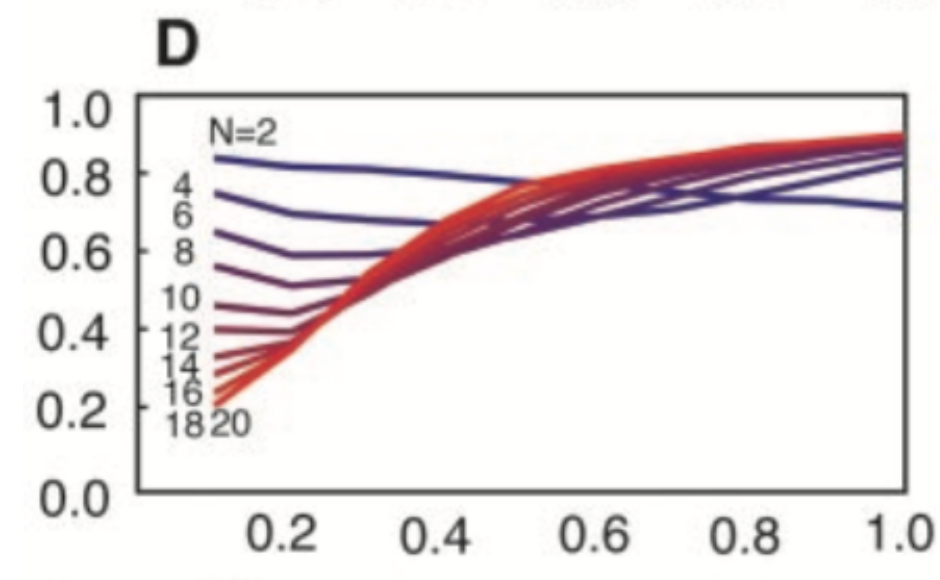


Kondoh 2003

Realism vs. Complexity

And intermediate between specific models and random matrix theory

Generalized modeling

(Source) (Drain)

$$\frac{\mathrm{d}}{\mathrm{dt}}B = S(B) - D(B)$$

Recruitment Mortality

Keep it GENERAL…
More 'accurate' wrt our knowledge
Can't simulate or solve for the f.p.

Gross et al. 2006
Yeakel et al. 2011

Establish B^* as a variable representing all *internal* equilibria of the system.

Build a new set of parameters representing the normalized variables of the generalized system:

$$\frac{\mathrm{d}}{\mathrm{dt}}B = S(B) - D(B)$$

$$\frac{\mathrm{d}}{\mathrm{dt}}b = \frac{S^*}{B^*}s(b) - \frac{D^*}{B^*}d(b)$$

$$b := \frac{B}{B^*}, \quad s(b) := \frac{S(B)}{S(B^*)}, \quad \text{and} \quad d(b) := \frac{D(B)}{D(B^*)}$$

$$\gamma = \frac{S^*}{B^*} = \frac{D^*}{B^*}$$

Rewrite in terms of *b*

$$\frac{\mathrm{d}}{\mathrm{dt}}b = \gamma(s(b) - d(b))$$ **PERTURB**

γ: biomass turnover rate

Gross et al. 2006
Yeakel et al. 2011

Stability of the generalized model

$$\frac{\partial}{\partial b}\dot{b} = \lambda = \frac{\partial}{\partial b}\gamma\left(s(b) - d(b)\right)$$

$$\frac{\partial}{\partial b}s(b) = s_b = \left.\frac{\partial \log S}{\partial \log B}\right|_* \sim \frac{\text{\% change in S}}{\text{\% change in B}}$$

Functional elasticities are the logarithmic derivatives

**Provides a nonlinear measure for the sensitivity of the function to variations in biomass

Elasticity of growth

$$\lambda = \gamma(s_b - d_b)$$

Elasticity of mortality

Gross et al. 2006
Yeakel et al. 2011

Elasticities characterize whole families of functional forms

$F(X) = c_1$	$\frac{\partial f(x)}{\partial x} = 0$	Constant	(independent gain / loss)
$F(X) = c_2 X$	$\frac{\partial f(x)}{\partial x} = 1$	Linear	(intrinsic growth)
$F(X) = -c_3 X^2$	$\frac{\partial f(x)}{\partial x} = 2$	Superlinear	(self limitation)

