Does one size fit all?

Joel E. Cohen
Rockefeller & Columbia Universities
New York, New York, USA

2008-04-05

SIZEMIC, Clare College Cambridge, UK

Collaborators in food web work

Carolin Banašek-Richter
Louis-Felix Bersier
Marie-France Cattin Blandenier
Jaap Bloem
Anton M. Breure
Frederic Briand
Ulrich Brose
Stephen R. Carpenter
Xin Chen*
Charles Godfray
Henri A. Den Hollander
Tomas Jonsson*
Jamie M. Kneitel
Janos Komlos
Tomas Luczak
Neo D. Martinez
Jane Memmott
Christine Mueller
Thomas Mueller*
Christian Mulder
Charles M. Newman
Zbigniew Palka
Stuart Pimm
Dave Raffaelli
Daniel C. Reuman*
Joan Saldaña
Van Savage
Daniella Schittler
Kenneth Schoenly*
Heikki Setälä
Guy Woodward
Peter Yodzis
Zhiming Zhou

*postdoctoral fellows, former or present

A food web

lists organisms persisting in one (bounded) location,

with all consumer-resource trophic relationships (frequent enough over some time period).

Organisms should be resolved to level of detail required to represent feeding interactions “faithfully” by some standard: guilds, genera, species, life stages, size categories, individuals, individual attributes.

The dawn of food webs: Karl Moebius

Moebius studied oyster beds in Kiel Bay, Germany, in 1877.

He was first to define the concept of an *ecological community*.

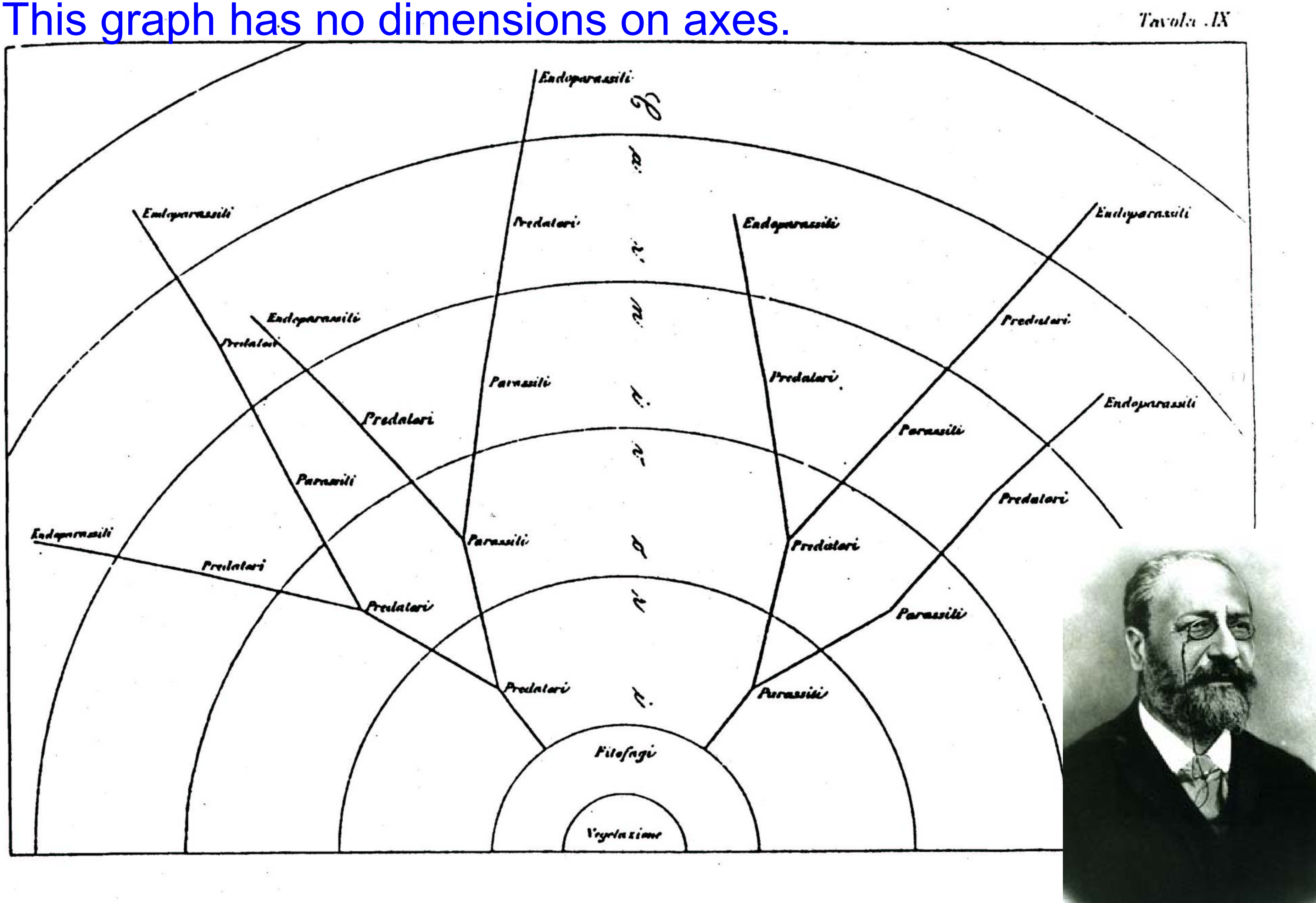
Moebius, K. 1877. *Die Auster und die Austernwirtschaft.* Berlin.

