Simplicity on the Other Side of Ecological Complexity?

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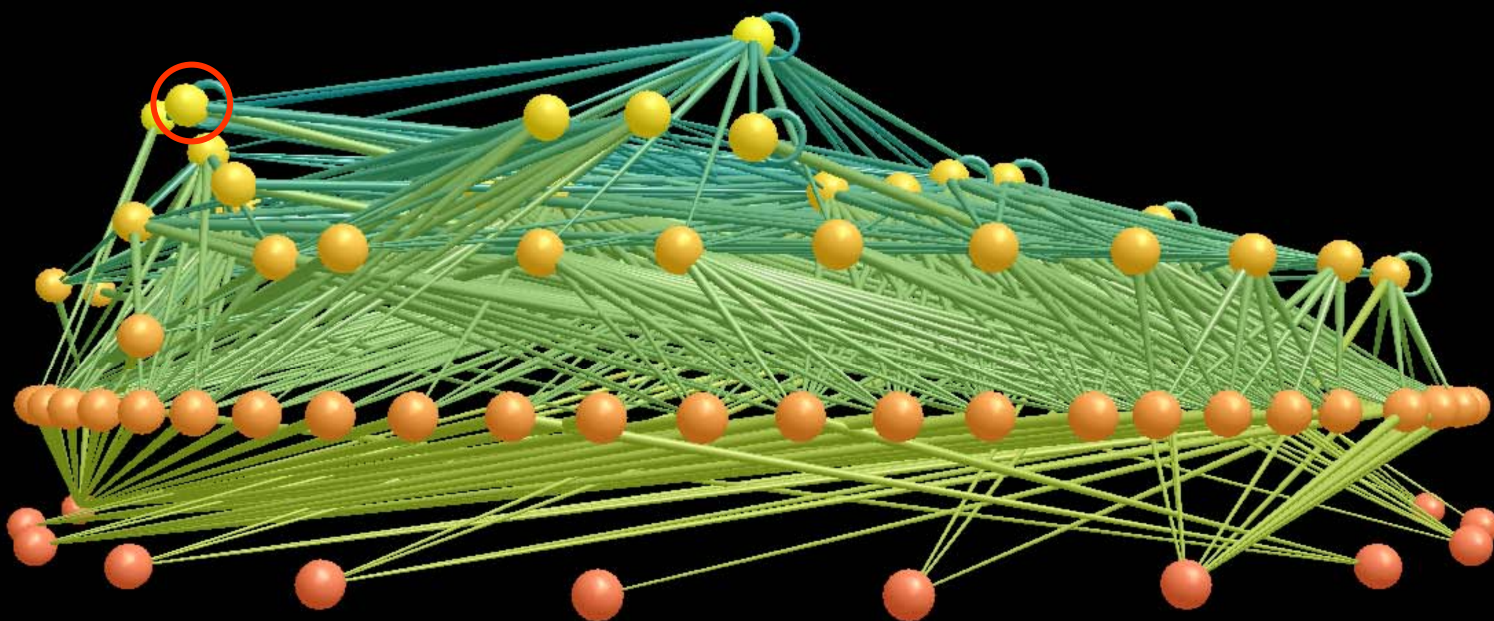
Benjamin
Cummings

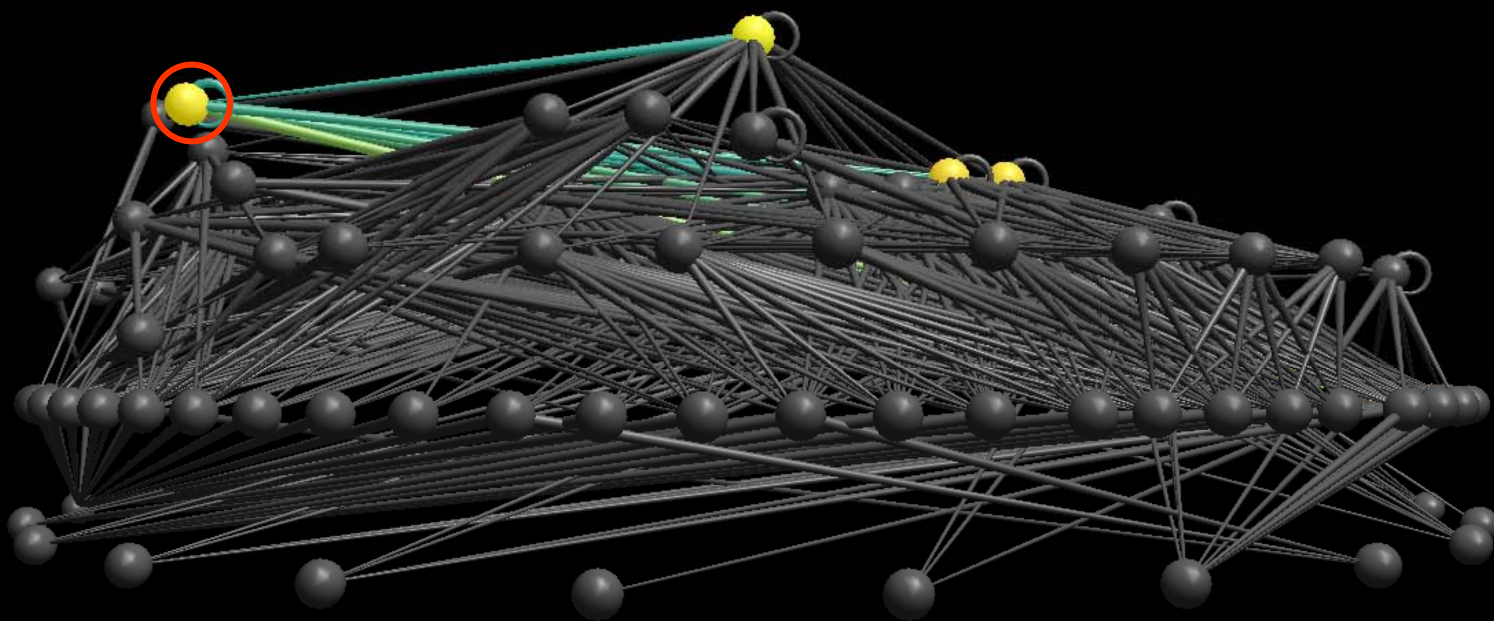
How can we predict the consequences of species loss in complex ecosystems?



Little Rock Lake Food Web (Martinez 1991)

How can we predict the consequences of species loss in complex ecosystems?

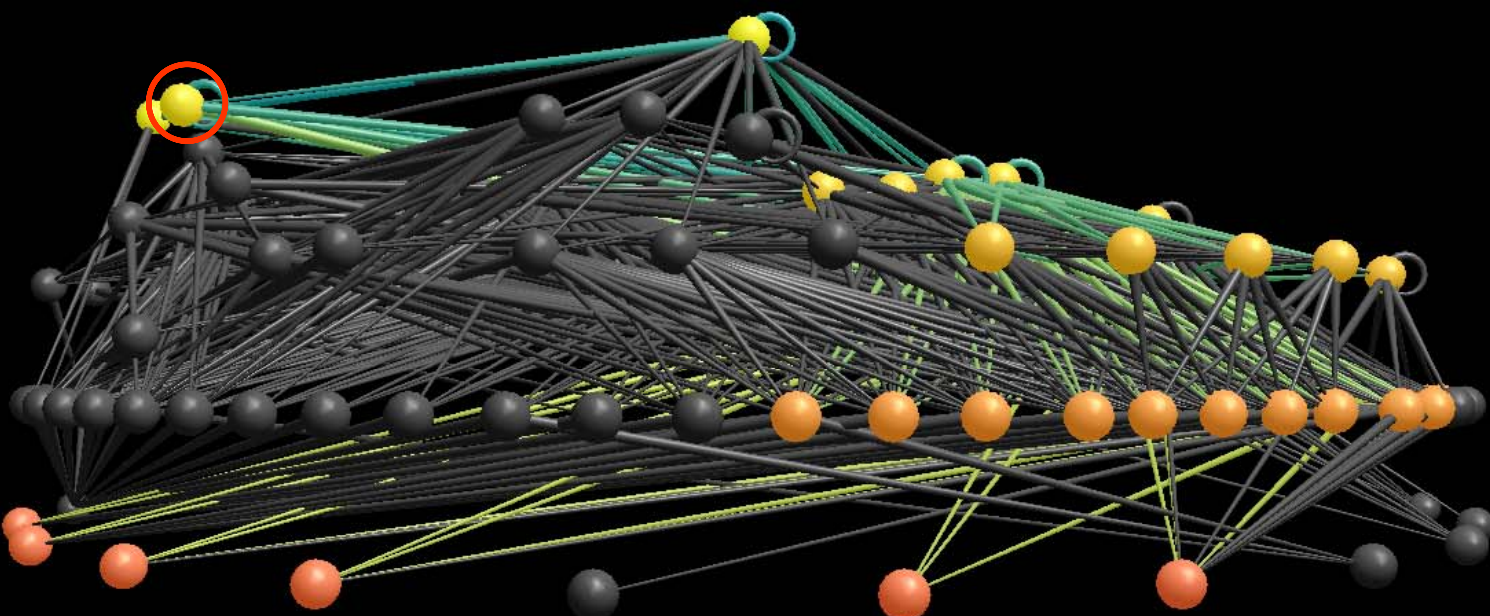
1 degree



Little Rock Lake Food Web (Martinez 1991)

How can we predict the consequences of species loss in complex ecosystems?

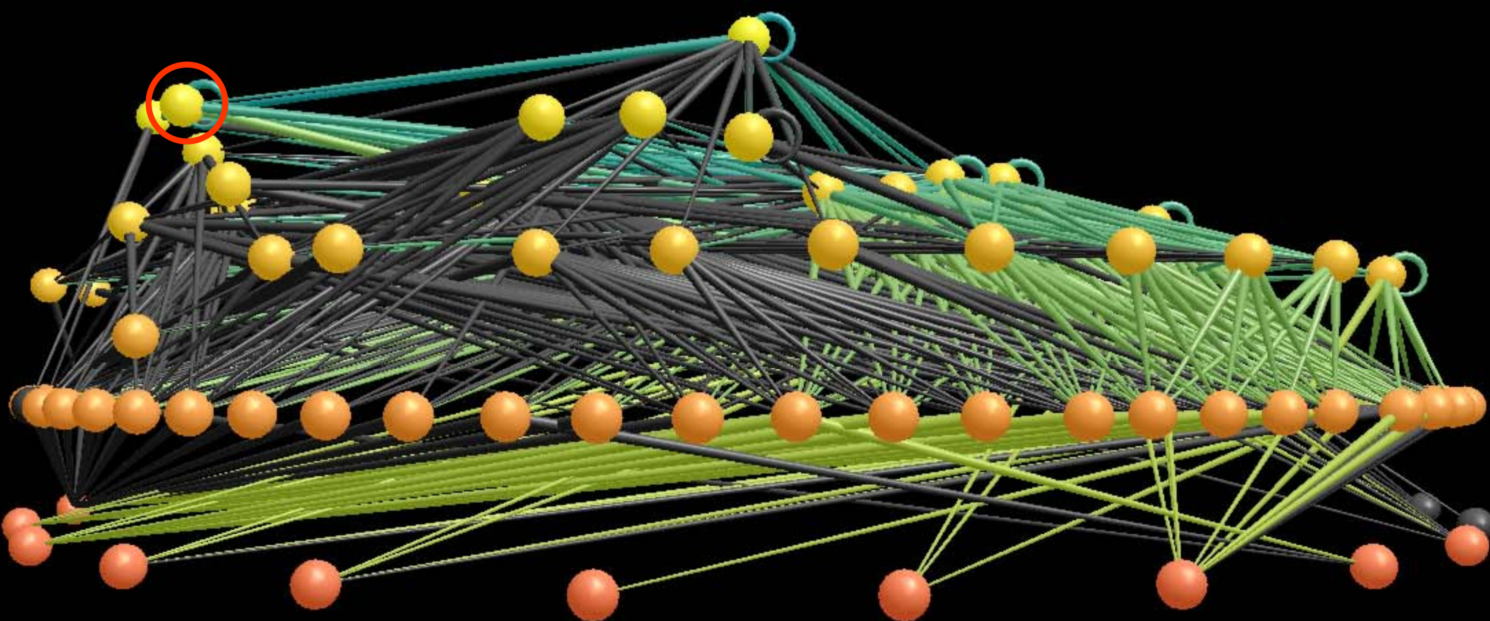
2 degrees



Little Rock Lake Food Web (Martinez 1991)

How can we predict the consequences of species loss in complex ecosystems?

3 degrees



Little Rock Lake Food Web (Martinez 1991)

Williams, Berlow, et al. PNAS 2002

some hope

metabolism

<1>

everything needs energy to stay alive

<2>

BIG things need more energy than small things

<2>

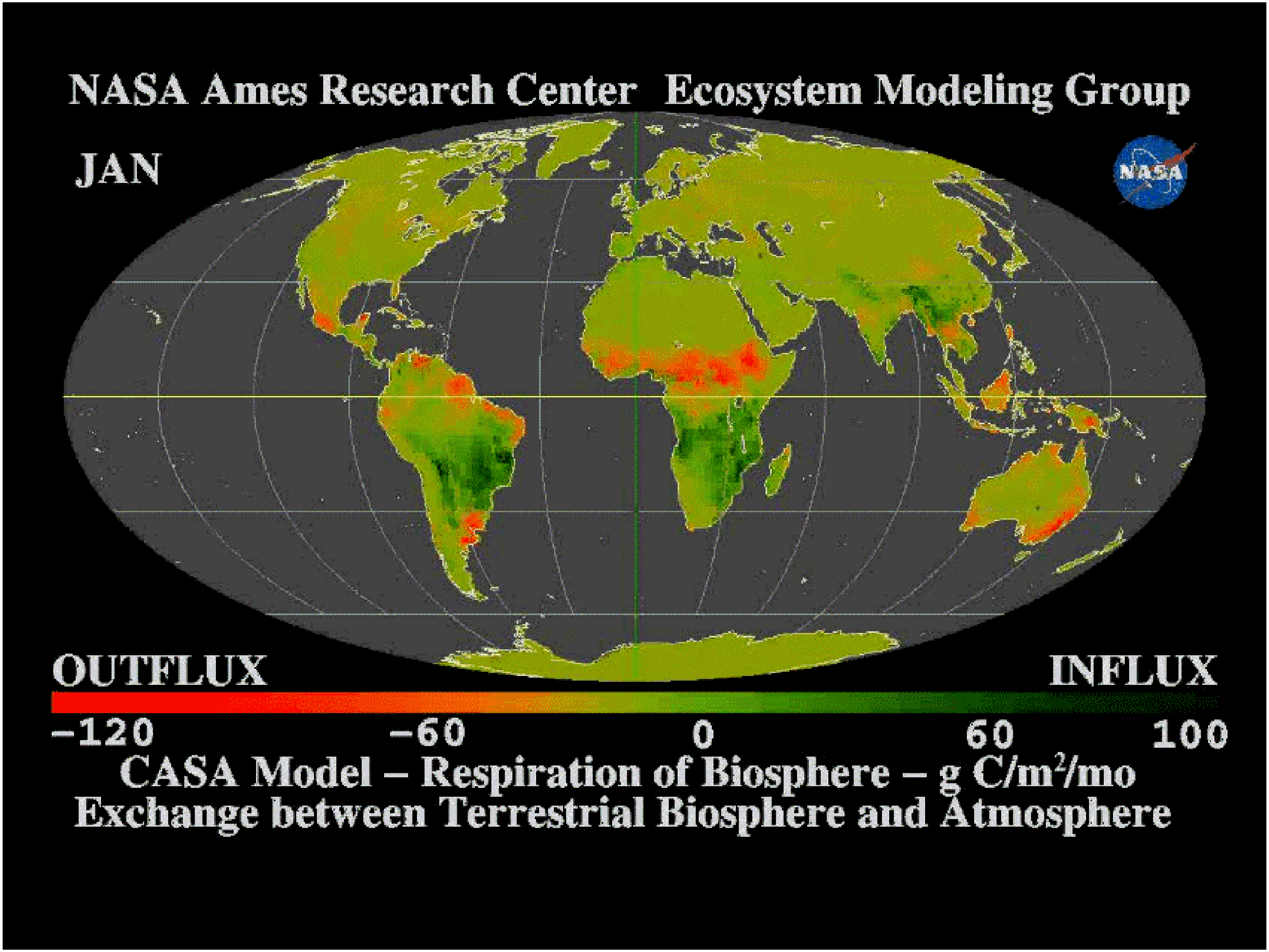
BIG things need(more)$^{3/4}$energy than small things

allometric scaling of metabolism with body size

Feeding is Universal

Food Webs are the foundation of Ecological Networks

Body Size should predict the strength of interactions in food webs


NASA Ames Research Center Ecosystem Modeling Group
JAN
NASA
OUTFLUX
INFLUX
-120
-60
0
60
100
CASA Model – Respiration of Biosphere – g C/m2/mo
Exchange between Terrestrial Biosphere and Atmosphere

Feeding is
Universal

Universal $\neq$ The Only Thing

Ubiquitous $\neq$ The Only Thing

non-metabolic interactions

Question

can we explain all interaction strengths
with body size (metabolism)?

can we explain all interaction strengths
with body size (metabolism)?

WHAT

can we explain

with body size (metabolism)?

WHAT NOT
can we explain
with body size (metabolism)?

repeat it

can we explain all interaction strengths
with body size (metabolism)?