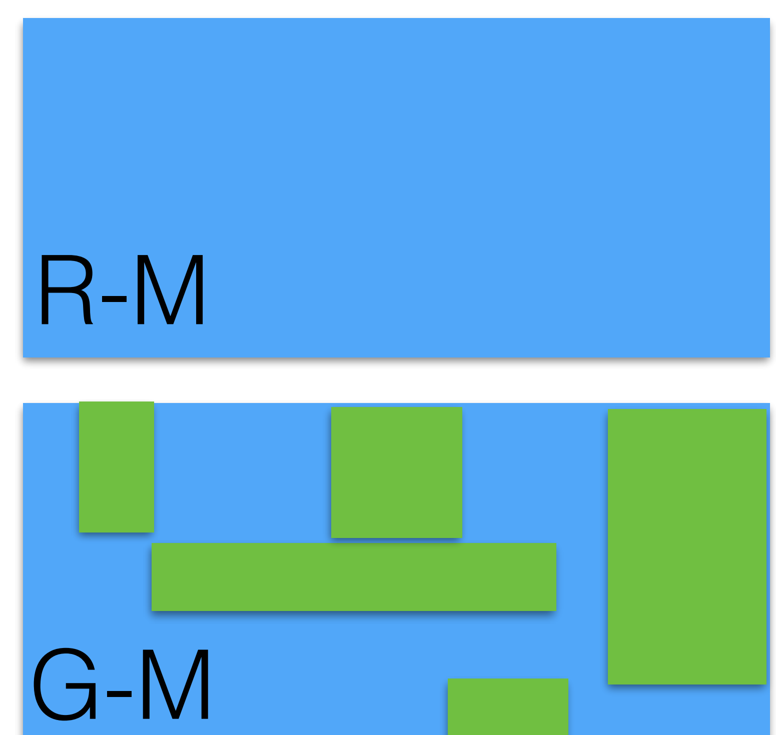
Additional benefits

-Sets realistic bounds to parameters that will go into the Jacobian**

-Depend on the state of the system at the time a measurement is made

-Error tolerant

More complex functions have elasticities as functions of the steady state

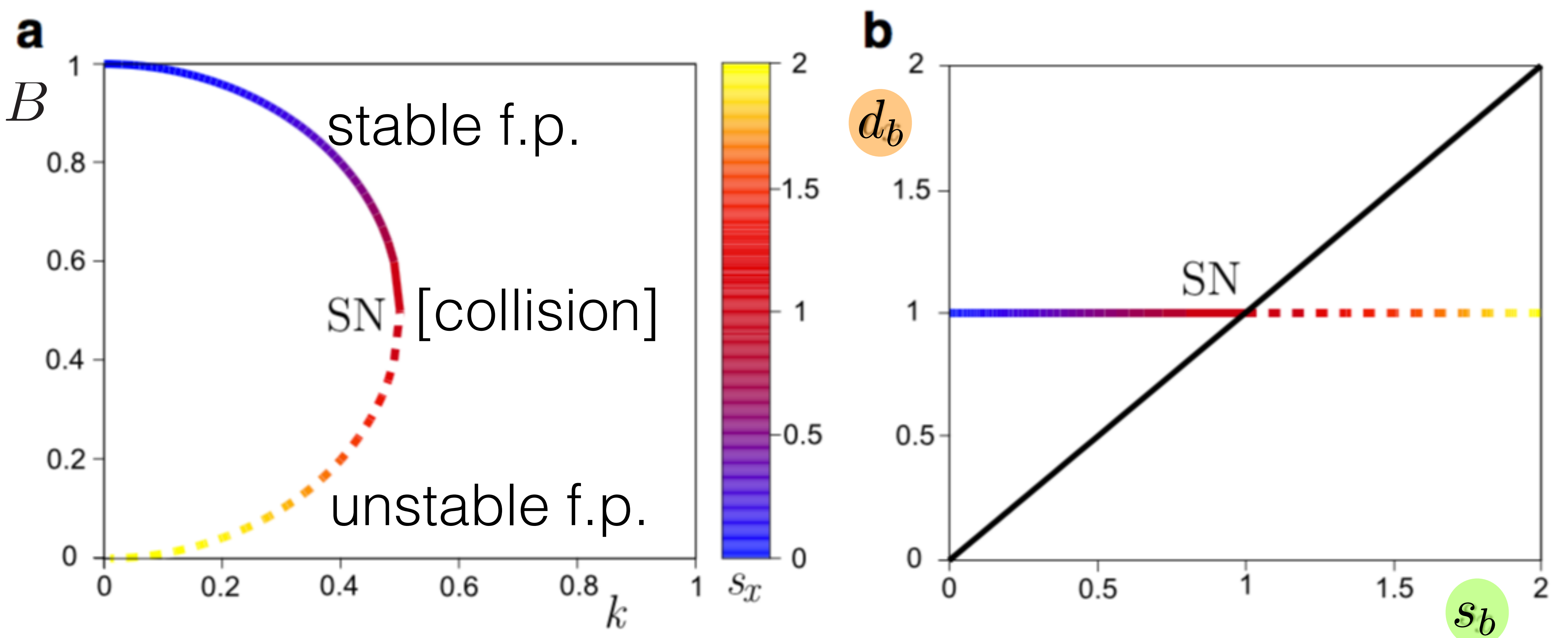


Gross et al. 2006
Yeakel et al. 2011

$$\frac{\mathrm{d}}{\mathrm{dt}}B = \frac{aB^2}{k^2 + B^2} - mB \qquad \frac{\mathrm{d}}{\mathrm{dt}}B = S(B) - D(B)$$

k = half-saturation value of growth

$$\lambda = \frac{\partial}{\partial b}\gamma\left(s(b) - d(b)\right) = \gamma\left(s_b - d_b\right)$$