WHAT

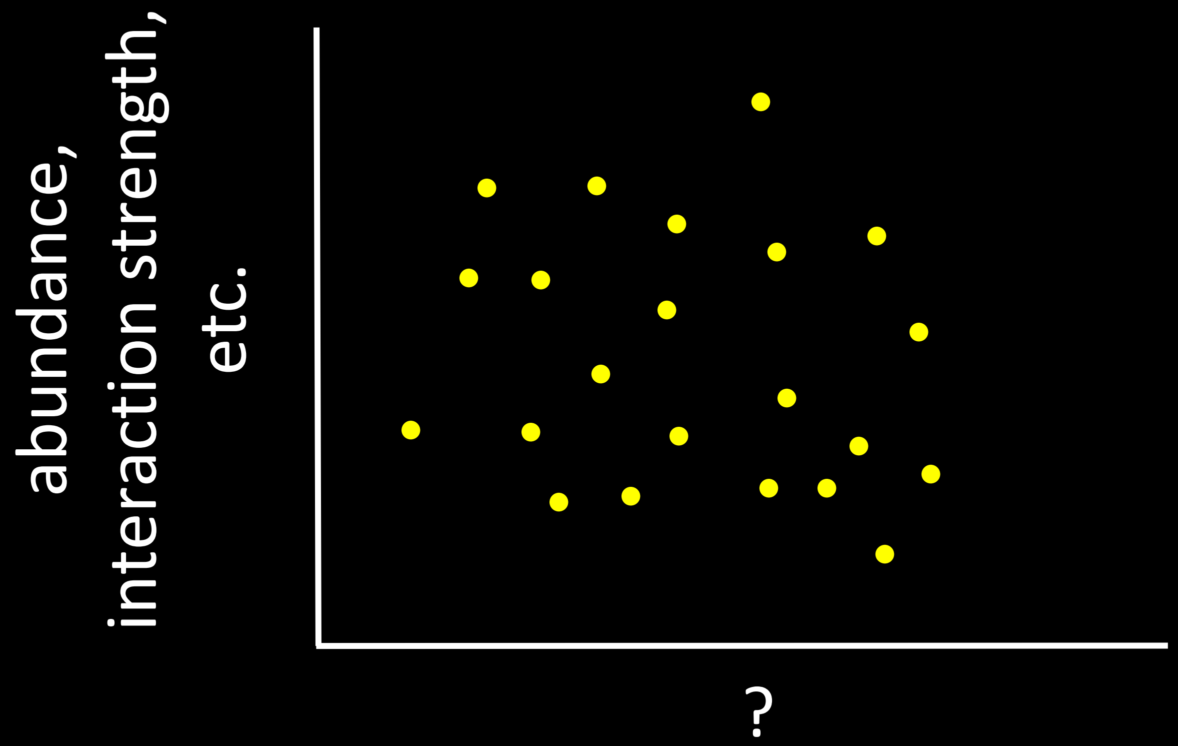
can we explain

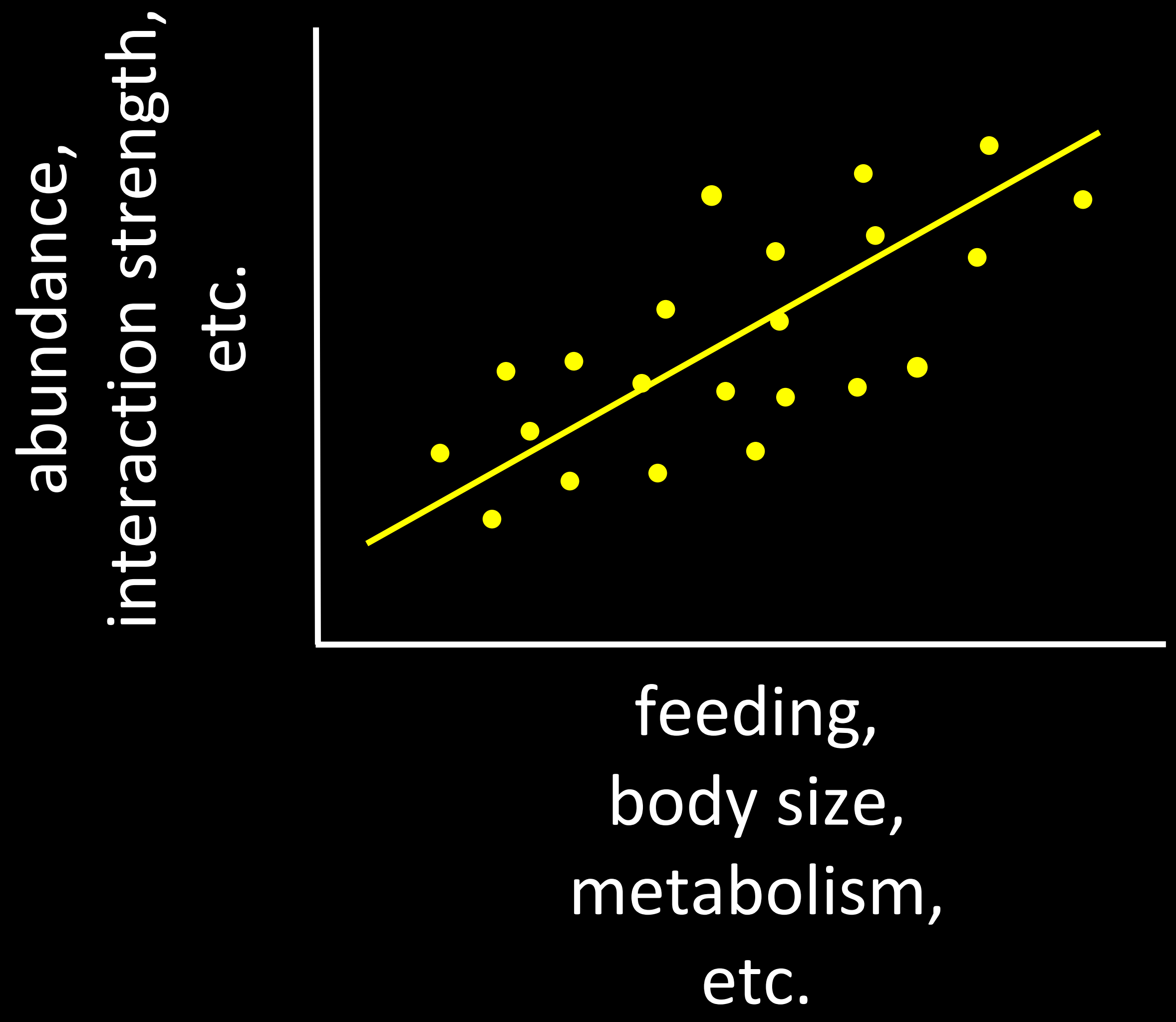
with body size (metabolism)?

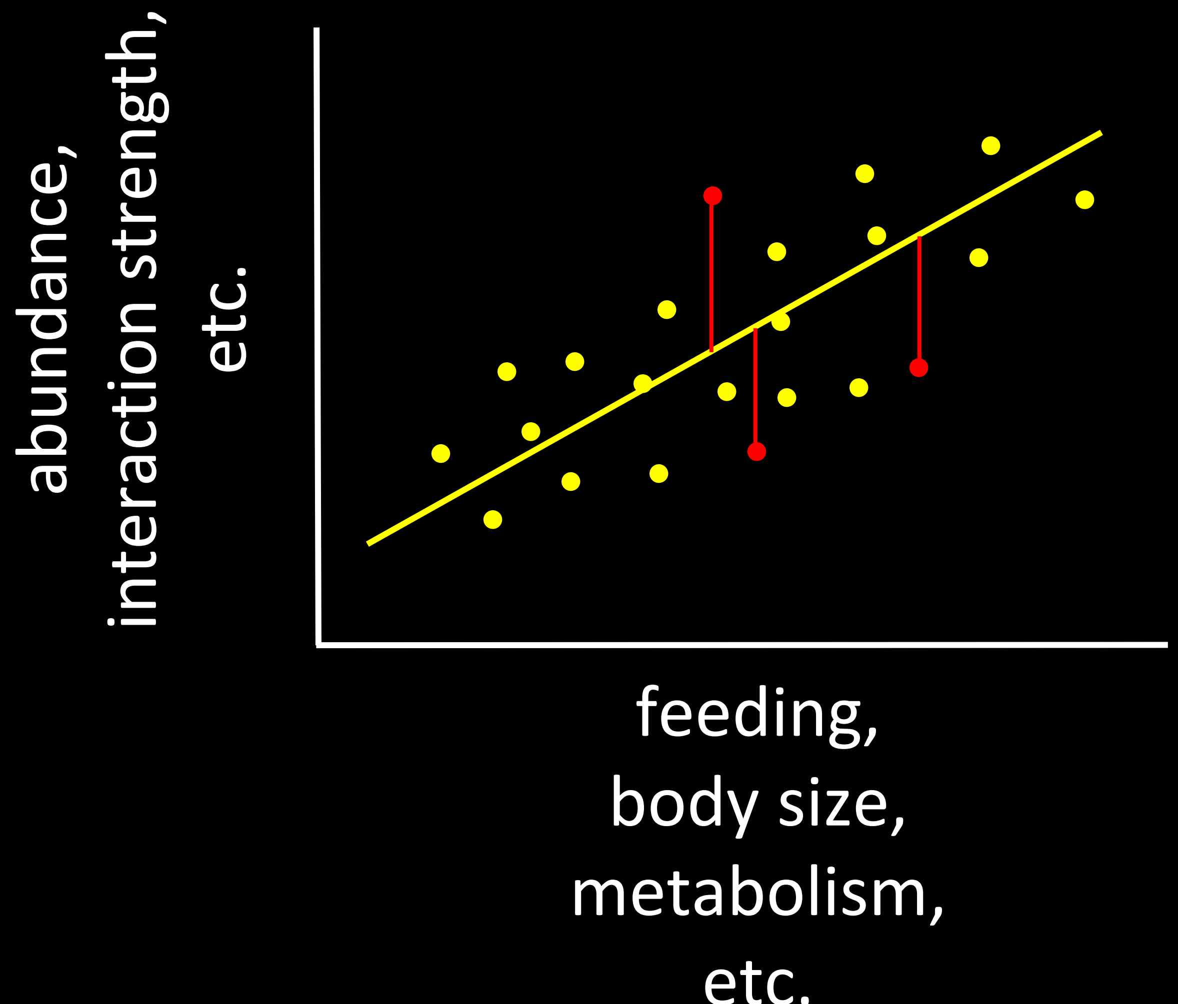
WHAT NOT

can we explain

with body size (metabolism)?


abundance,
interaction strength,
etc.
?


abundance,
interaction strength,
etc.
feeding,
body size,
metabolism,
etc.


abundance,
interaction strength,
etc.
feeding,
body size,
metabolism,
etc.

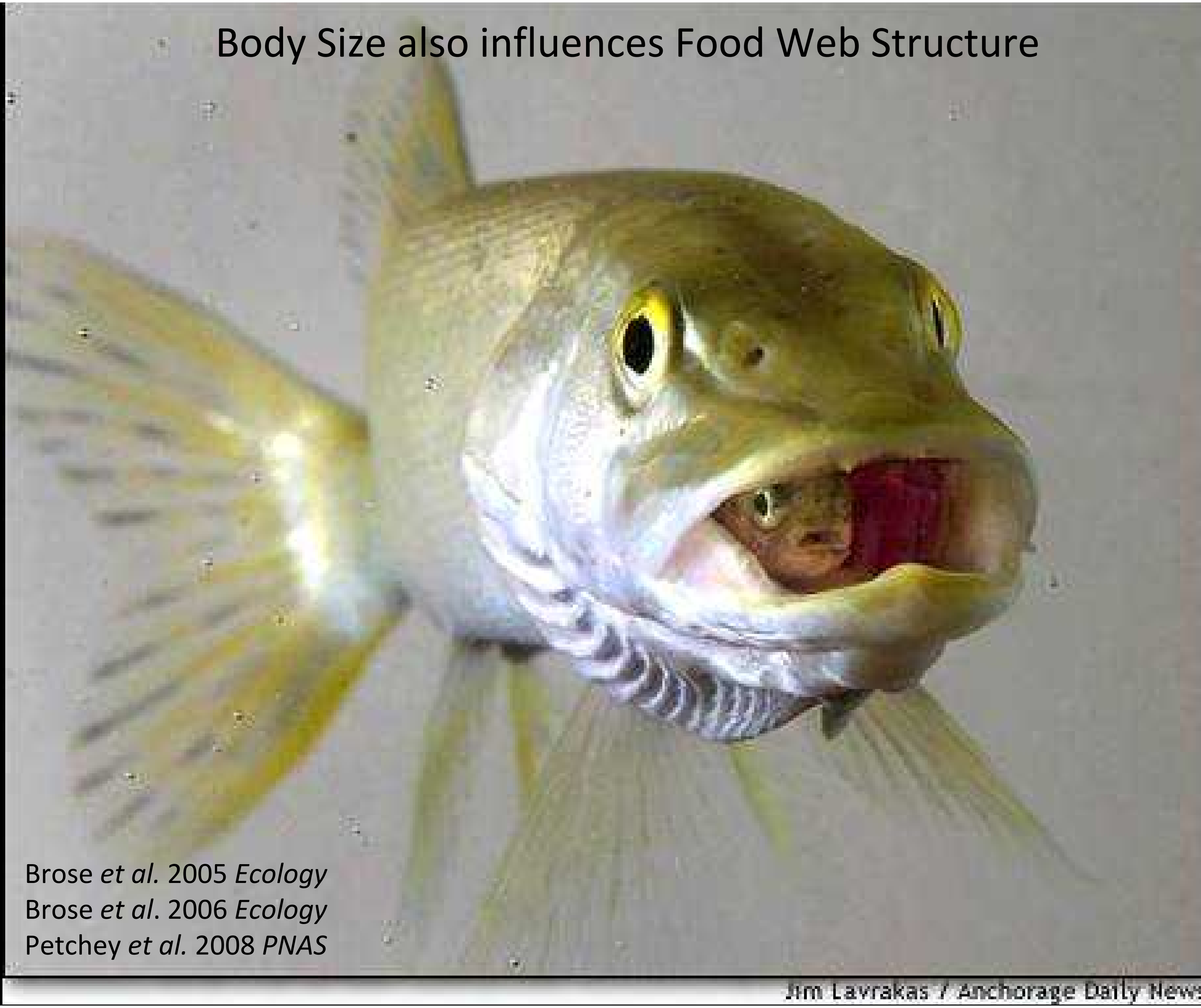
can we

describe a *metabolic baseline* of interactions

in complex networks?

can we
detrend metabolism
in complex networks?

Body Size also influences Food Web Structure



Brose *et al.* 2005 *Ecology*
Brose *et al*. 2006 *Ecology*
Petchey *et al.* 2008 *PNAS*

if *each link* obeys allometric rules
are those rules preserved at the *network scale*?

if *each link* obeys allometric rules
will body size predict
the effect of species loss *in the network*?

does

more complex = more complicated?

Approach

Simulation Results

Real World


Sierra Nevada
Research Institute

Approach:

<1>

Simulate species dynamics in a wide variety of networks

stochastic variation in structural and dynamic parameters

Approach:

<2>

all feeding links governed by (body size)$^{3/4}$

Approach:

<3>

delete each species and measure effects on all others

Approach:

<4>

Track variation for each simulation

interaction strengths
network level structure
neighborhood structure
species attributes
link attributes

Approach:

<5>

mine the variability for what best explains interaction strengths

The Model

coupled
The Models

<1>

Food Web Structure: *Niche Model*

(Williams and Martinez 2000)

<2>

Predator-Prey Interactions: *Bio-energetic Model*

(Yodzis and Innes 1992, Brose et al. 2005, 2006 Eco Letts)

<3>

Plant population dynamics: *Plant-Nutrient Model*

(Tilman 1982, Huisman and Weissing 1999)

Bioenergetic Predator-Prey Dynamics

Biomass$_i$ at time *t*

$$B_i' = \boxed{-x_i B_i} + \boxed{\sum_{j=resources} x_i y B_i F_{ij}} - \boxed{\sum_{j=consumers} x_j y B_j F_{ji} / e_{ji}}$$

Biomass of each species (*i*) at time (*t*) is balance of

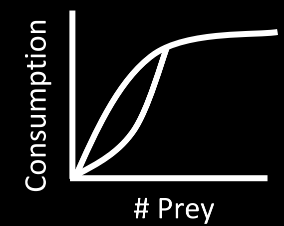
1. *gain* from consuming prey species
2. *loss* to being consumed by other species
3. *loss* to metabolism

Bioenergetic Predator-Prey Dynamics

Biomass$_i$ at time *t*

mass-specific metabolic rate

Functional Response



$$B_i' = -x_i B_i + \sum_{j=resources} x_i y B_i F_{ij} - \sum_{j=consumers} x_j y B_j F_{ji} / e_{ji}$$

assimilation efficiency

max metabolic-specific ingestion rate

x_i, y_i scale with body size
(body size correlated with web structure)

Bioenergetic Predator-Prey Dynamics (Plants)

mass-specific growth rate

metabolic loss

loss to herbivores

$$B_i' = r_i G_i B_i - x_i B_i - \sum_{j=consumers} x_j y B_j F_{ji} / e_{ji}$$

Nutrient-Dependent Growth of Plants

r_i, x_j, y scale with body size

Nutrient-Dependent Growth of Plants

Concentration of Nutrients
determined by
Supply
Turnover
Consumption

$$G_i(N) = MIN\left(\frac{N_1}{K_{1i}+N_1}, \frac{N_2}{K_{2i}+N_2}\right)B_i(t)$$

plant growth rate

Growth determined by most limiting Nutrient

Half saturation conc. for uptake of that Nutrient

Generate a food web (Niche Model)

↓

Calculate trophic level for each species

↓

Apply plant-nutrient model to plants, predator-prey model to rest.

↓

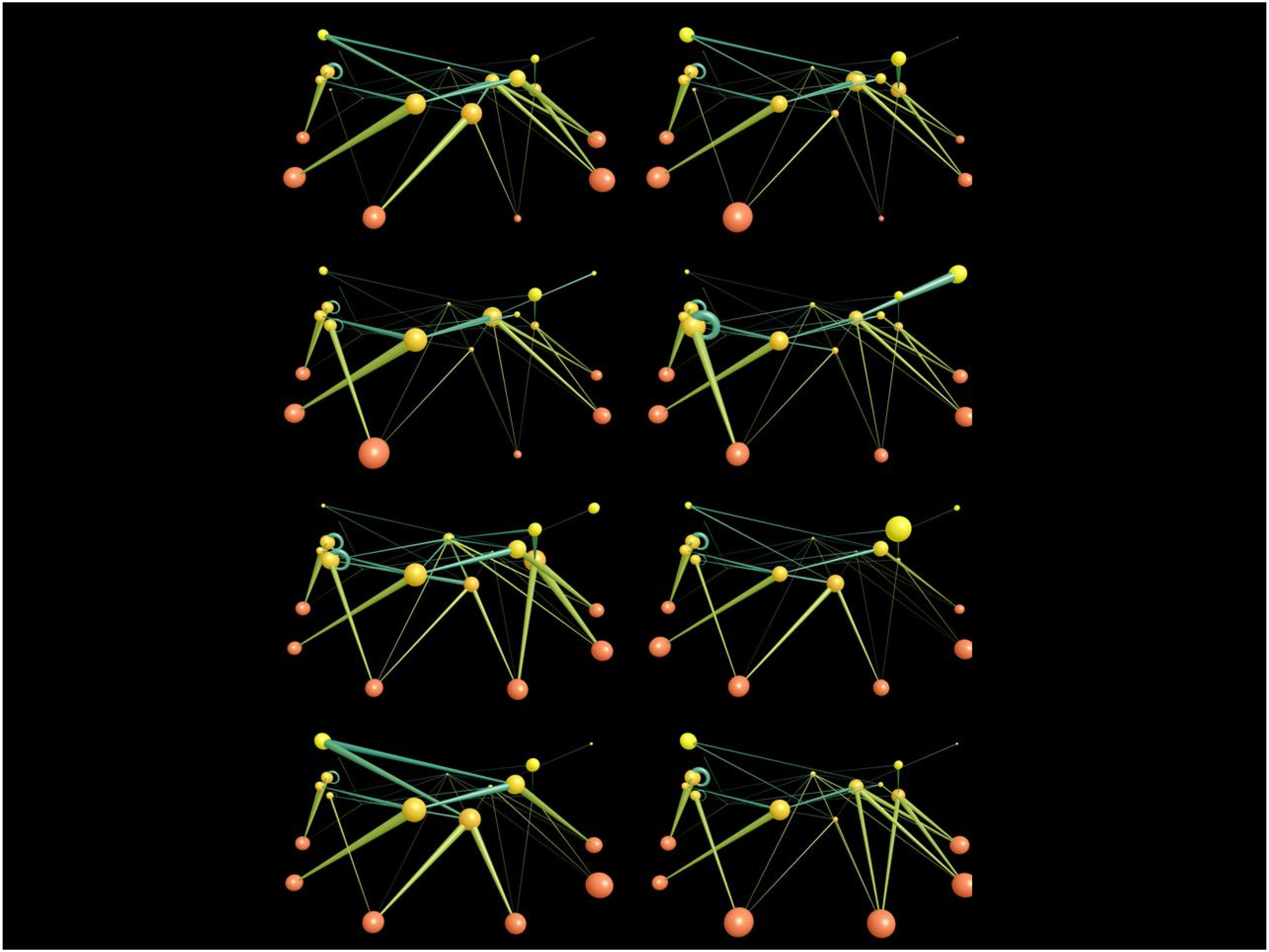
Assign body sizes based on trophic level (mean pred: prey ratio = 10)

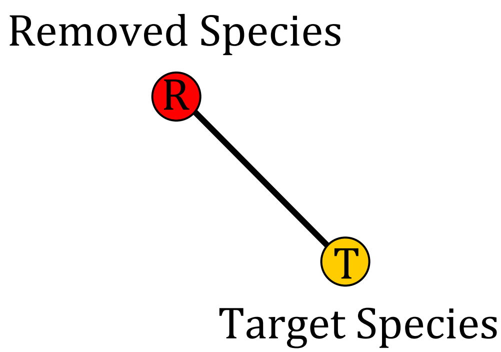
↓

Run simulation with each species deleted individually
to generate a *complete removal matrix*

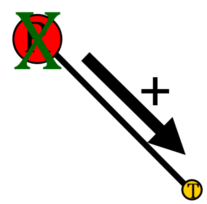
↓

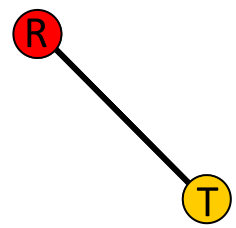
Repeat for all species and for 600 Niche Model webs