Yeakel et al. 2011

Realism vs. Complexity

And intermediate between specific models and random matrix theory

Generalized modeling on a larger scale

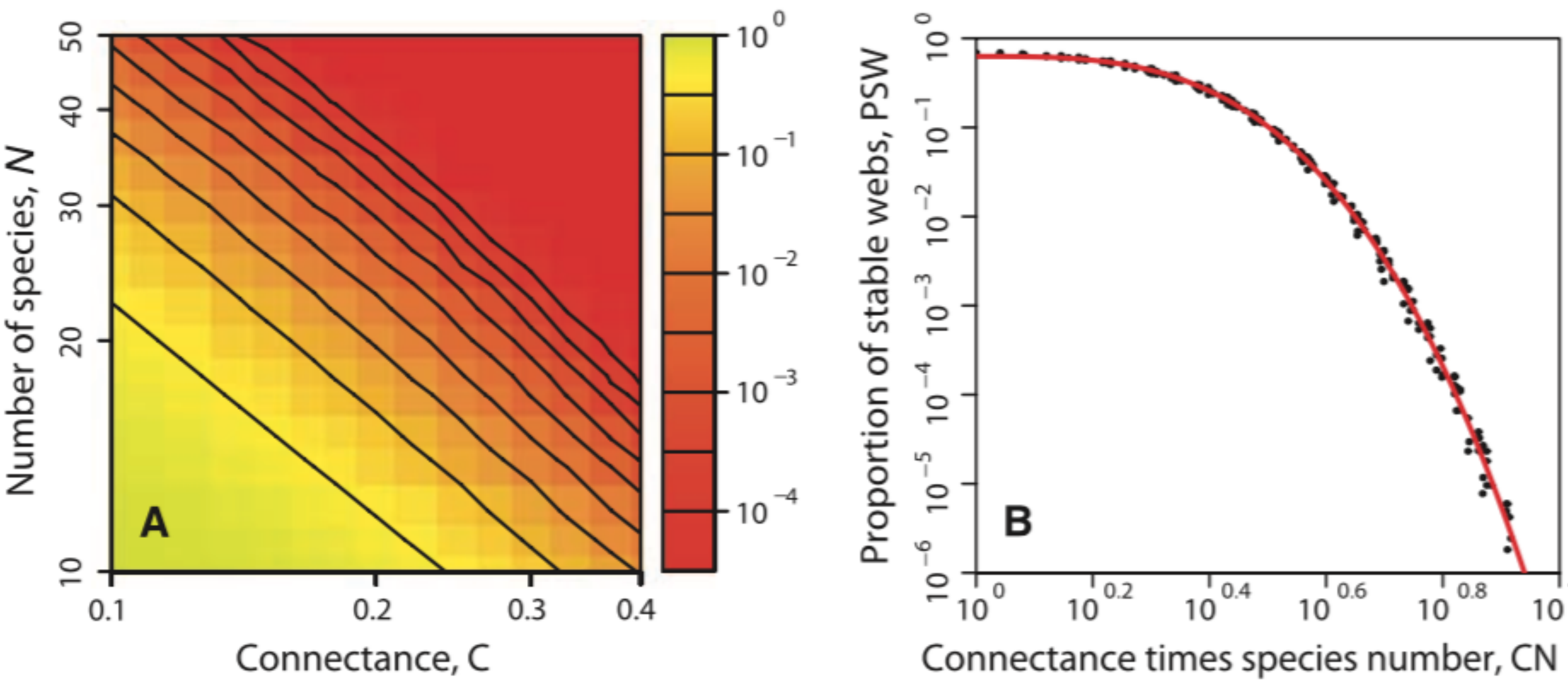
$$\dot{X}_i = S_i(X_i) + F_i(X_1, ..., X_N) - M_i(X_i) - \sum_{j=1}^{N} G_{ij}(X_1, ..., X_N)$$

Growth from 1° prod.

Growth from pred.

Intrinsic mort.