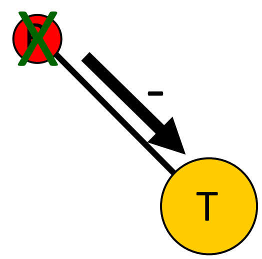
Removed Species
R
T
Target Species




R
T

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

population $I = B_{T+} - B_{T-}$



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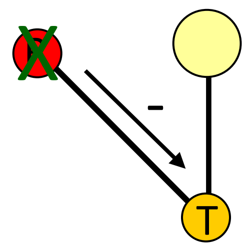

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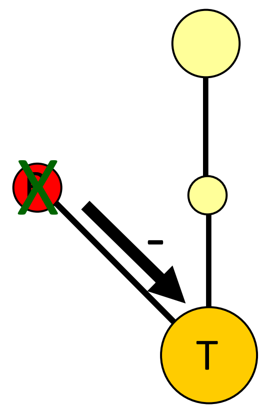

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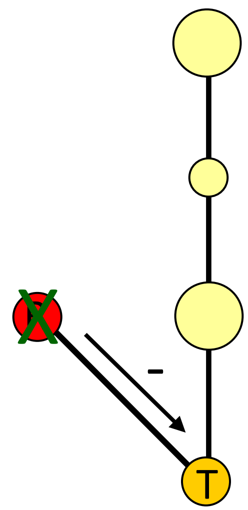

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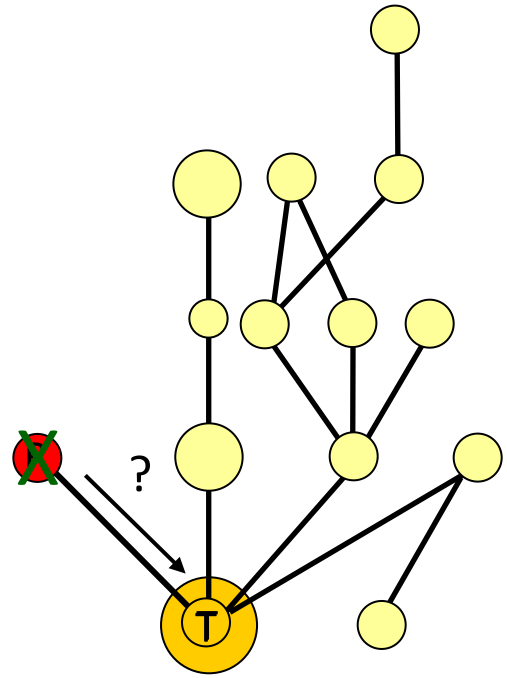

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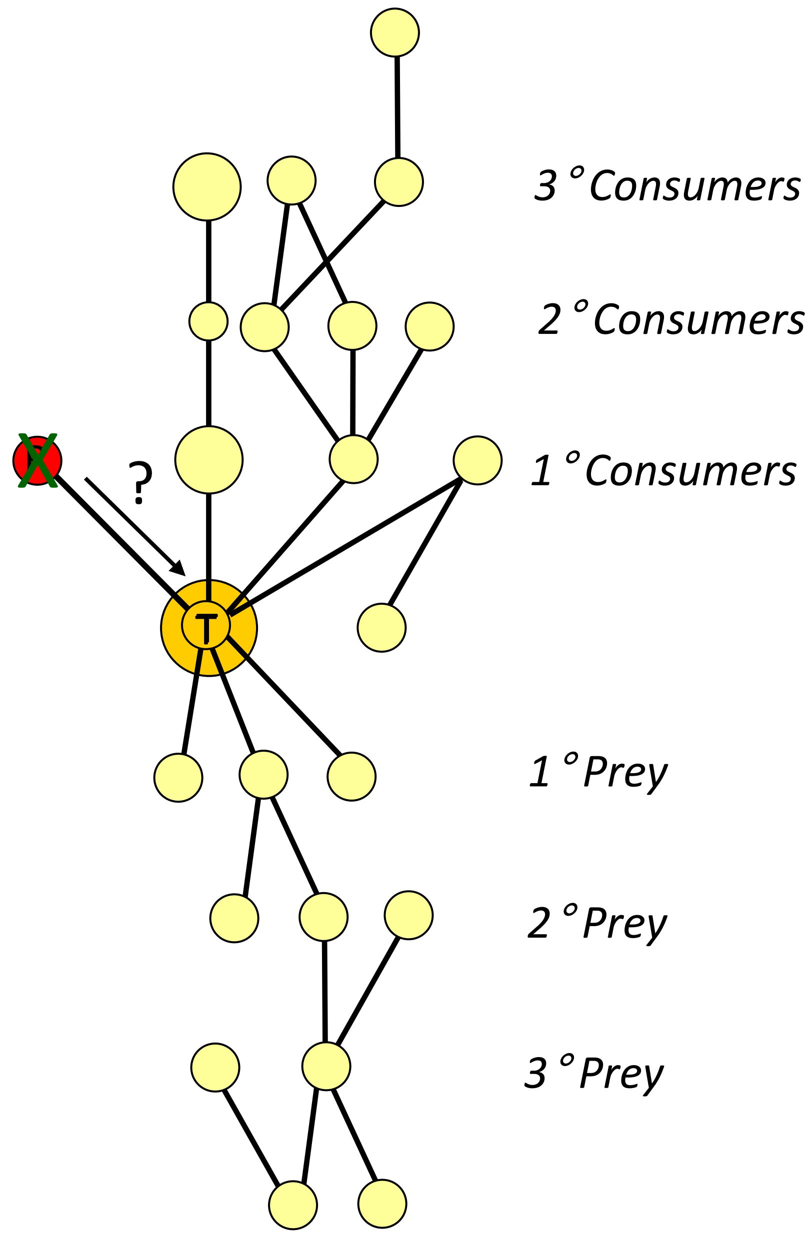

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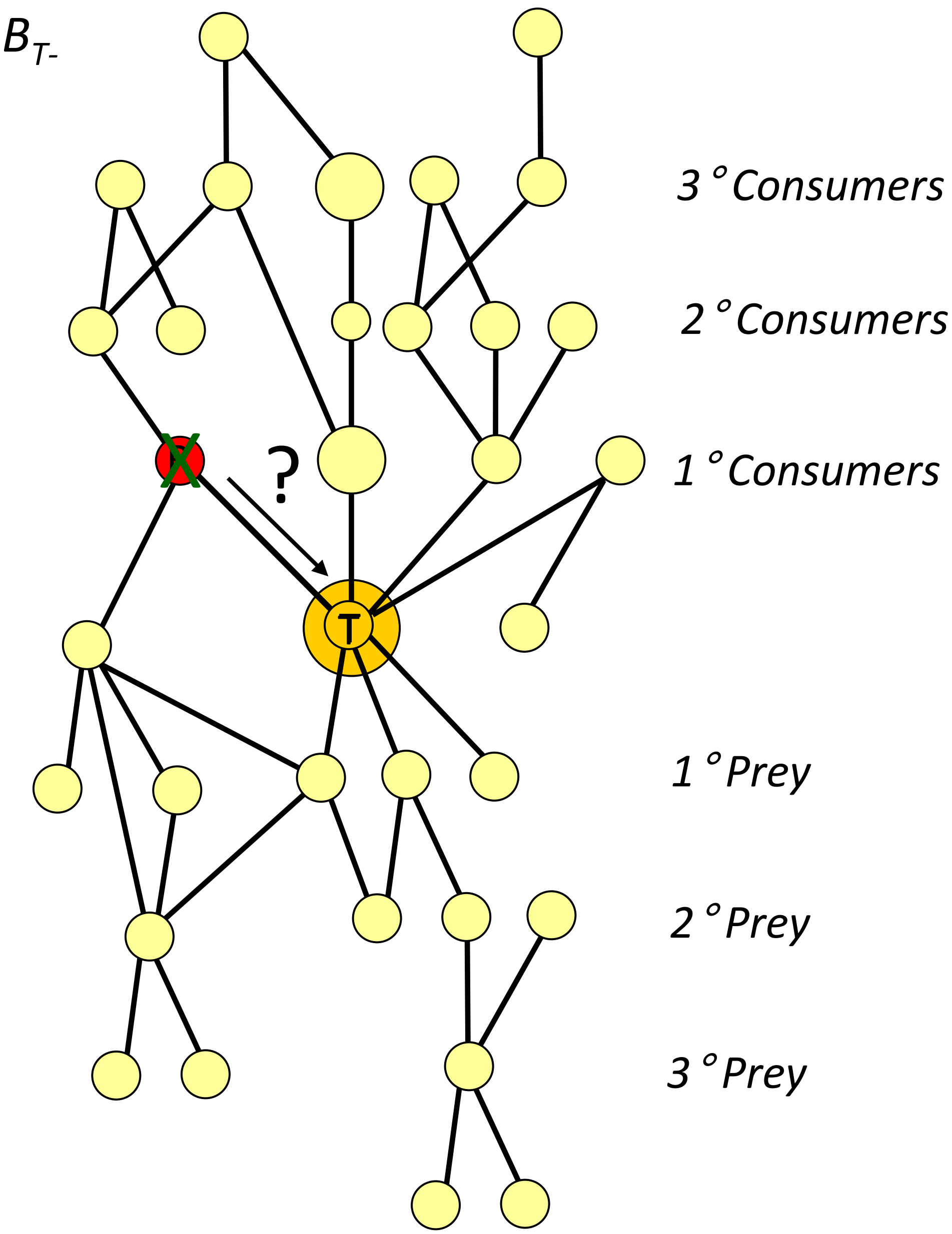
population $I = B_{T+} - B_{T-}$



add
noise

track the consequences of that noise

add noise:

<1>

Web Structure
size, connectance, architecture

add noise:

<2>

Animal Attributes
metabolic and max consumption rate,
pred-prey body size ratio
functional response type
predator interference

add noise:

<3>

Plant Attributes
growth rate
half saturation concentrations

track:

90 predictors to explain

variation in the strengths of

254,032 interactions among

12,116 species in

600 webs

track:

<1>

Global network structure

<2>

Species attributes of *R* and *T*

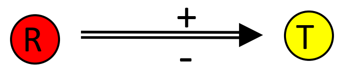
<3>

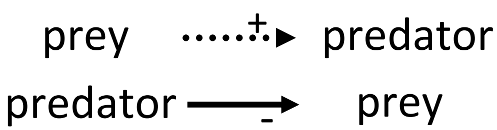
Local network structure around each *R* and *T*

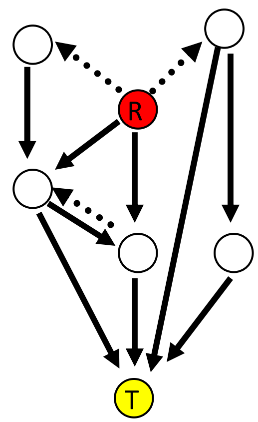
<4>

Attributes of the interaction

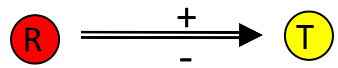
attributes of the interaction

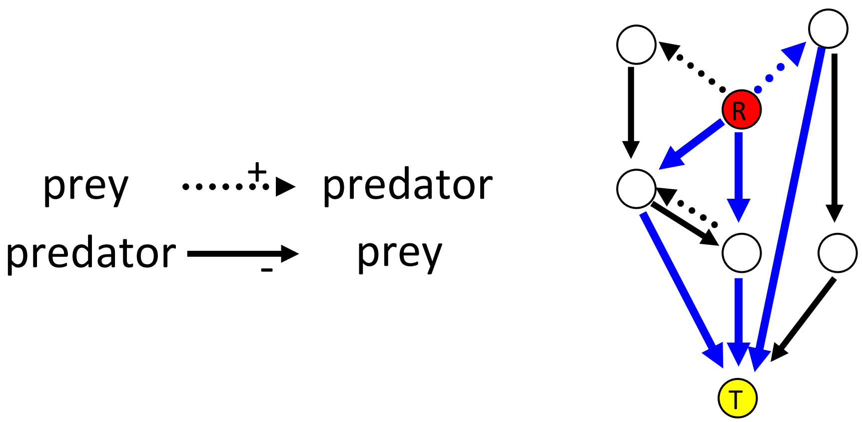






attributes of the interaction

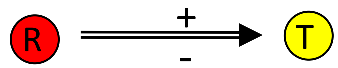


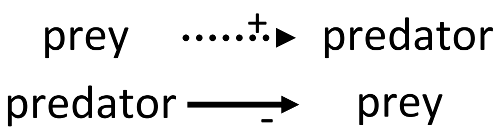


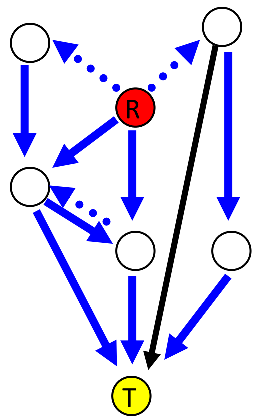
shortest path = 2 degrees

2 degree paths: +, +, -

attributes of the interaction





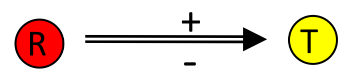


shortest path = 2 degrees

2 degree paths: +, +, -

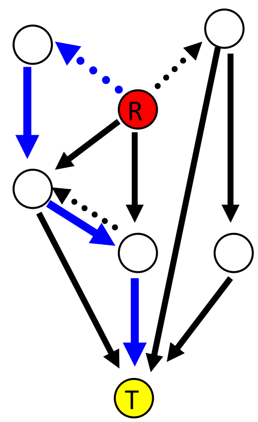
3 degree paths: +, +, +, -

attributes of the interaction



prey ····+► predator

predator —-► prey



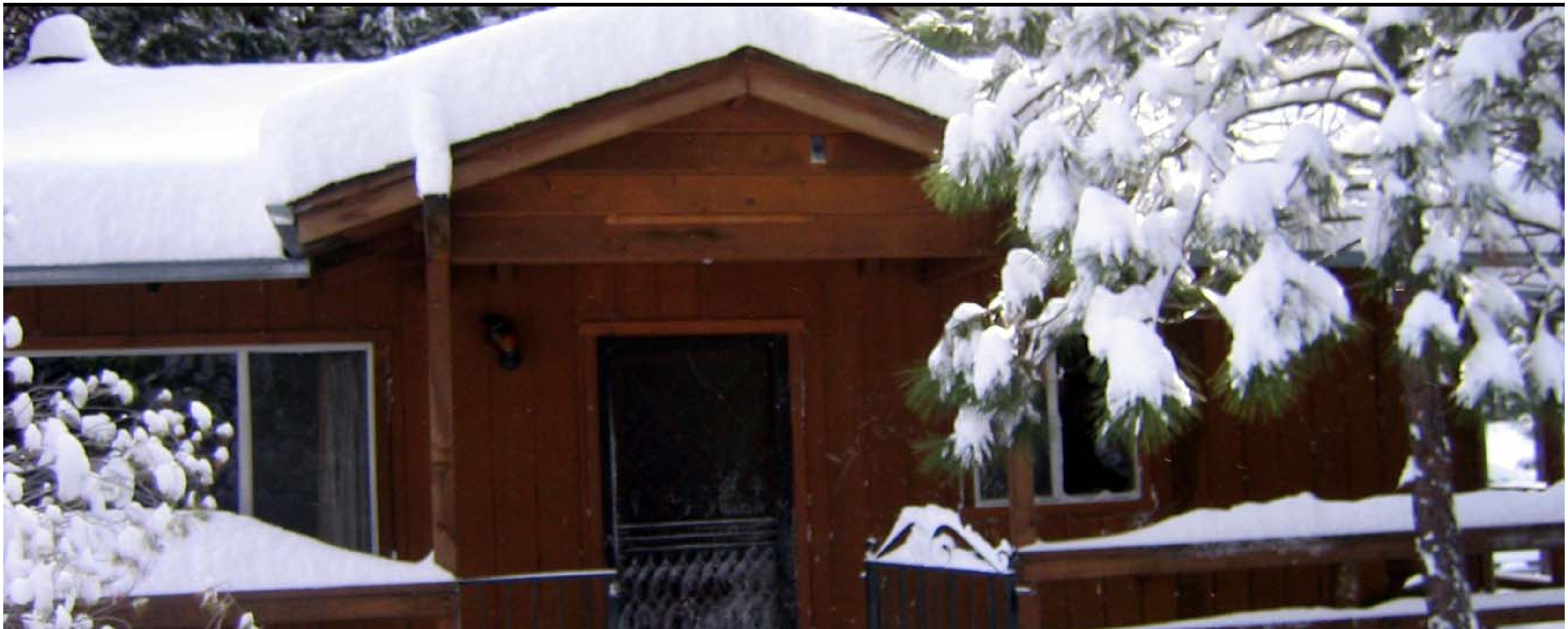
shortest path = 2 degrees

2 degree paths: +, +, -
3 degree paths: +, +, +, -
4 degree paths: -

sign shortest path = +1
sign next shortest path = +2
un-weighted sum (shortest + next shortest) = +3
weighted sum (shortest + (next shortest / 2)) = +2

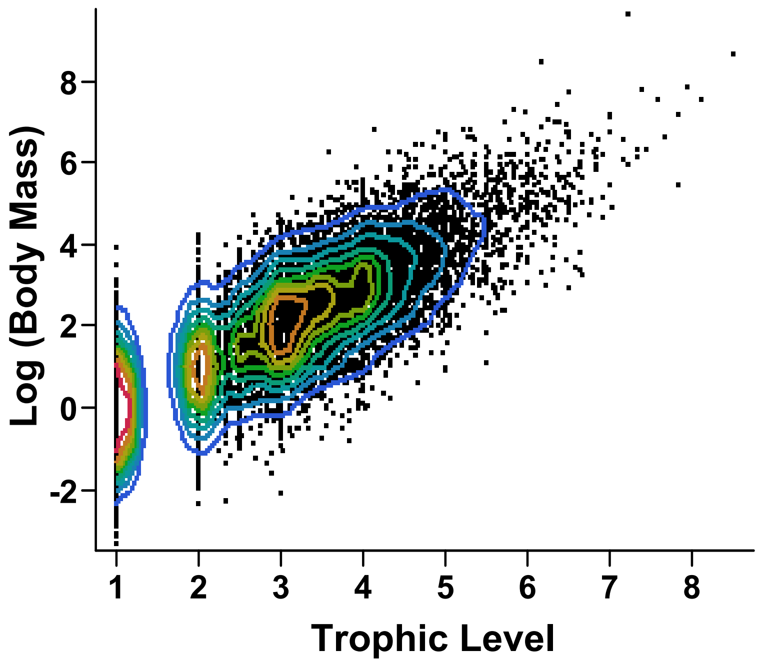
before **after**


101

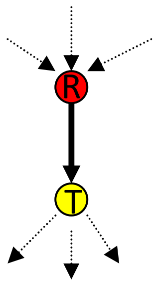


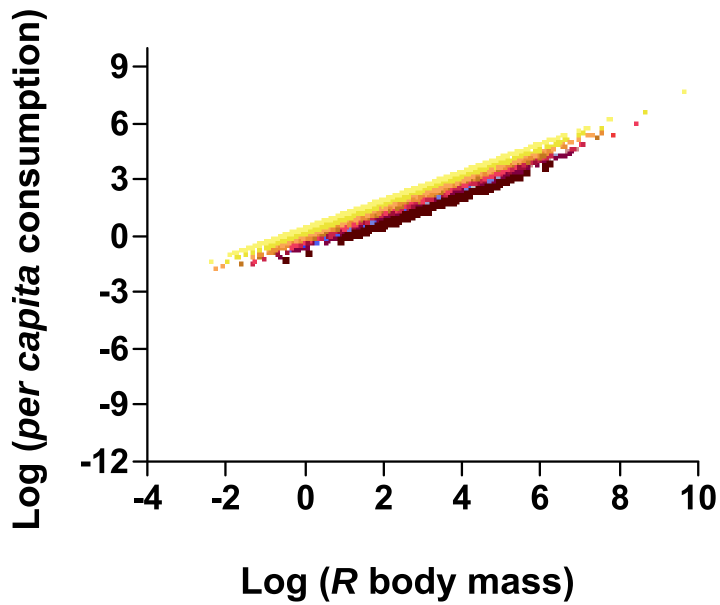


Body Size and Food Web Structure



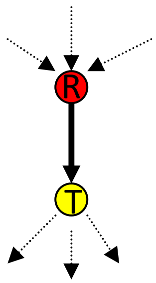
Each Feeding Interaction Scales with (Body Size)$^{3/4}$

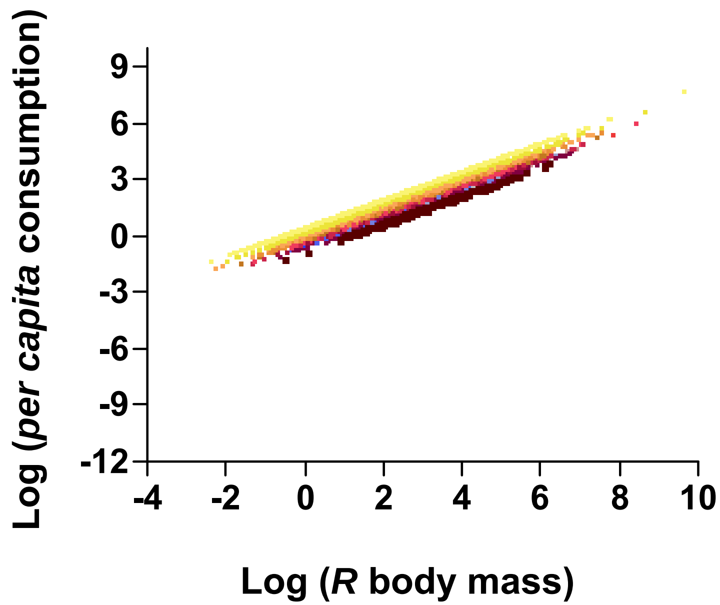




R^2 = 0.90
Slope = 0.74

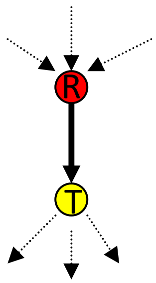
Per Capita Linear Interaction Strength = *Per Capita* Removal Interaction Strength?