Mort. due to predation



Gross et al. 2009

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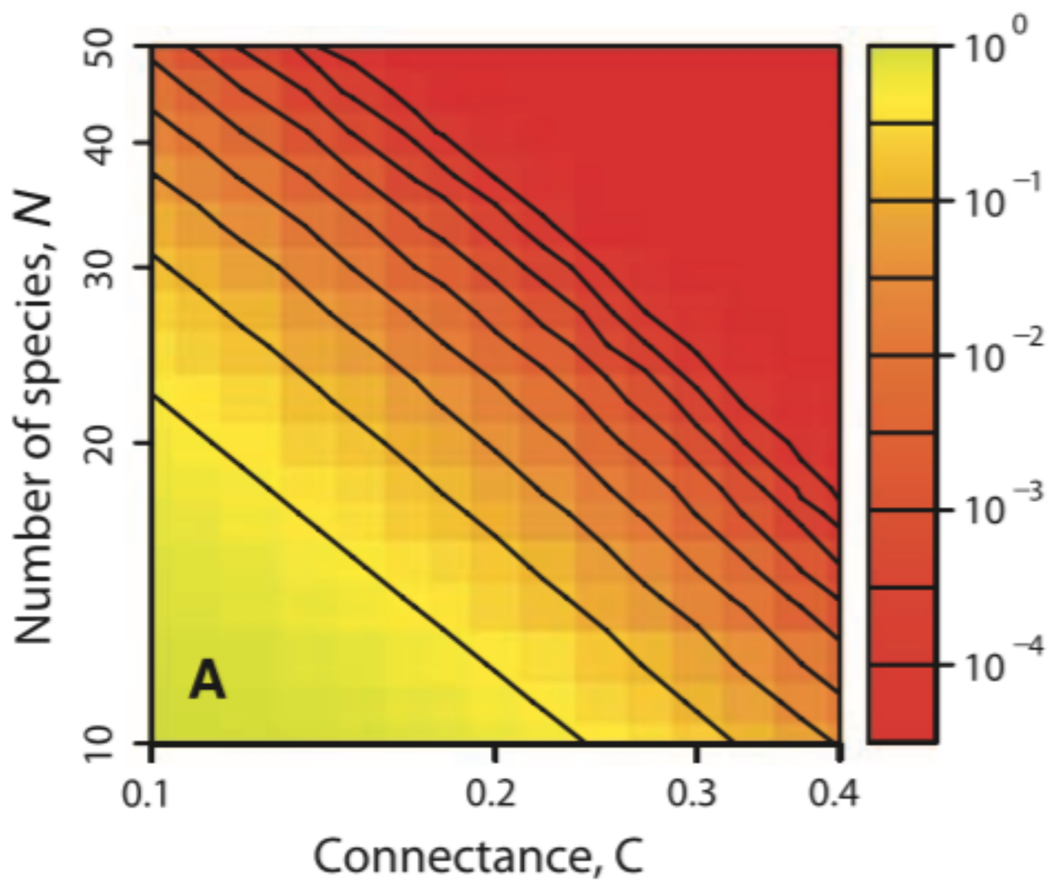
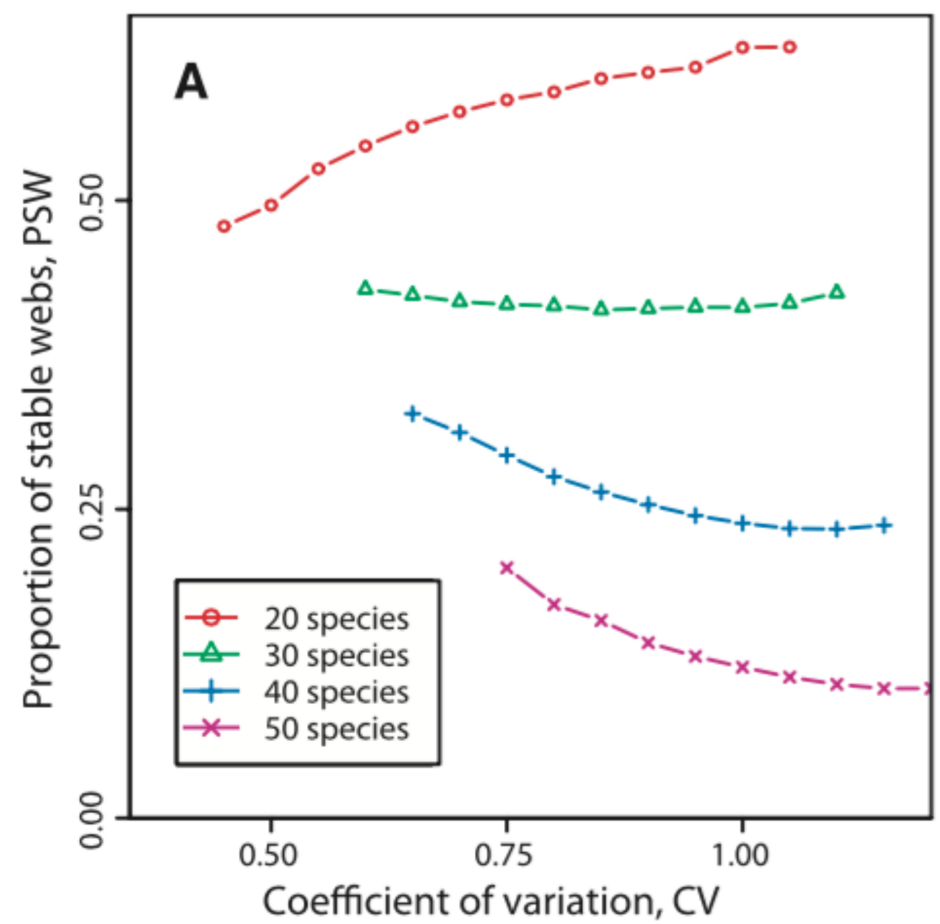
Growth from 1° prod. | Growth from pred. | Intrinsic mort. | Mort. due to predation