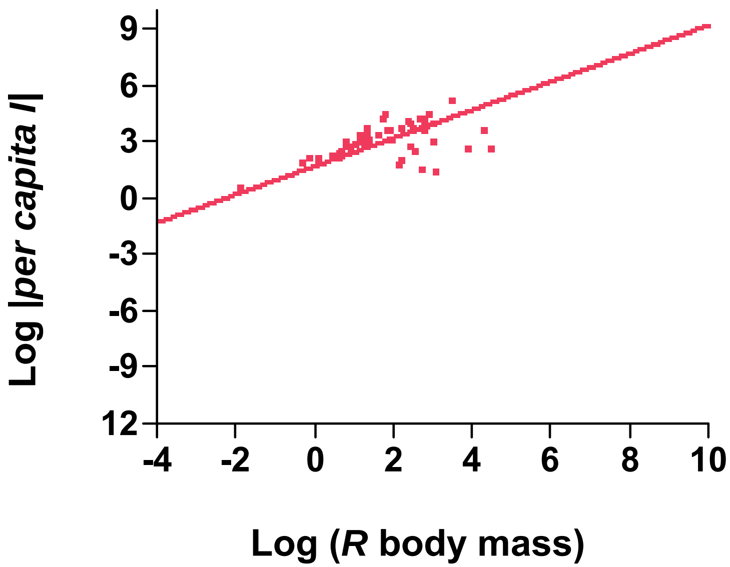




$R^2 = 0.90$
Slope = 0.74

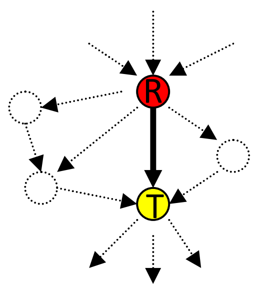
Per Capita Removal Interaction Strength

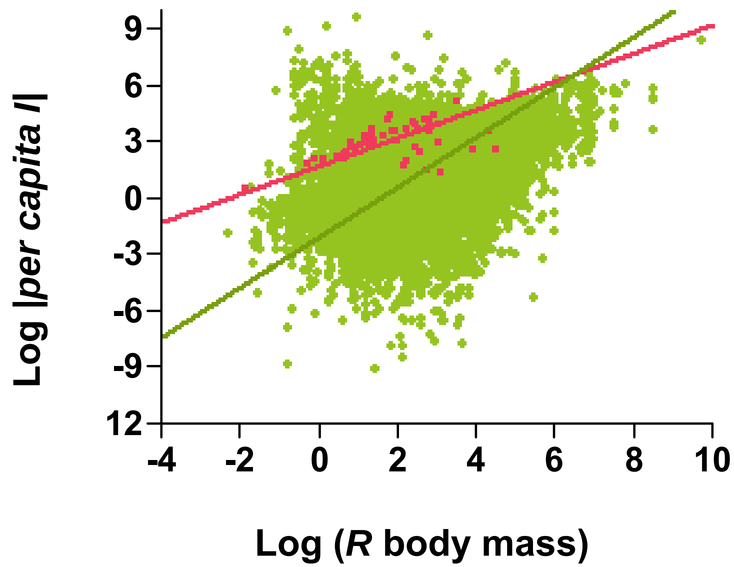




$R^2 = 0.32$
Slope = 0.74

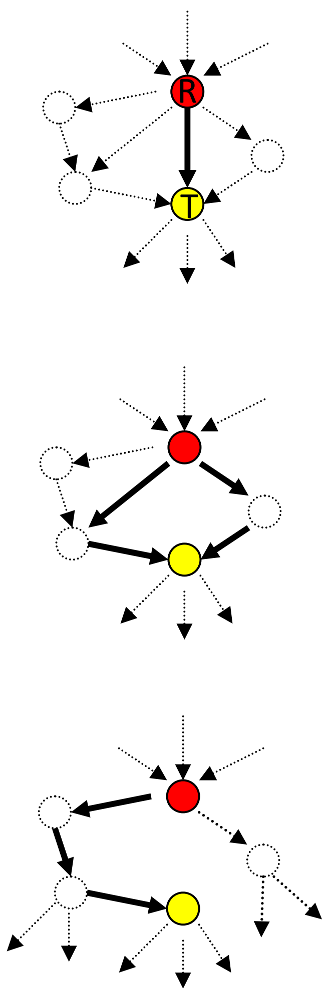
Per Capita Removal Interaction Strength

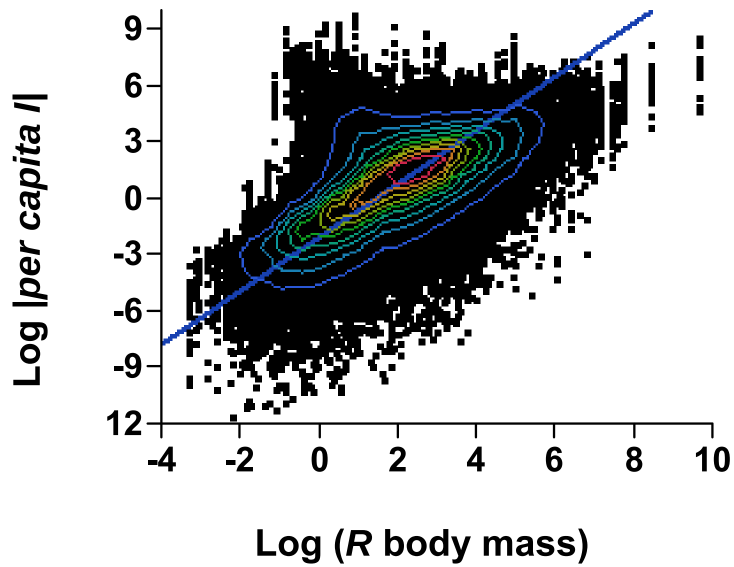




R^2 = 0.14
Slope = 1.3

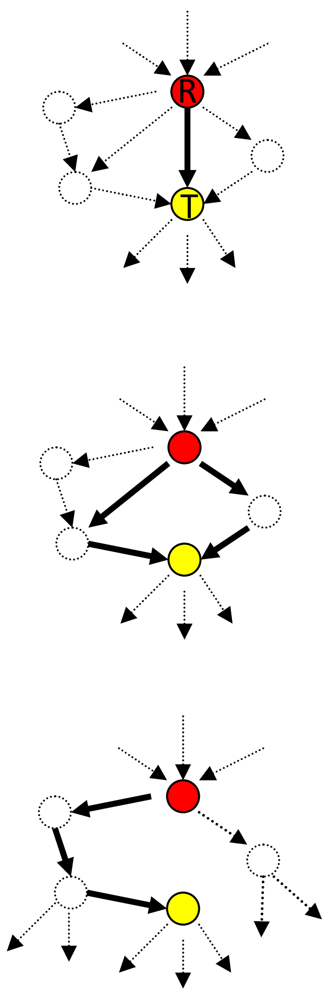
Per Capita Removal Interaction Strength

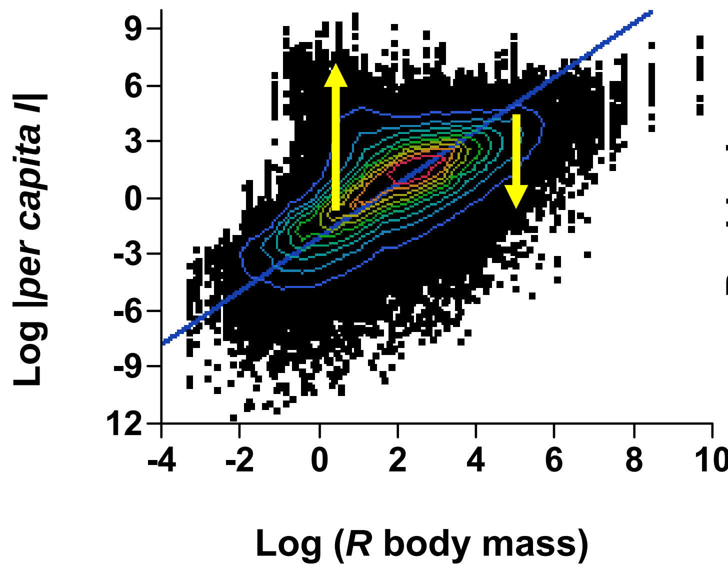


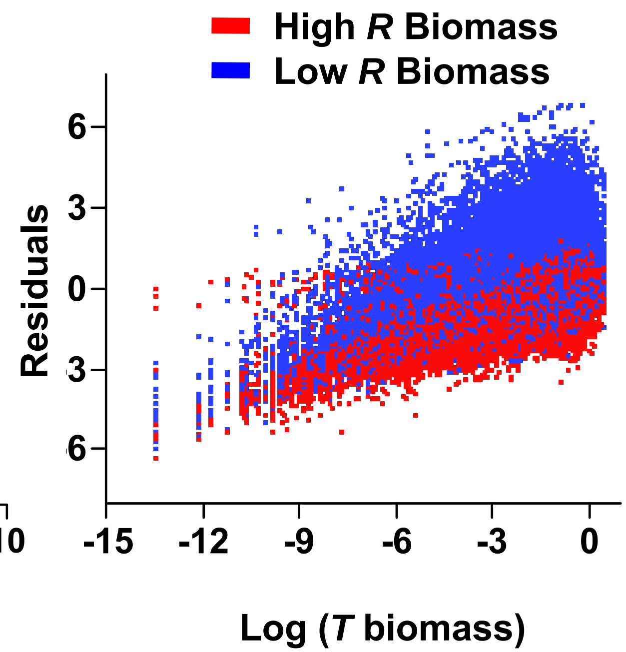


R^2 = 0.45
Slope = 1.4

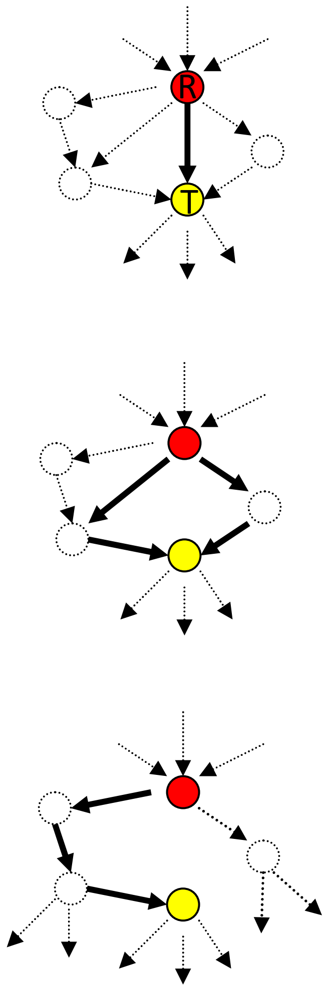
Per Capita Removal Interaction Strength

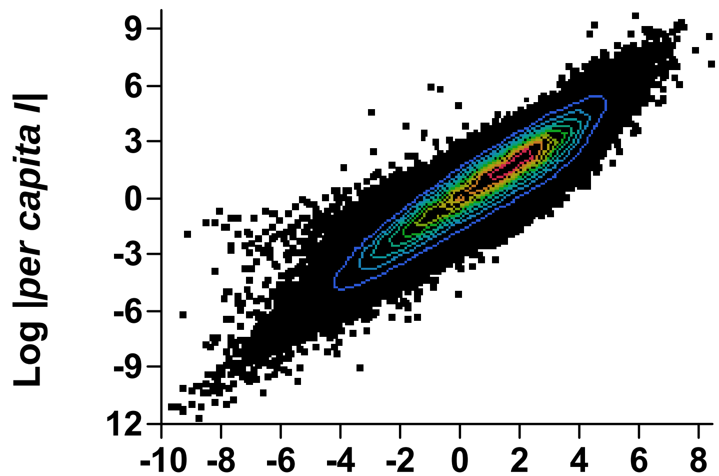






Per Capita Interaction Strength





Predicted by:
Log (T biomass) +
Log (R biomass) +
Log (R body mass)

R^2 = 0.88

population *I*

(population interaction strength)

population *I*

(total effect on T of removing R)

Classification and Regression Trees (CART):

of the 90 variables tracked

best predictors of both
sign and *magnitude* of population *I*

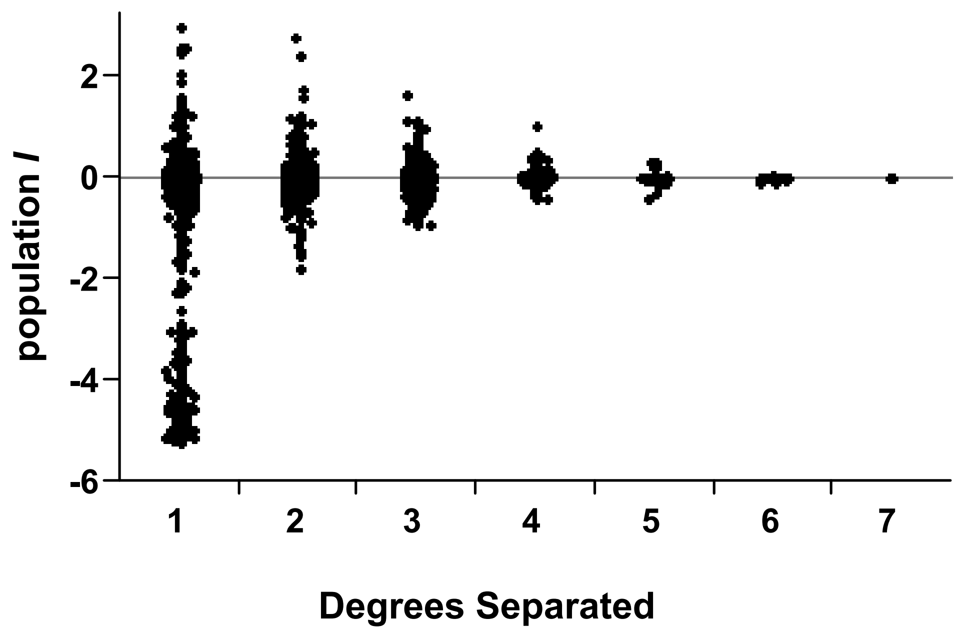
Classification and Regression Trees (CART):

of the 90 variables tracked

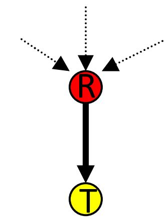
best predictors of both
sign and *magnitude* of population *I*

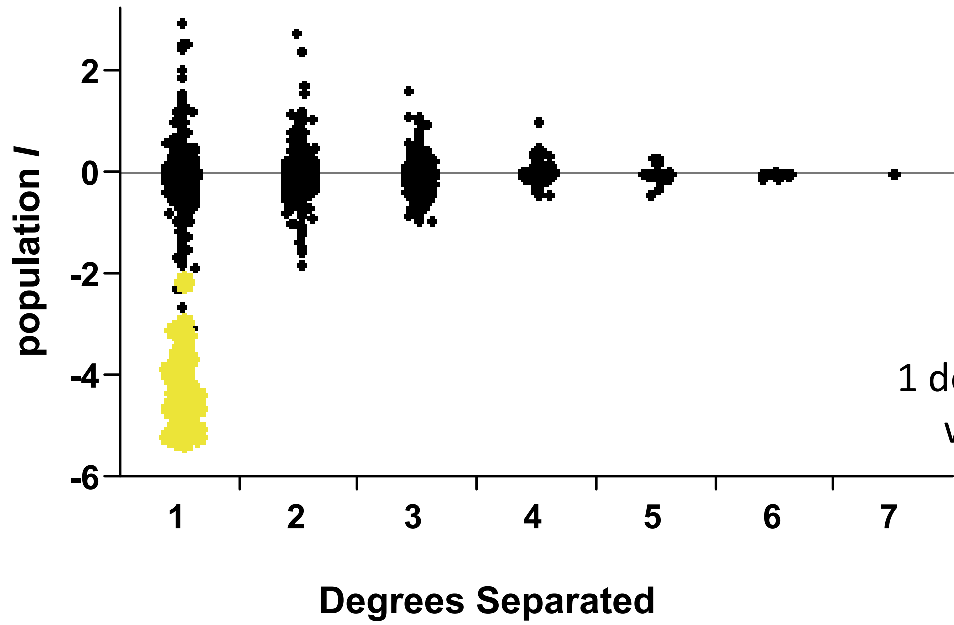
$R^2 = 0.86 – 0.89$

Weighted Sum Path Signs
T biomass
R biomass
Degrees Separated
Simple Chains
T trophic level