Gross et al. 2009

Big webs behave differently than small webs

$$\dot{X}_i = S_i(X_i) + F_i(X_1, ..., X_N) - M_i(X_i) - \sum_{j=1}^{N} G_{ij}(X_1, ..., X_N)$$

Growth from 1° prod.

Intrinsic mort.

Growth from pred.

Mort. due to predation

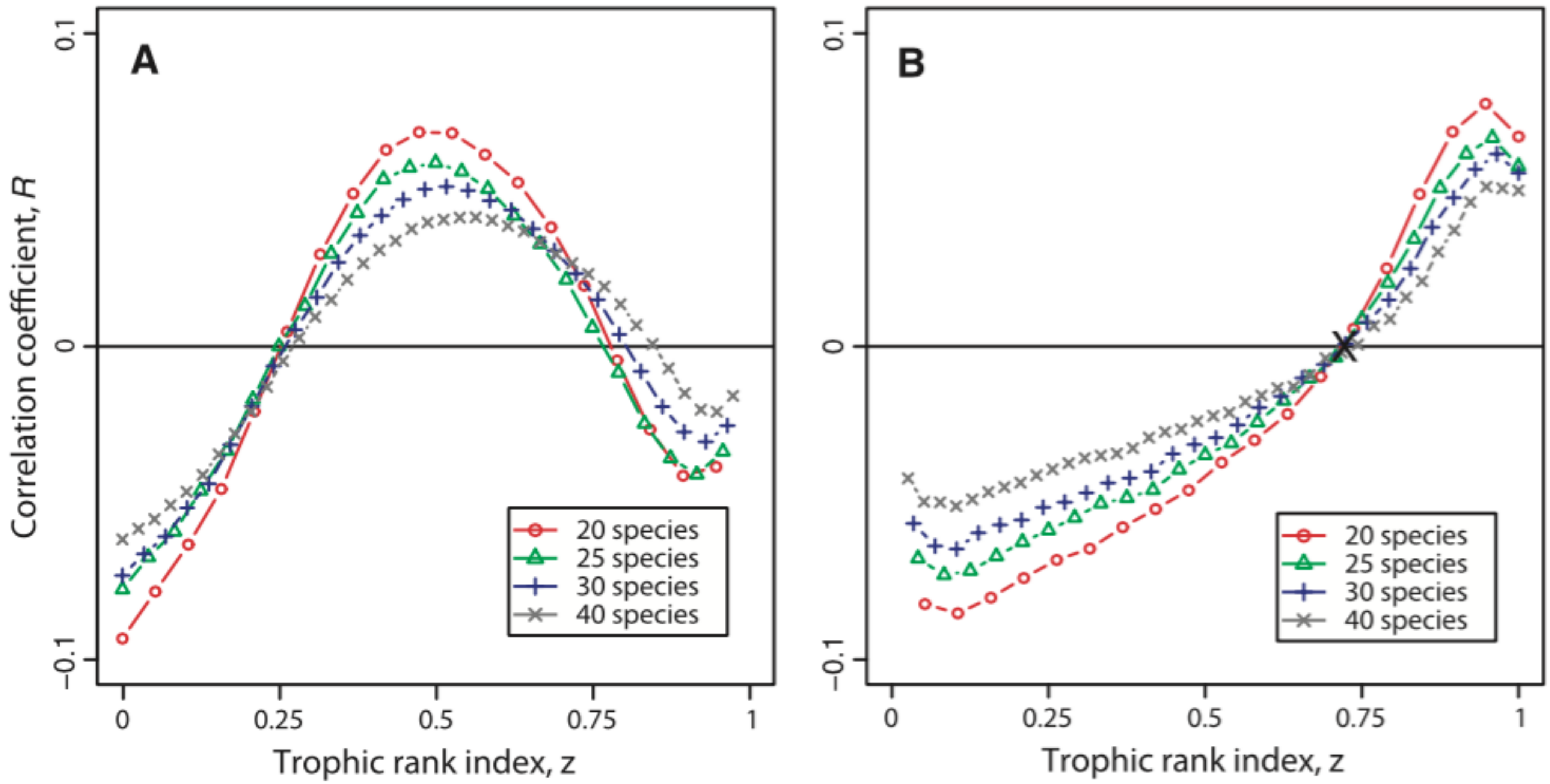
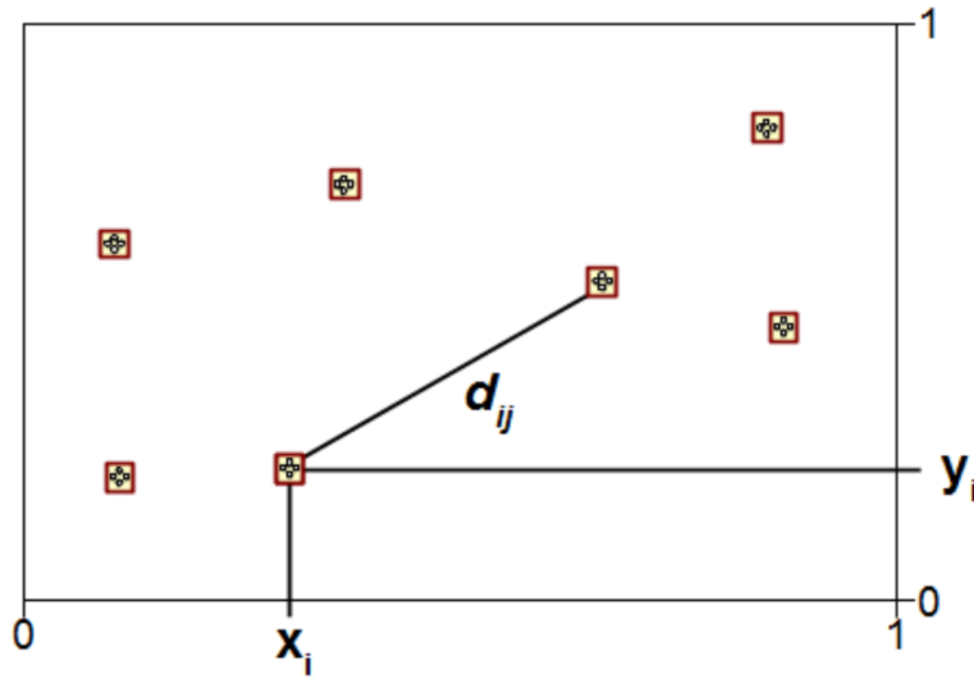