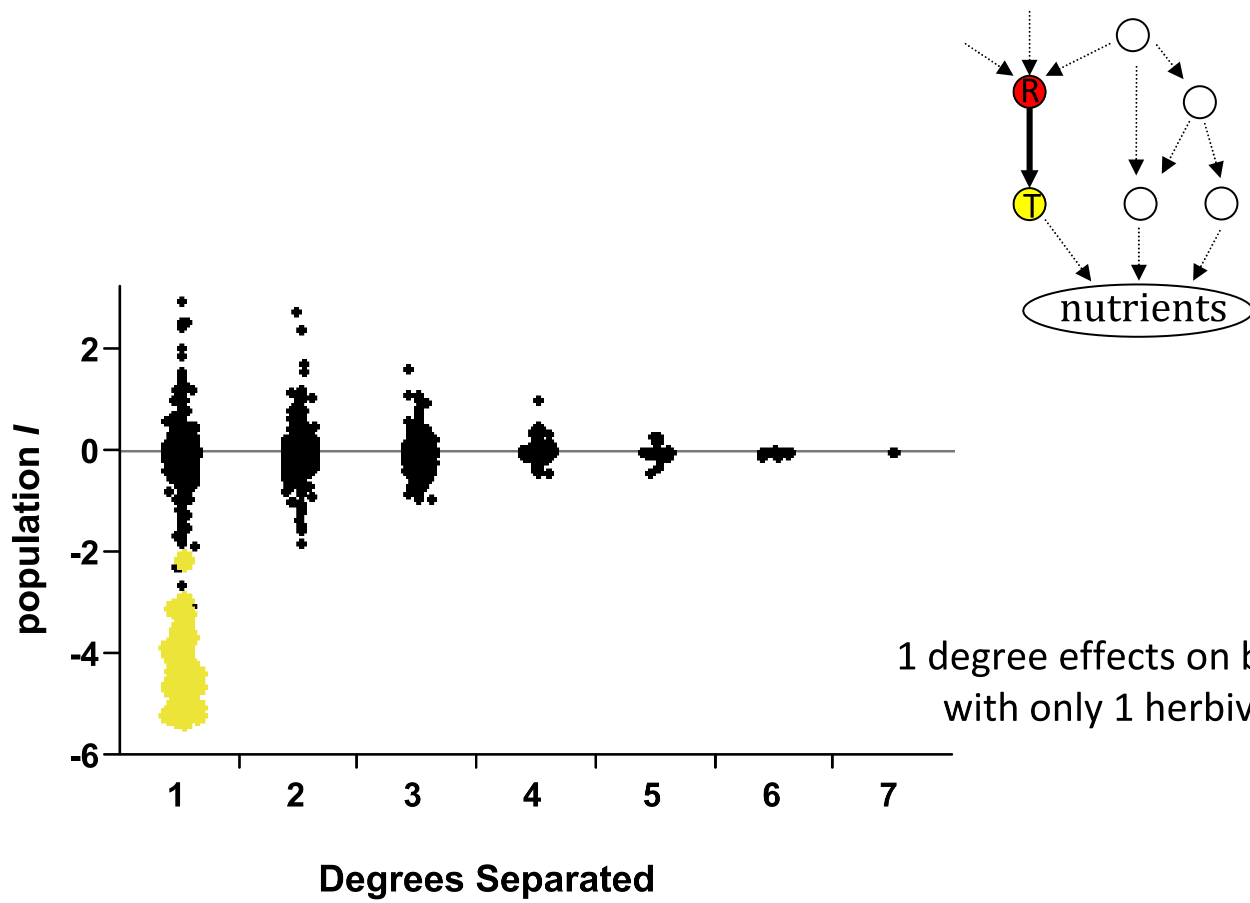


population I
2
0
-2
-4
-6
1
2
3
4
5
6
7
Degrees Separated

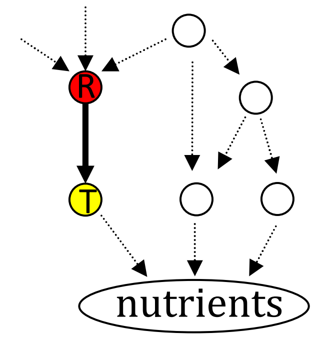


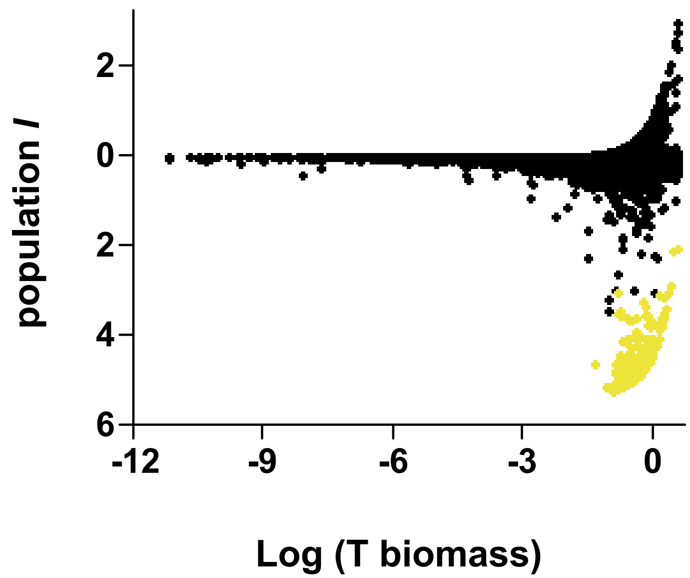


1 degree effects on basal T
with only 1 herbivore

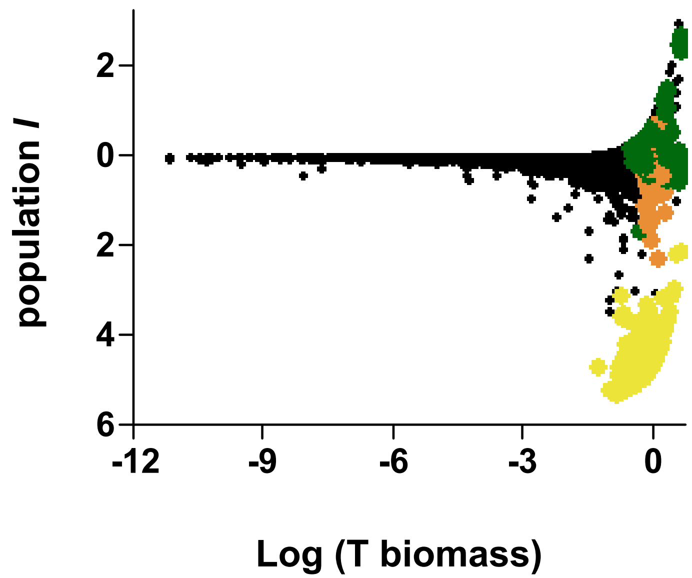


1 degree effects on basal T
with only 1 herbivore





1 degree effects on basal T
with only 1 herbivore



weighted sum path signs > 0

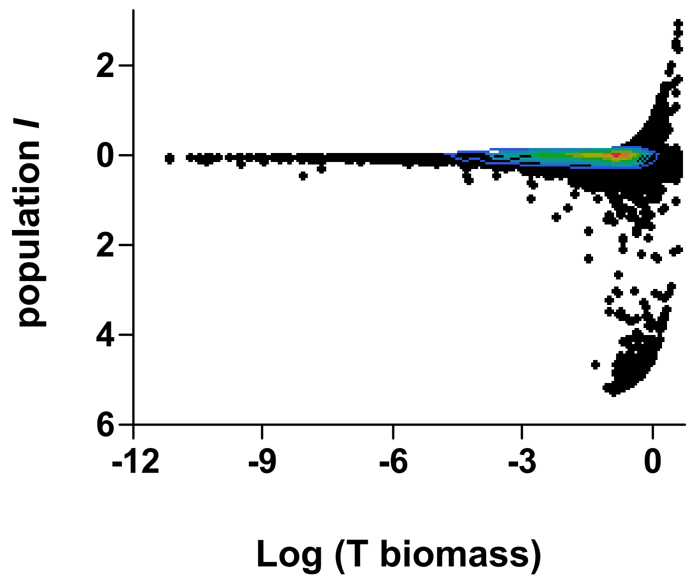
high biomass R and T

weighted sum path signs < 0

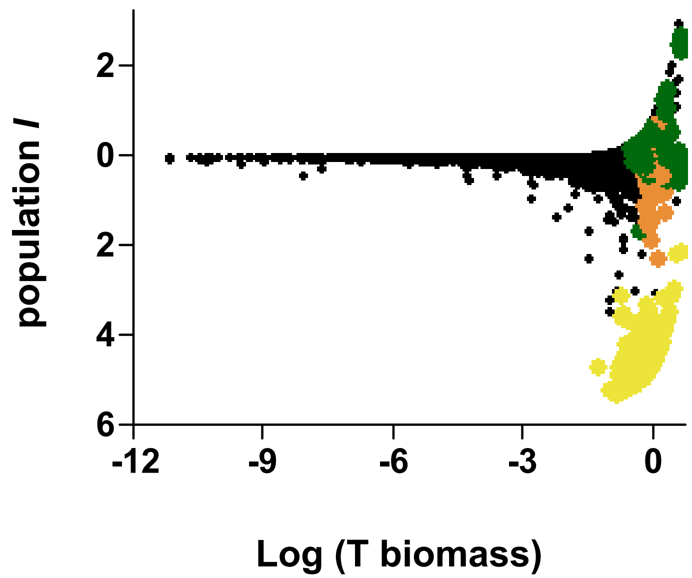
1 degree effects on basal T
with only 1 herbivore

some issues

interaction strengths are log-normally distributed



sign and magnitude explained by different things



weighted sum path signs > 0

high biomass R and T

weighted sum path signs < 0

weighted sum path signs < 0

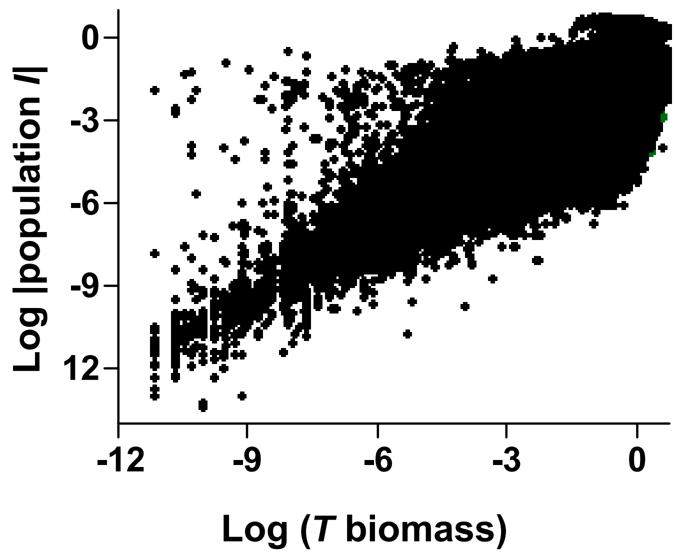
Classification and Regression Trees (CART)
on *log transformed* Interaction Strengths

of the 90 variables tracked

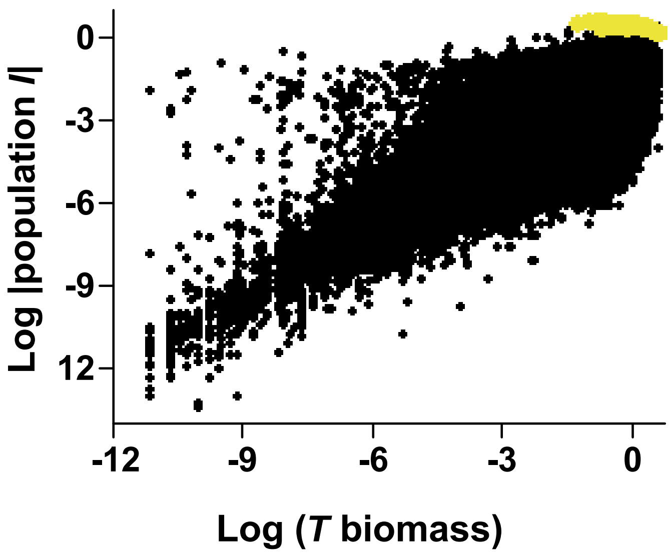
best predictors of
absolute magnitude of log(population *I*)

T biomass
R biomass
(Degrees Separated)

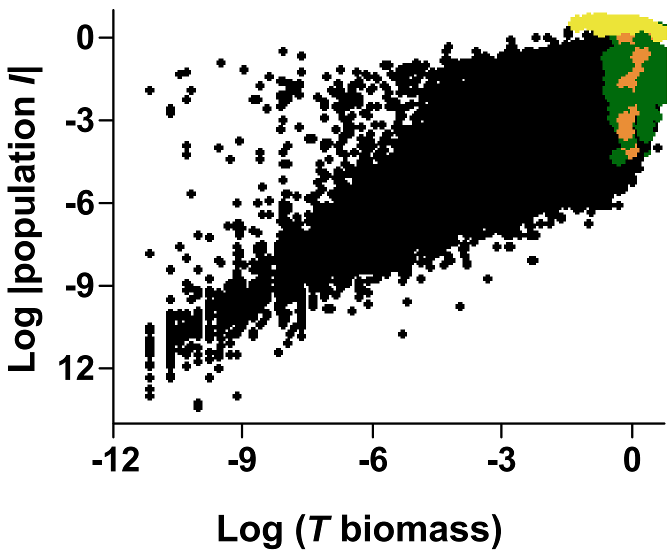
$R^2 = 0.65$

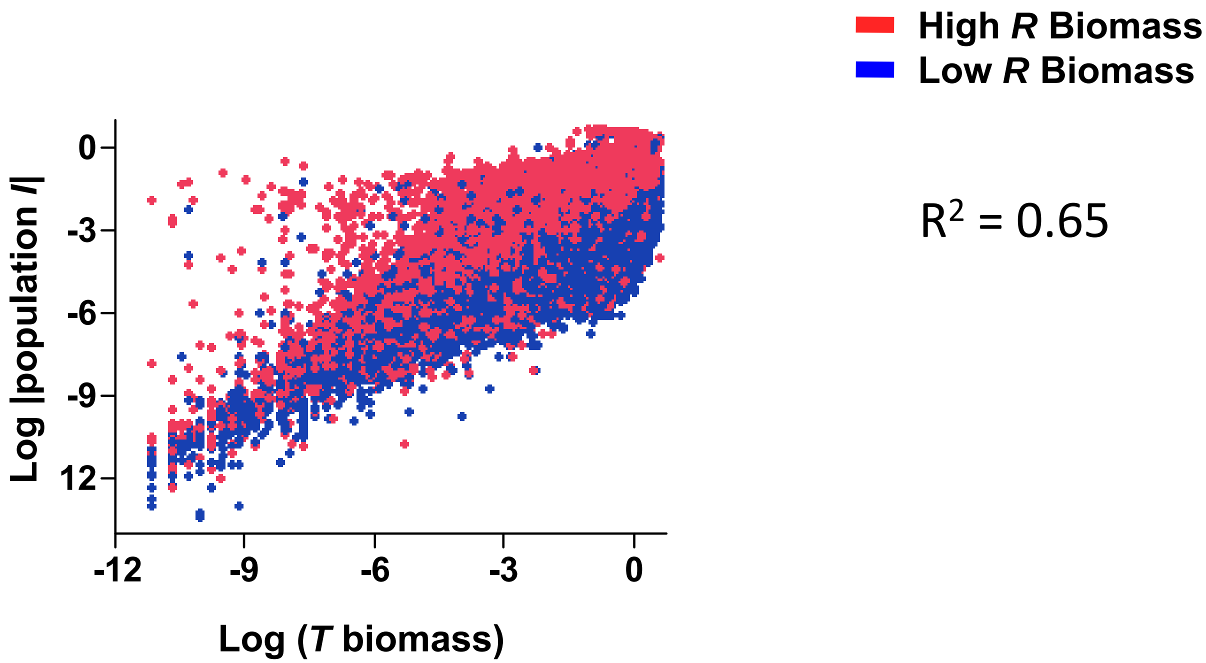


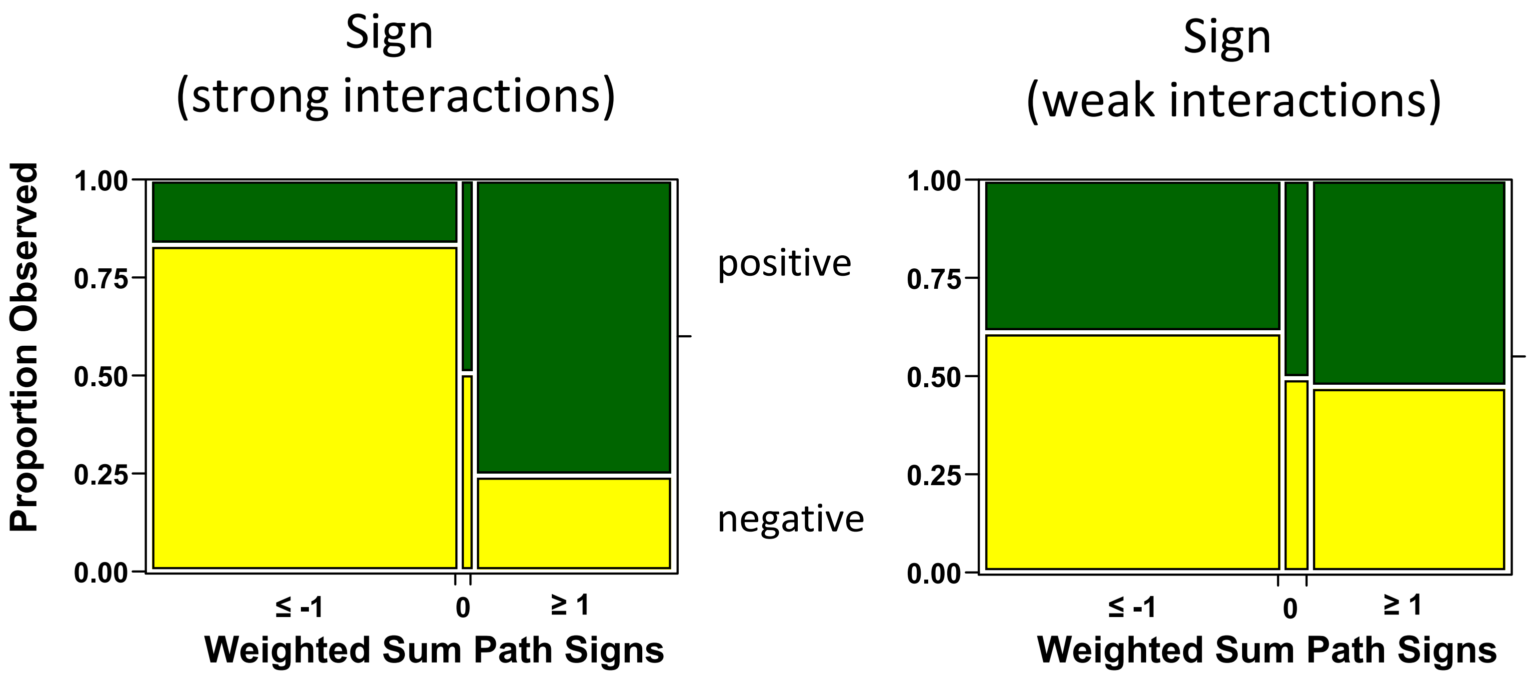
Log |population I|
0
-3
-6
-9
12
-12
-9
-6
-3
0
Log (T biomass)



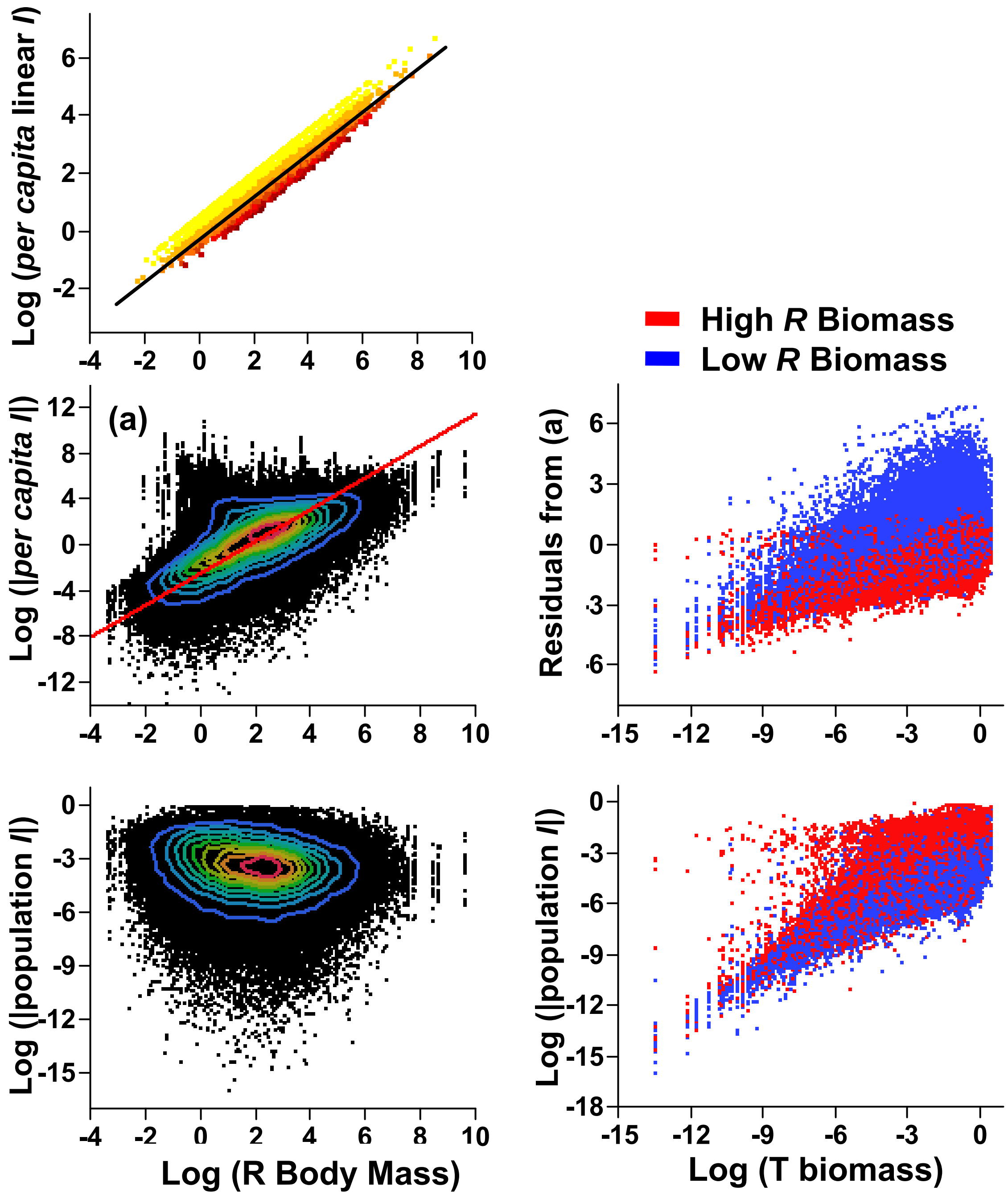
Log |population I|
0
-3
-6
-9
12
-12
-9
-6
-3
0
Log (T biomass)


Log |population I|
0
-3
-6
-9
12
-12
-9
-6
-3
0
Log (T biomass)


High R Biomass
Low R Biomass
R2 = 0.65
Log |population I|
0
-3
-6
-9
12
-12
-9
-6
-3
0
Log (T biomass)



Sign
(strong interactions)
Proportion Observed
1.00
0.75
0.50
0.25
0.00
≤ -1
0
≥ 1
Weighted Sum Path Signs
positive
negative
Sign
(weak interactions)
1.00
0.75
0.50
0.25
0.00
≤ -1
0
≥ 1
Weighted Sum Path Signs



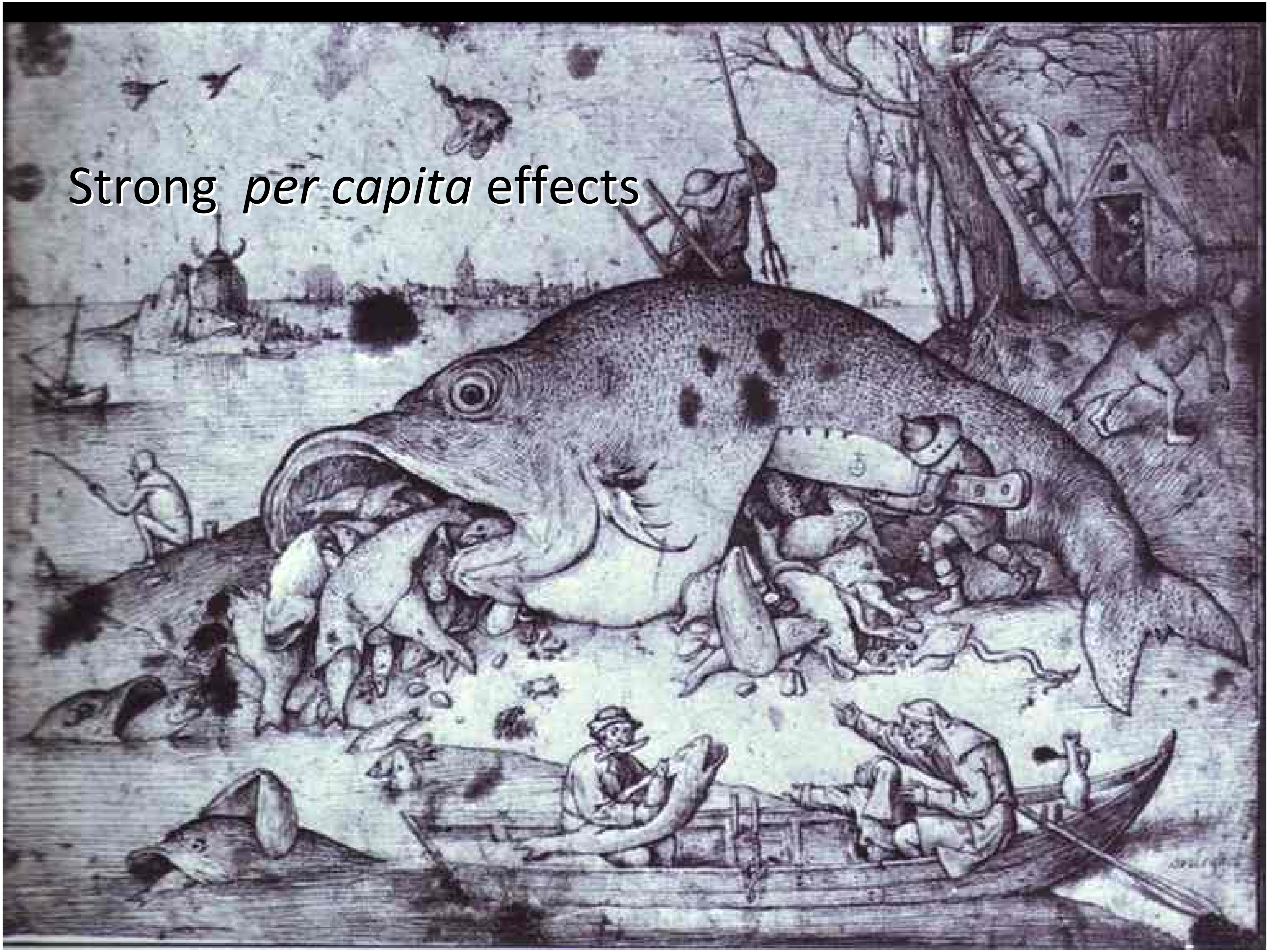
Summary:

1. 3/4 scaling disappears in complex networks

2. strongest *per capita I*: large bodied, low biomass *R* effects on high biomass *T*
$R^2 = 0.88$

3. strongest population *I*: high biomass *R* effects on high biomass *T*
$R^2 = 0.65$

Strong *per capita* effects



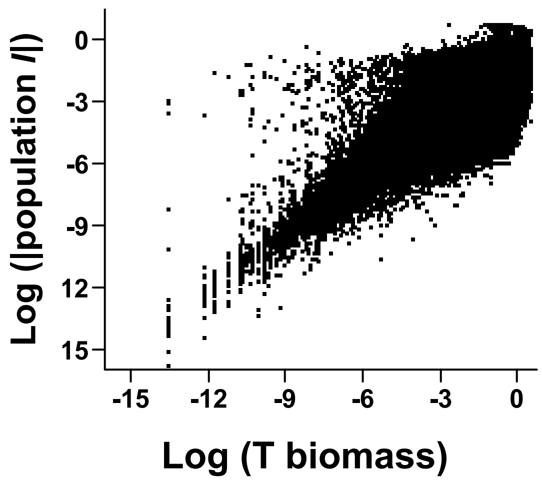
Strong population effects

How can it be so simple?

Is it circular?

predicting: $(B_{T+} - B_{T-})$
using: B_{T+}

B_{T+} = T biomass (R present)
B_{T-} = T biomass (R removed)

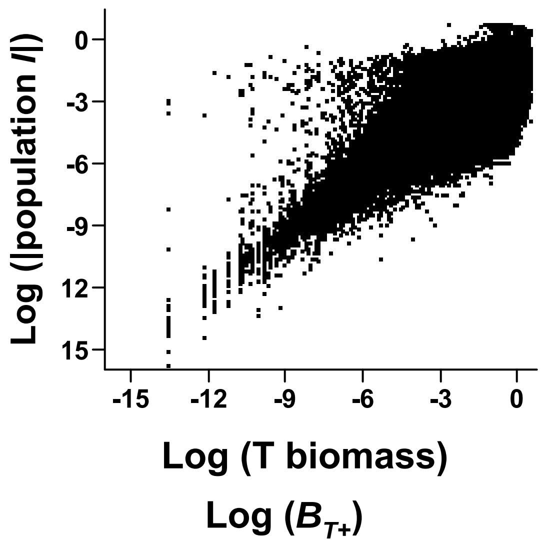


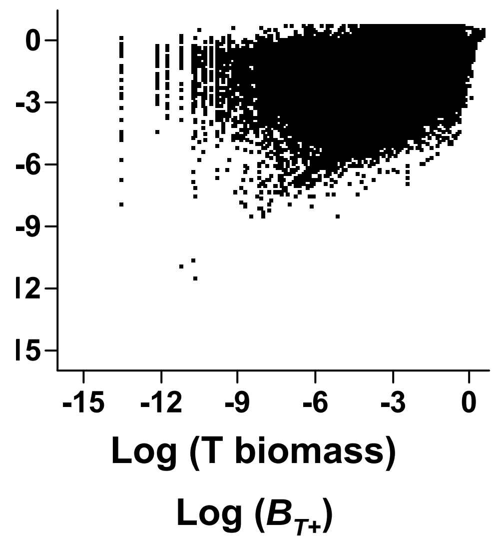
Log (B_{T+})

Is it circular?

predicting: $(B_{T+} - B_{T-})$ → 2° extinction of T
using: B_{T+}

reshuffled interactions

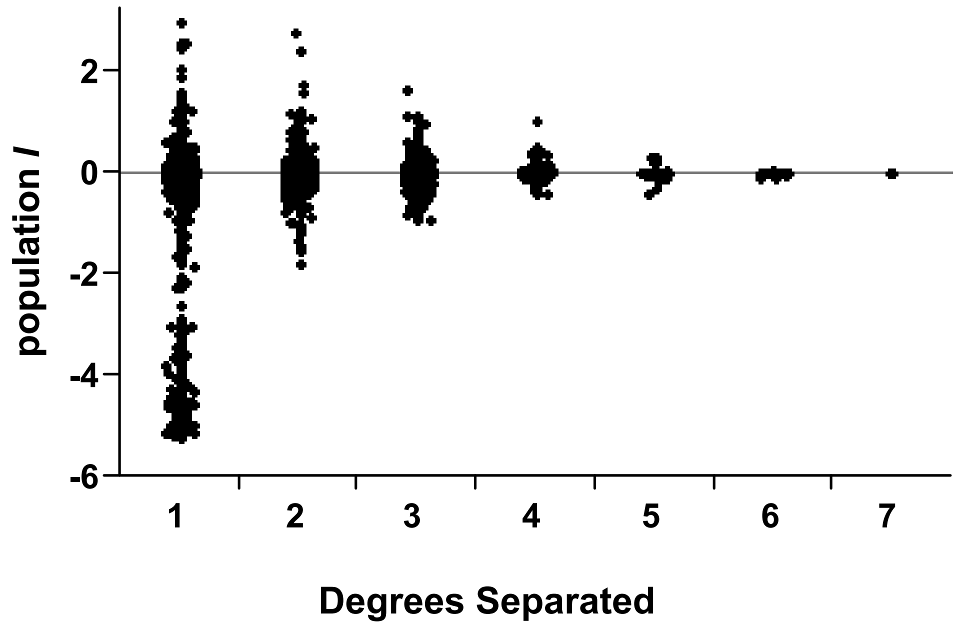




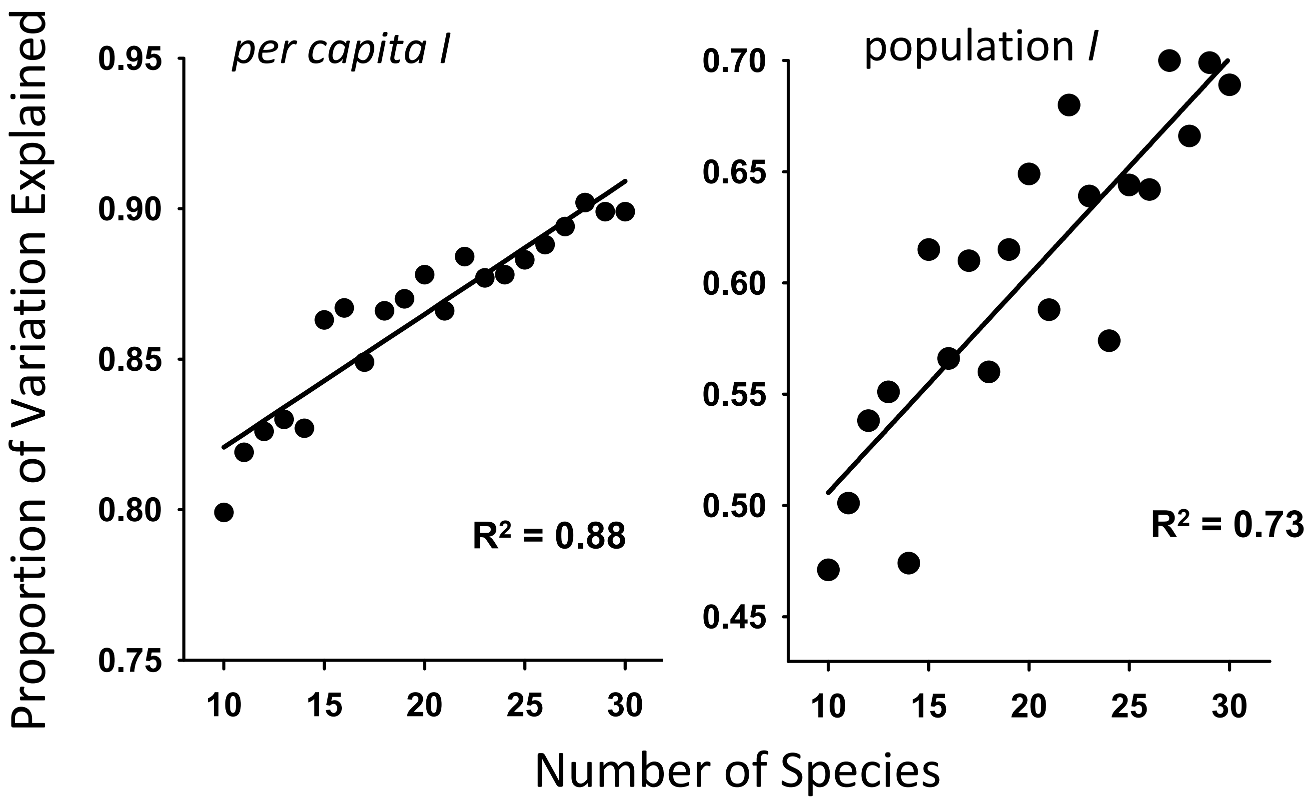
$R^2 = 0.59$

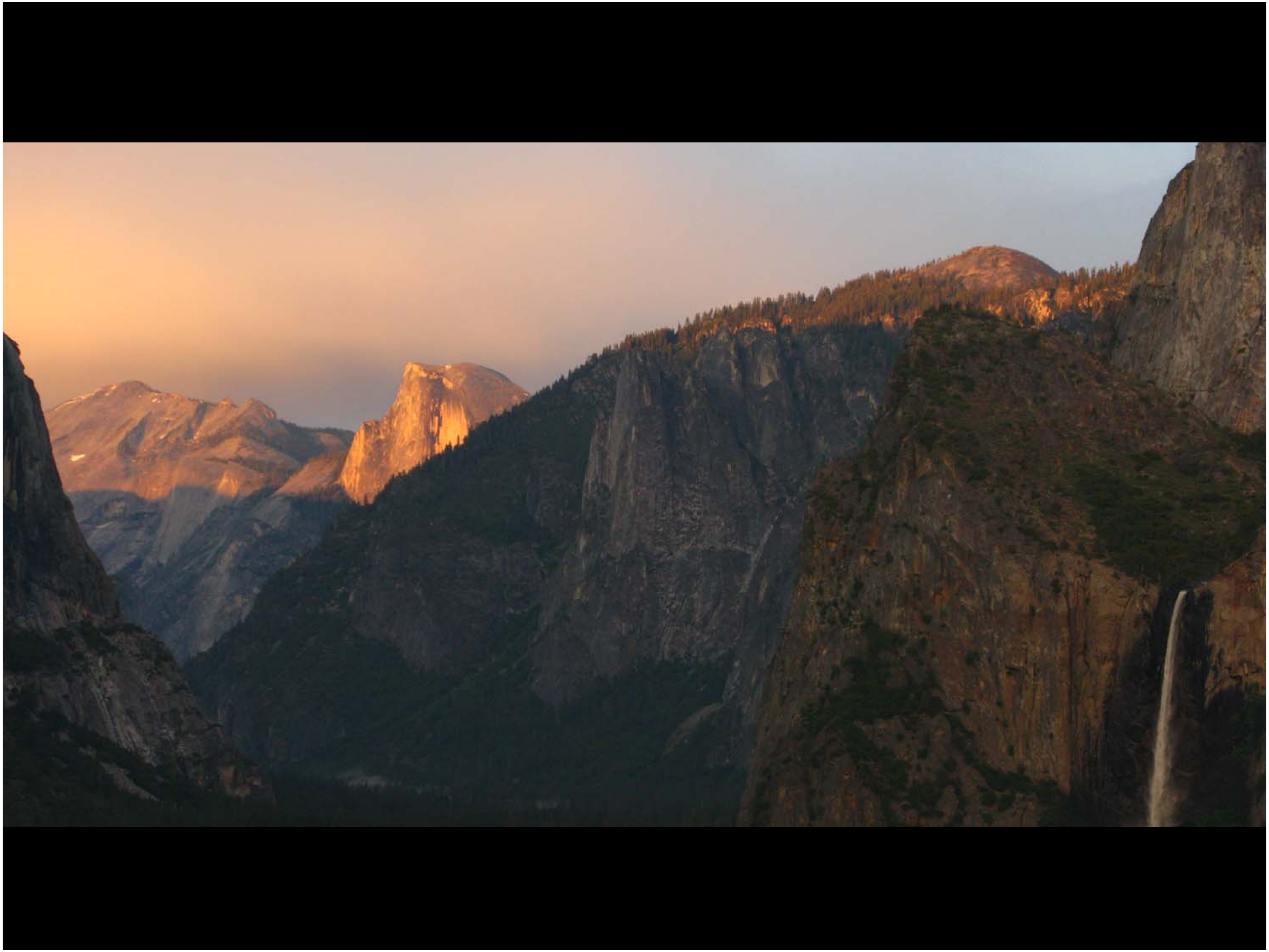
$R^2 = 0.19$

Chains of interactions tend to dampen with distance



More Complex is More Simple





What about the real world?

Predictions:

<1>

Purely metabolic interactions
should be well predicted by simple attributes of *R* and *T*.

Predictions:

<2>

Deviations from simple metabolic predictions should point to strong non-metabolic influences.

Goal:

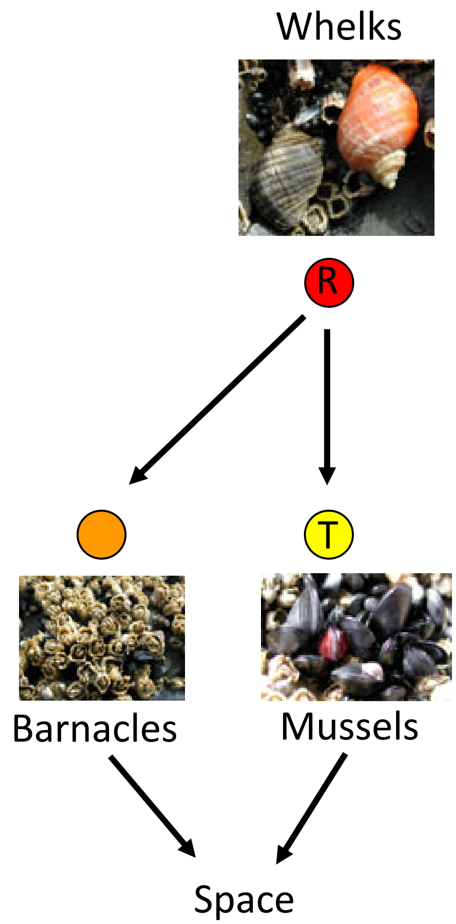
De-trend the "metabolic baseline" of complex systems
to gain insight into other important ecological processes.