Fig. 4. Dependence of food-web stability on the distribution of links. (**A**) Correlation of stability with the number of predator species preying on a focal species, in dependence on the trophic position of the focal species as measured by its trophic-rank index *z*. Stability is enhanced if most species prey upon intermediate species, which are characterized by indices around *z* = 0.5. (**B**) Correlation of stability with the number of prey species predated upon by a focal species, in dependence on the trophic position of the focal species. Stability is enhanced if apical predators are generalists, whereas intermediate predators are specialists.

Gross et al. 2009

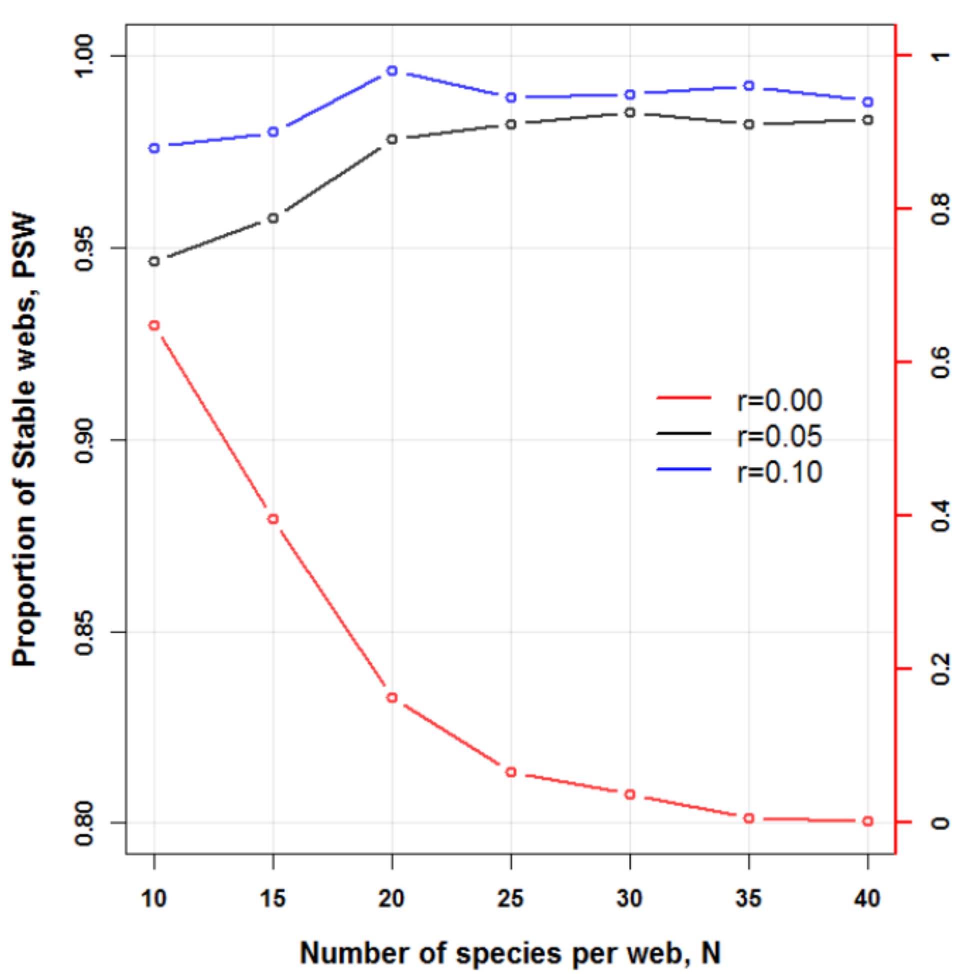
Food webs in SPACE

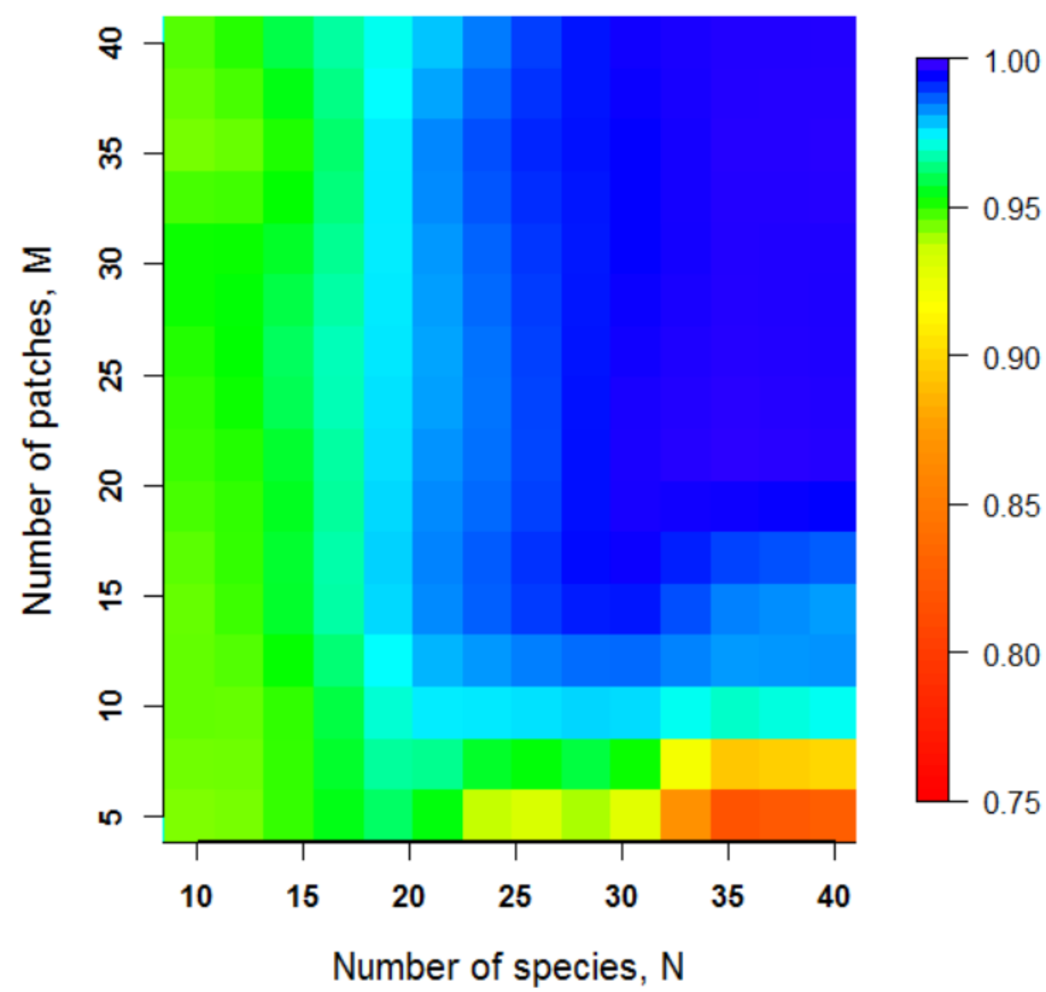


Lars Rudolf

r = fraction of gain by immigration

Thilo Gross

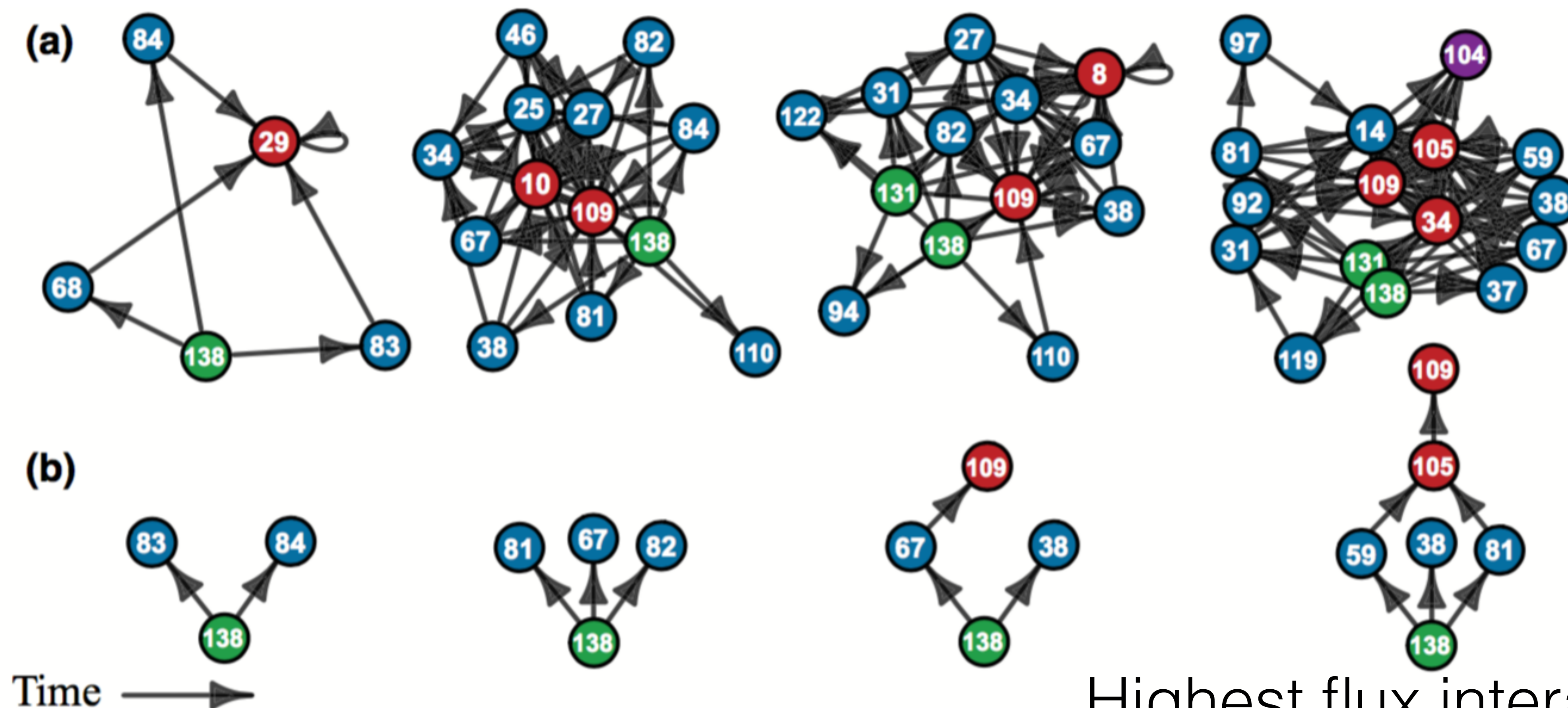




PSW

Food webs in TIME

Exploring assembly from microcosm experiments



Highest flux interactions

"Webs experiencing different colonisation rates had stable topologies despite significant species turnover, suggesting that some features of network architecture emerge early and change little through assembly. But webs experiencing low colonisation rates showed less variation in the magnitudes of trophic fluxes, and were less likely to develop coupled fast and slow resource channels – a common feature of published webs. **Our results reveal that food web structure develops according to repeatable trajectories that are strongly influenced by colonisation rate.**"

Fahimipour & Hein, 2014