Successfully
Predict

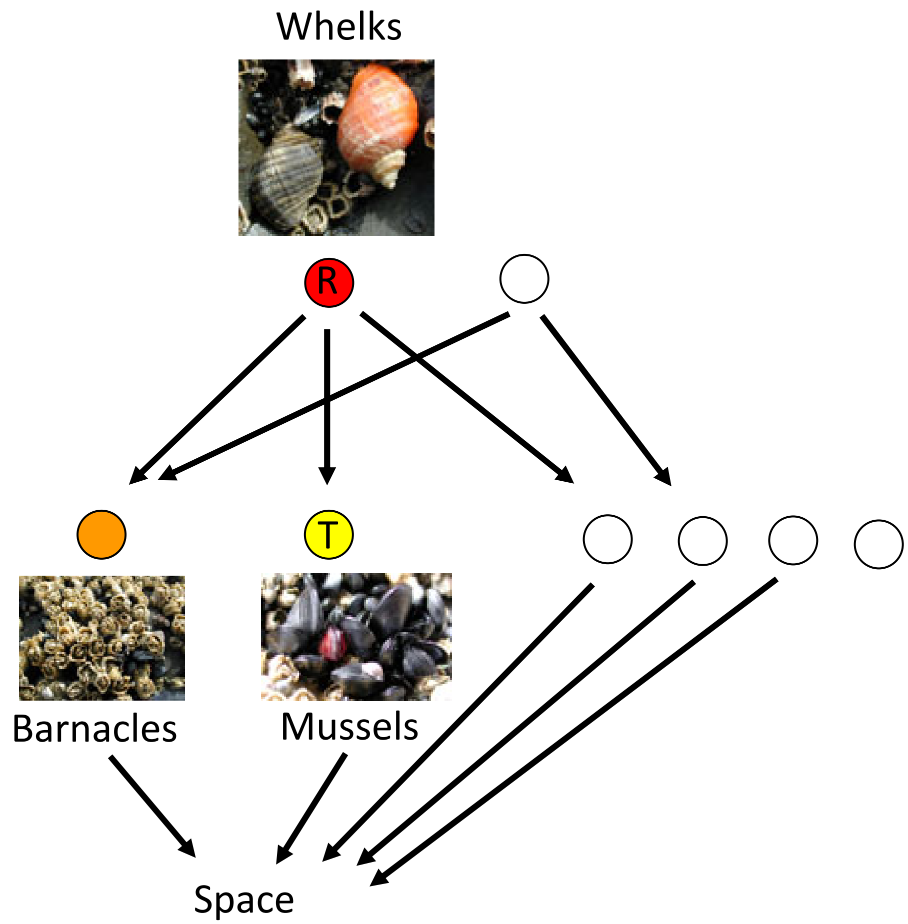
Predictably

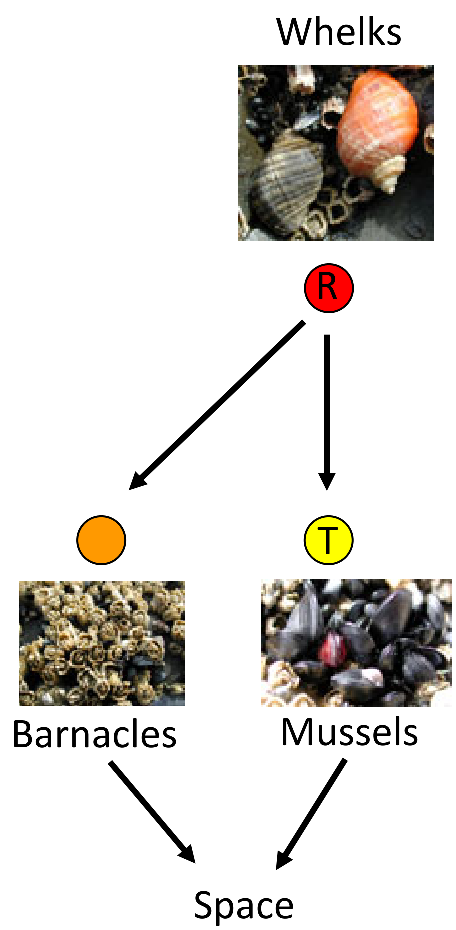
Fail

Berlow 1999 *Nature* 398:330

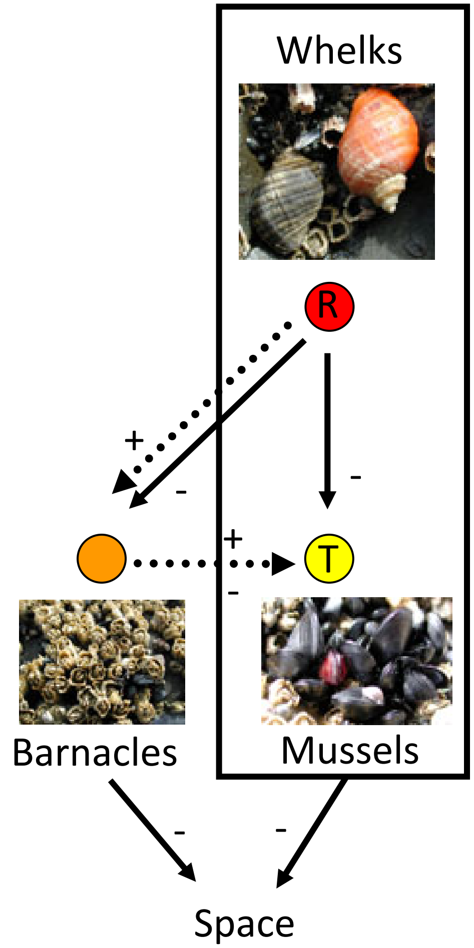

Whelks
R
T
Barnacles
Mussels
Space

Field Experiment Conditions

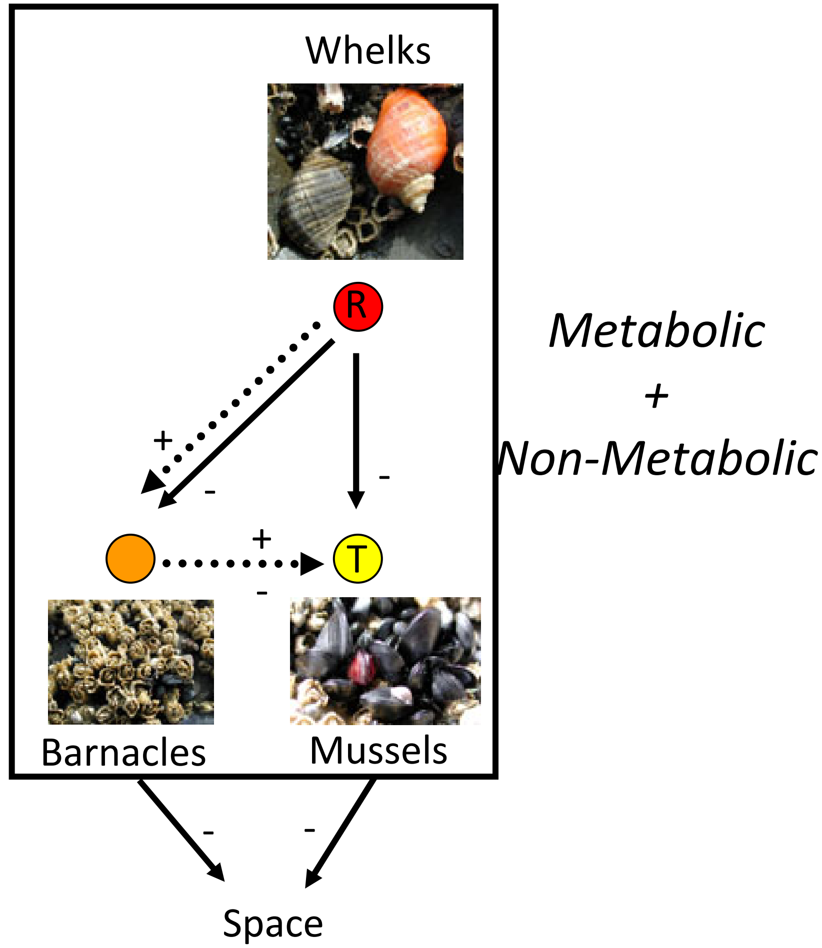


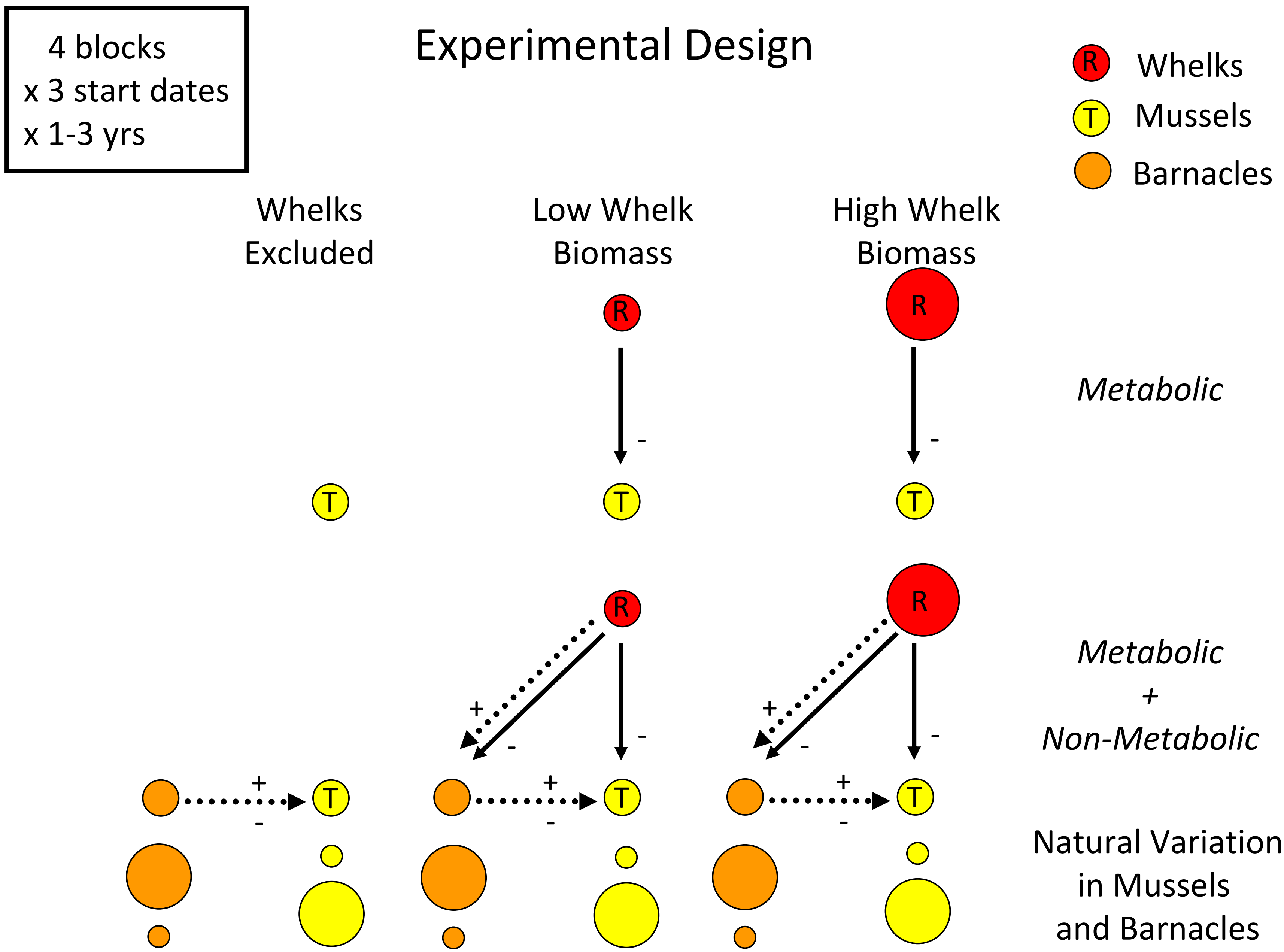


Whelks
R
T
Barnacles
Mussels
Space

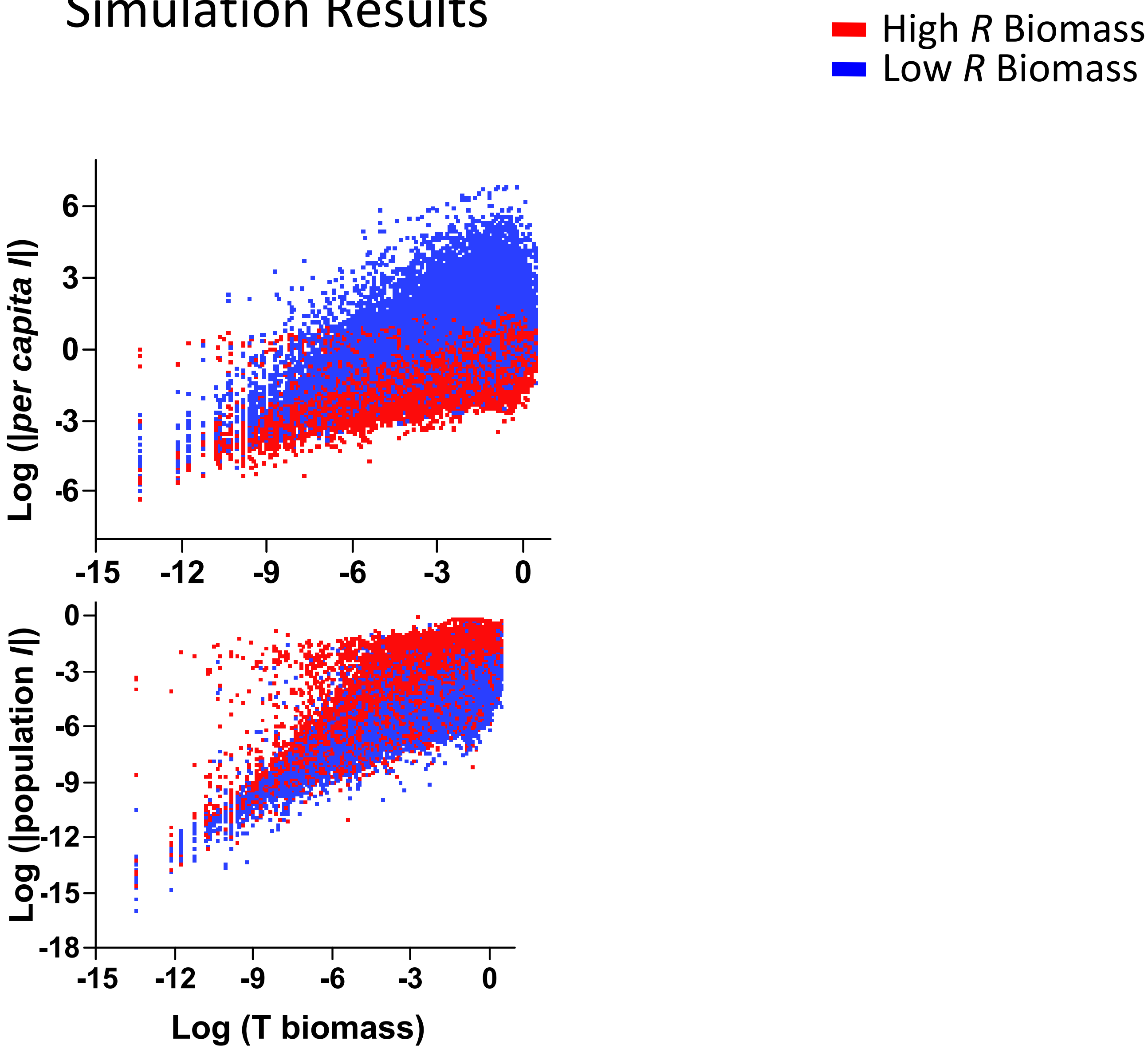


Metabolic

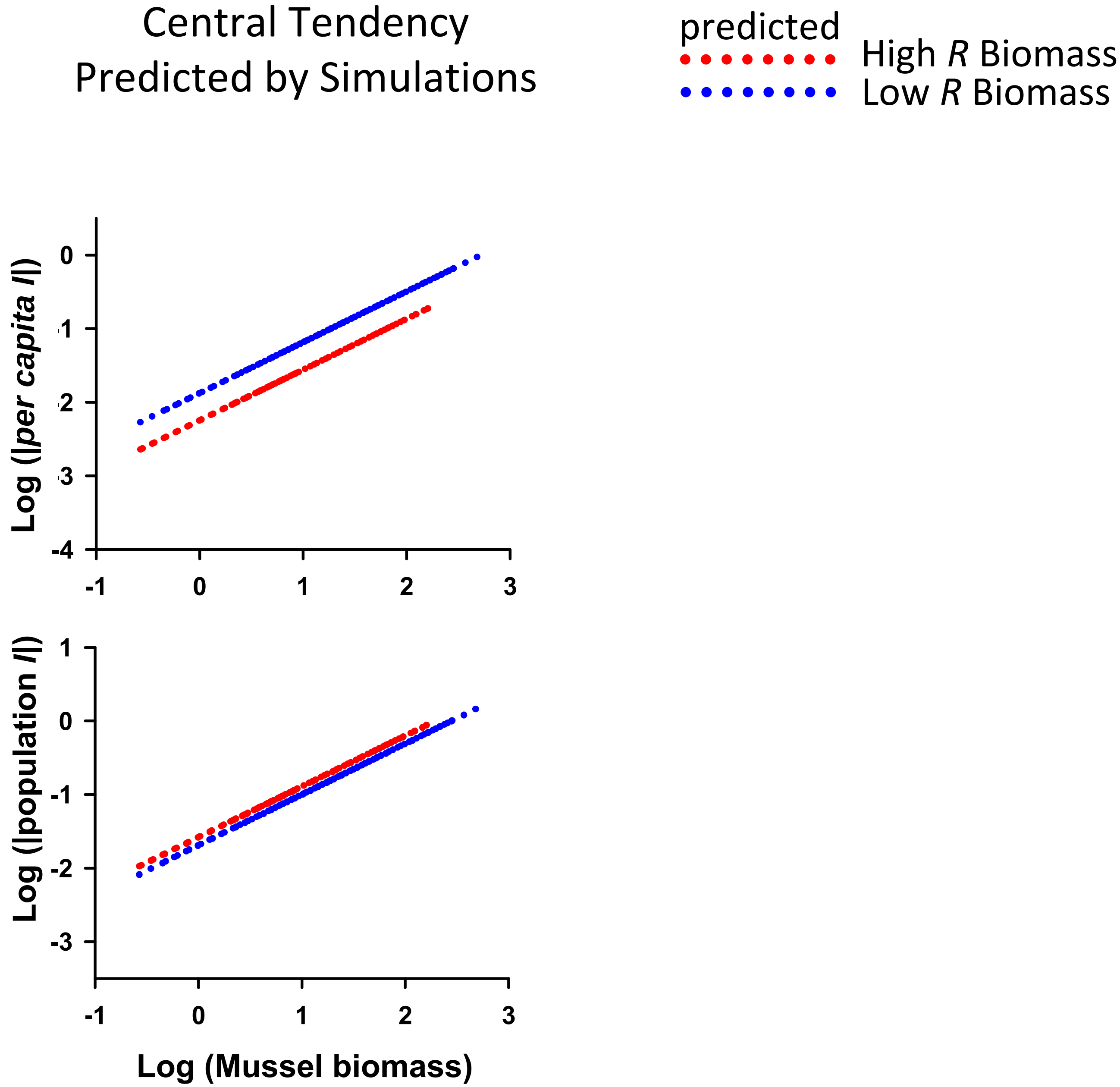

Whelks
R
+
-
-
+
T
-
Barnacles
Mussels
-
-
Space
Metabolic
+
Non-Metabolic

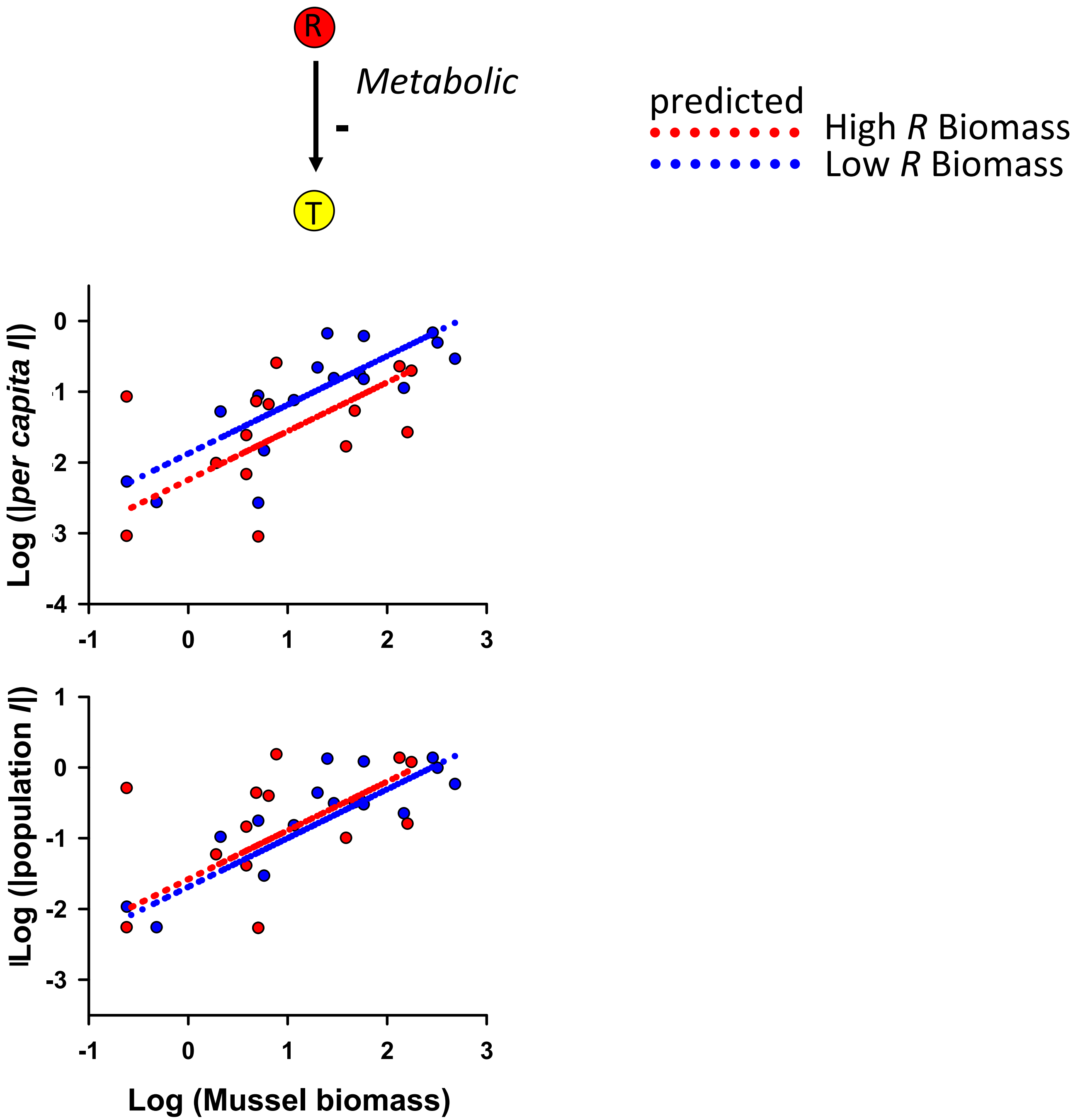

4 blocks
x 3 start dates
x 1-3 yrs
Experimental Design
R Whelks
T Mussels
Barnacles
Whelks Excluded
Low Whelk Biomass
High Whelk Biomass
Metabolic
Metabolic + Non-Metabolic
Natural Variation in Mussels and Barnacles

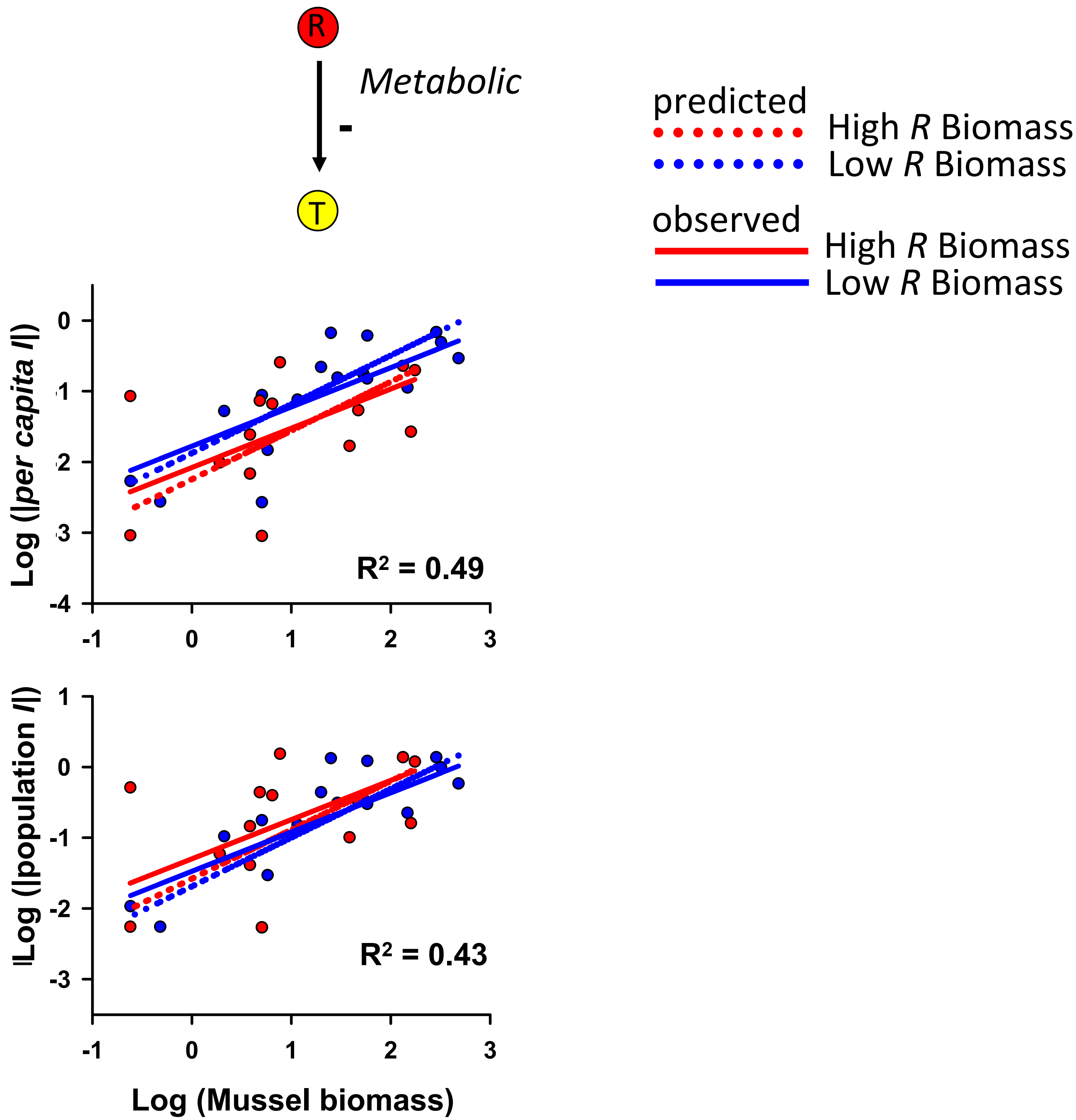
Simulation Results

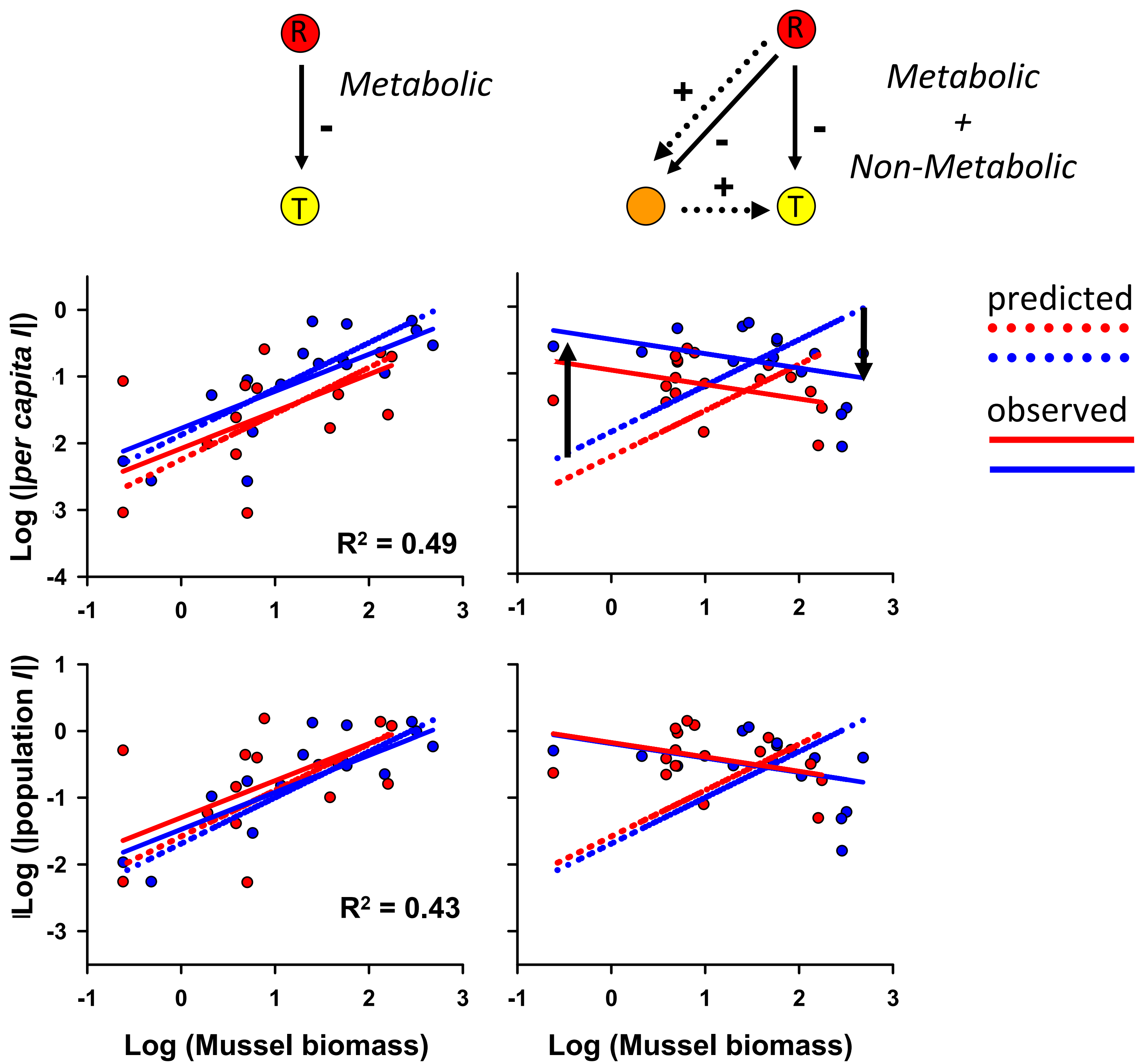


Central Tendency
Predicted by Simulations




R
Metabolic
-
T
predicted
High R Biomass
Low R Biomass
Log (|per capita I|)
0
-1
-2
-3
-4
-1
0
1
2
3
Log (|population I|)
1
0
-1
-2
-3
-1
0
1
2
3
Log (Mussel biomass)


R
Metabolic
-
T
predicted
High R Biomass
Low R Biomass
observed
High R Biomass
Low R Biomass
Log (|per capita I|)
R² = 0.49
Log (|population I|)
R² = 0.43
Log (Mussel biomass)



R
T
Metabolic
-
R
T
+
-
-
+
Metabolic
+
Non-Metabolic
predicted
observed
Log (|per capita I|)
R² = 0.49
Log (|population I|)
R² = 0.43
Log (Mussel biomass)
Log (Mussel biomass)

Summary

<1>
¾ power law signal disappears and
new simple patterns emerge in a network context.

<2>
magnitude of *per capita* and population *I*
explained by 2-3 simple species attributes (of 90)

<3>
effects dampen with distance
more complex = more simple

<4>
predictable fit and lack-of-fit in field experiment

Conclusions

<1>

metabolic "webbiness" of life not necessarily a big source of uncertainty.
"module" approaches may be appropriate

<2>

metabolic "null model" may describe
a universal *baseline* of species interactions in a complex network.

<3>

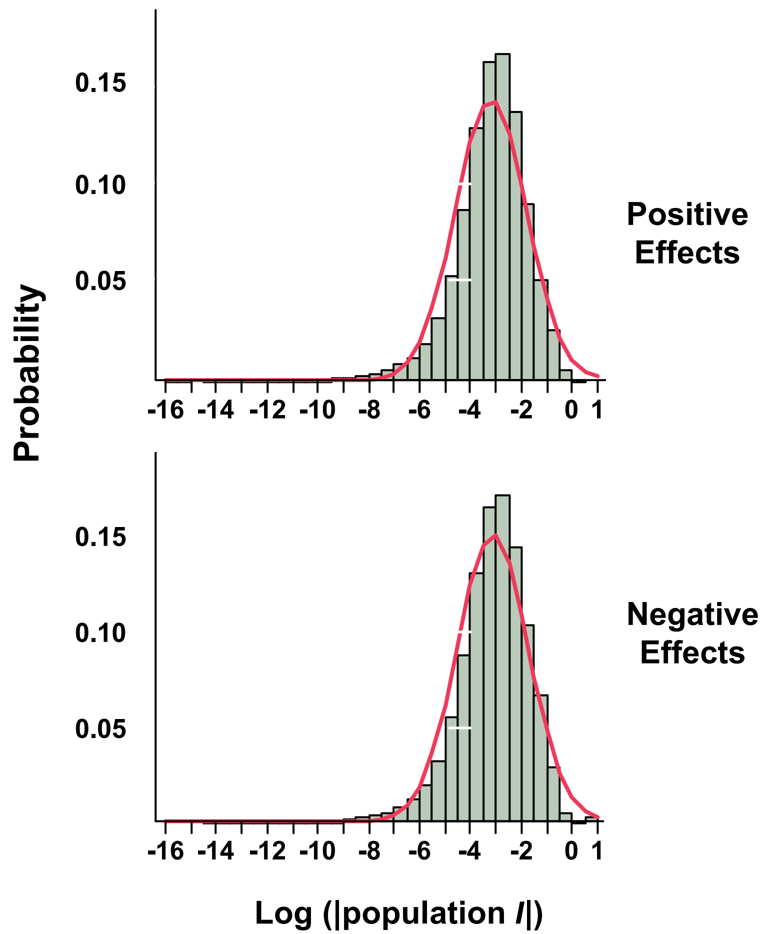
"de-trend" metabolism in ecological networks
to better understand non-metabolic interactions and processes

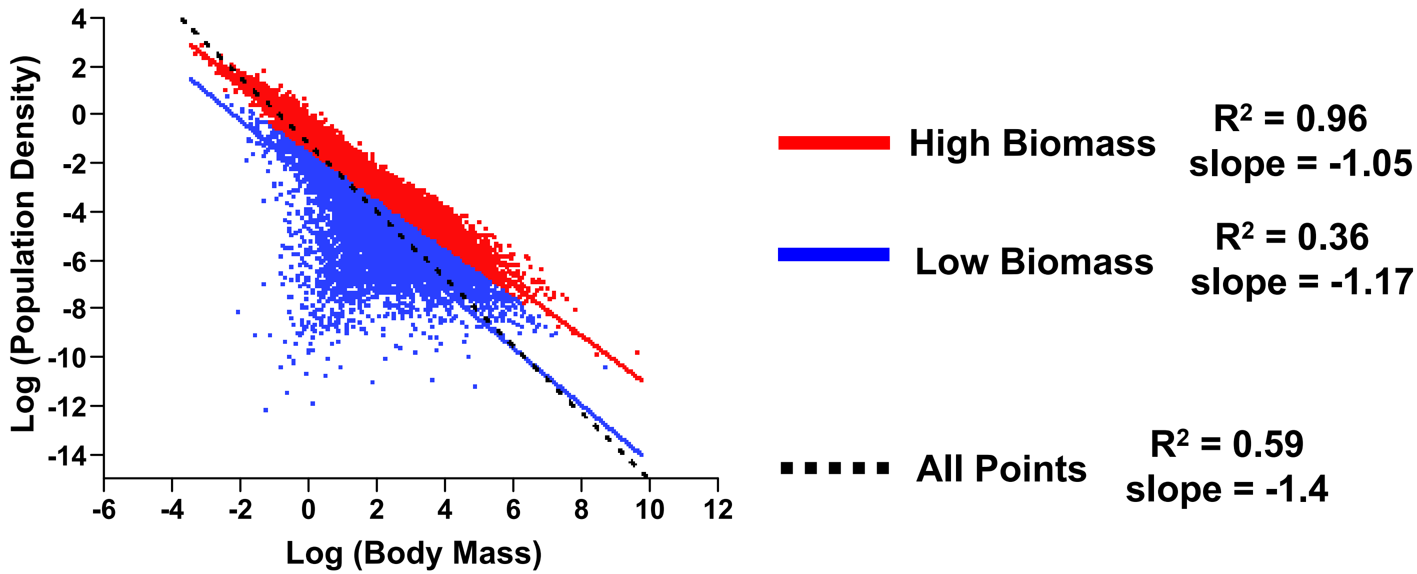
Acknowledgements

Alexander von Humboldt Foundation

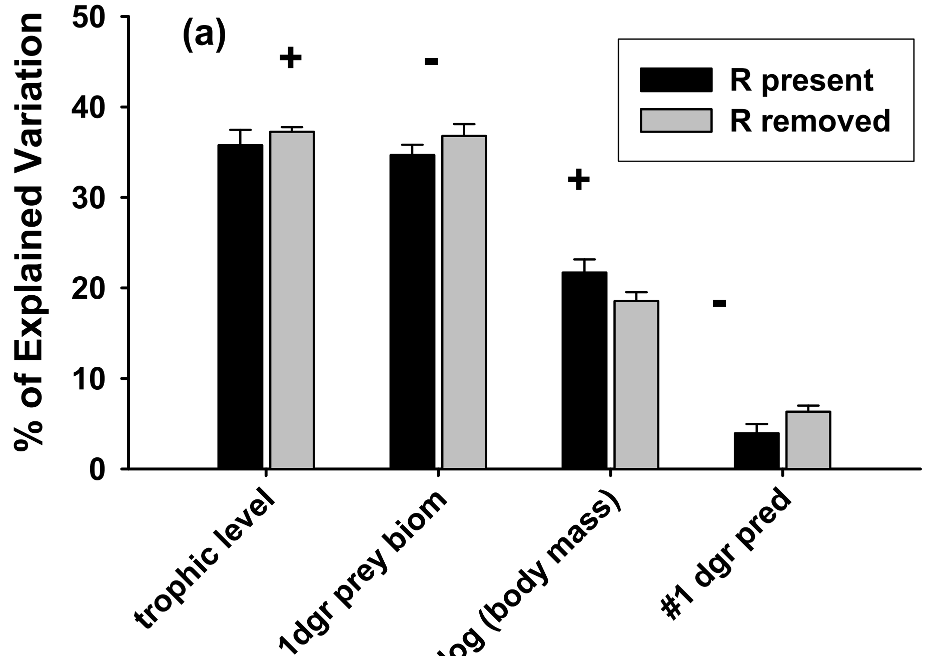
"I would not give a fig for simplicity on this side of complexity,
but I'd give my life for the simplicity on the other side of complexity"

Oliver Wendell Holmes, Jr.


Probability
0.15
0.10
0.05
-16 -14 -12 -10 -8 -6 -4 -2 0 1
Positive Effects
Negative Effects
Log (|population *I*|)



Log (Population Density)
4
2
0
-2
-4
-6
-8
-10
-12
-14
-6
-4
-2
0
2
4
6
8
10
12
Log (Body Mass)
High Biomass
R^2 = 0.96
slope = -1.05
Low Biomass
R^2 = 0.36
slope = -1.17
All Points
R^2 = 0.59
slope = -1.4



n = 5 random subsamples
of 10,000 interactions

Chains of interactions tend to dampen with distance