Definition (Moebius 1877): An ecological community is

"a group of living beings of which the numbers and types of species and individuals correspond to the average external conditions, which are subject to reciprocal influences, and which maintain themselves permanently in a specified area by reproduction."

L. Camerano food web (1880)

This graph has no dimensions on axes.



Food web directed graph

Lorenzo Camerano probably drew first food web directed graph (1880), probably inspired by tree of life in Darwin's *Origin of Species*.

"Trophic level" is implicit in his drawings.

Dynamic cascade described in text.

Camerano, L. 1880. Dell'equilibrio dei viventi merce la reciproca distruzione. *Atti della Reale Accademia delle Scienze di Torino* 15:393-414.

Food web predation matrix

Stephen Alfred Forbes probably first used predation matrix to represent food webs (1880): sometimes qualitative, sometimes quantitative.

Forbes, Stephen Alfred, 1880. On the food of young fishes. *Illinois Laboratory of Natural History Bulletin* 1:66-79.

Quantitative predation matrix (1880)

No. specimens

Length

Relative abundance in diet

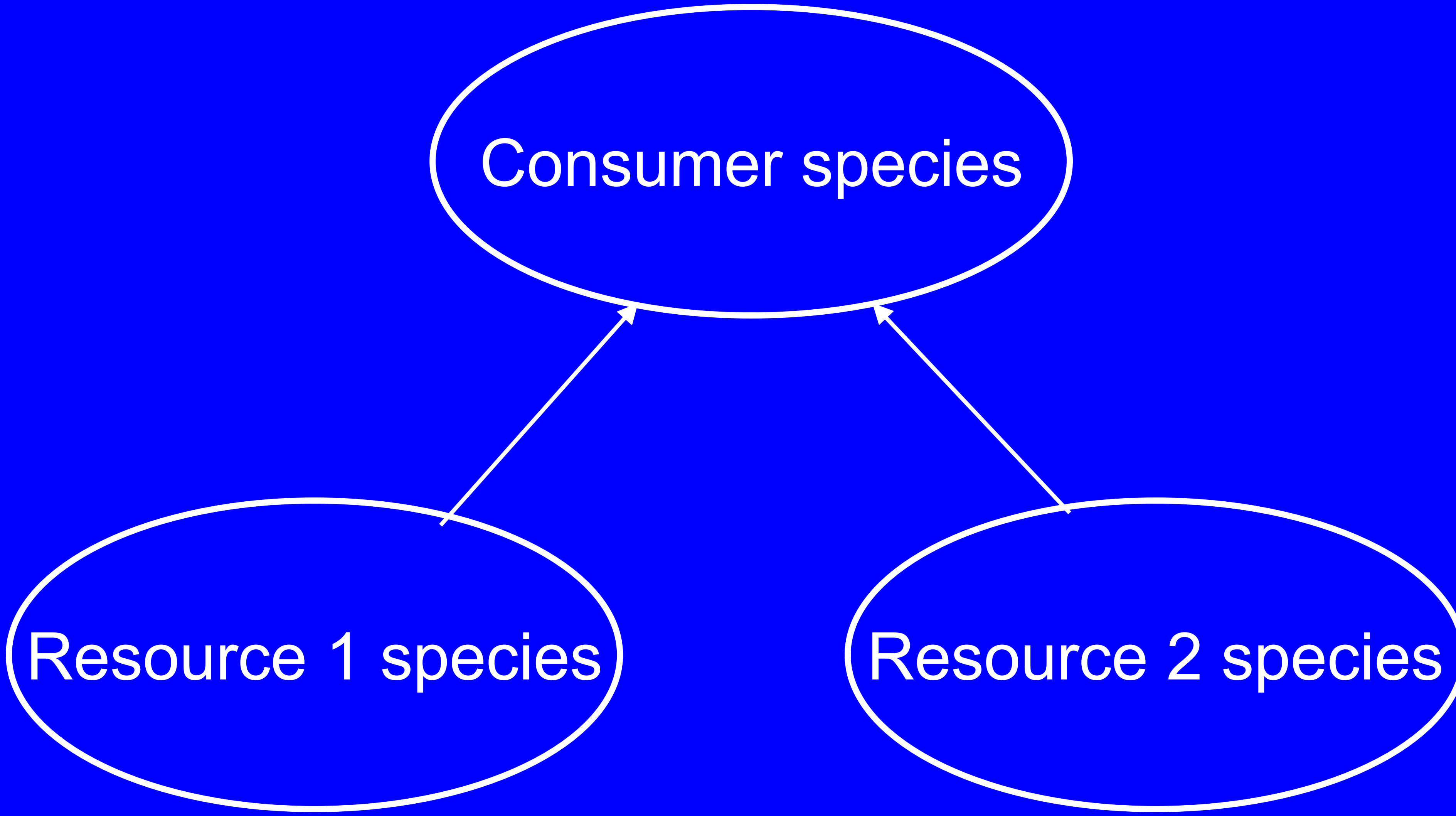
Stephen Alfred Forbes

TABLE OF FOOD OF YOUNG FISHES.

	Perca.	Morone.	Centrarchidæ.*	Haploidonotus.	Esox.	Dorysoma.	Cyprinidæ, sp.	Semotilus.	Notropis.
Number of specimens	6	1	43	1	1	12	1	3	2
Size in inches	1@1¼	1¼	⅝@2	1⅛	1¼	½@1¾	⅝	⅝@1	1½
KINDS OF FOOD.	Ratios in which each element of food was found.								
I. FISHES		50			40				
Dorysoma		50							
II. MOLLUSKS			†						
III. INSECTS	08		28	100		02	75		
1. *Diptera* (larvæ)	08		26	75		02	75		
Chironomus	08		26	75		02	75		
Corethra						†			
2. *Hemiptera* (young)			†						
Corixa			†						
3. *Neuroptera* (larvæ)			02	25					
Ephemeridæ				25					
Palingenia				25					
IV. HYDRACHNIDÆ			†						
V. CRUSTACEA	92	50	72		60	90	25	07	100
Amphipoda (young)			02		20				
Entomostraca	92	50	70		40	90	25	07	100
Cladocera	52	40	42		40	42	25		100
Sididæ			02						
Daphniidæ	50		36		20	34	25		100
Lynceidæ	02		04		20	04			
Leptodoridæ						02			
Ostracoda			09			†			
Copepoda	40	10	19			48		07	
VI. ALGÆ						08		93	

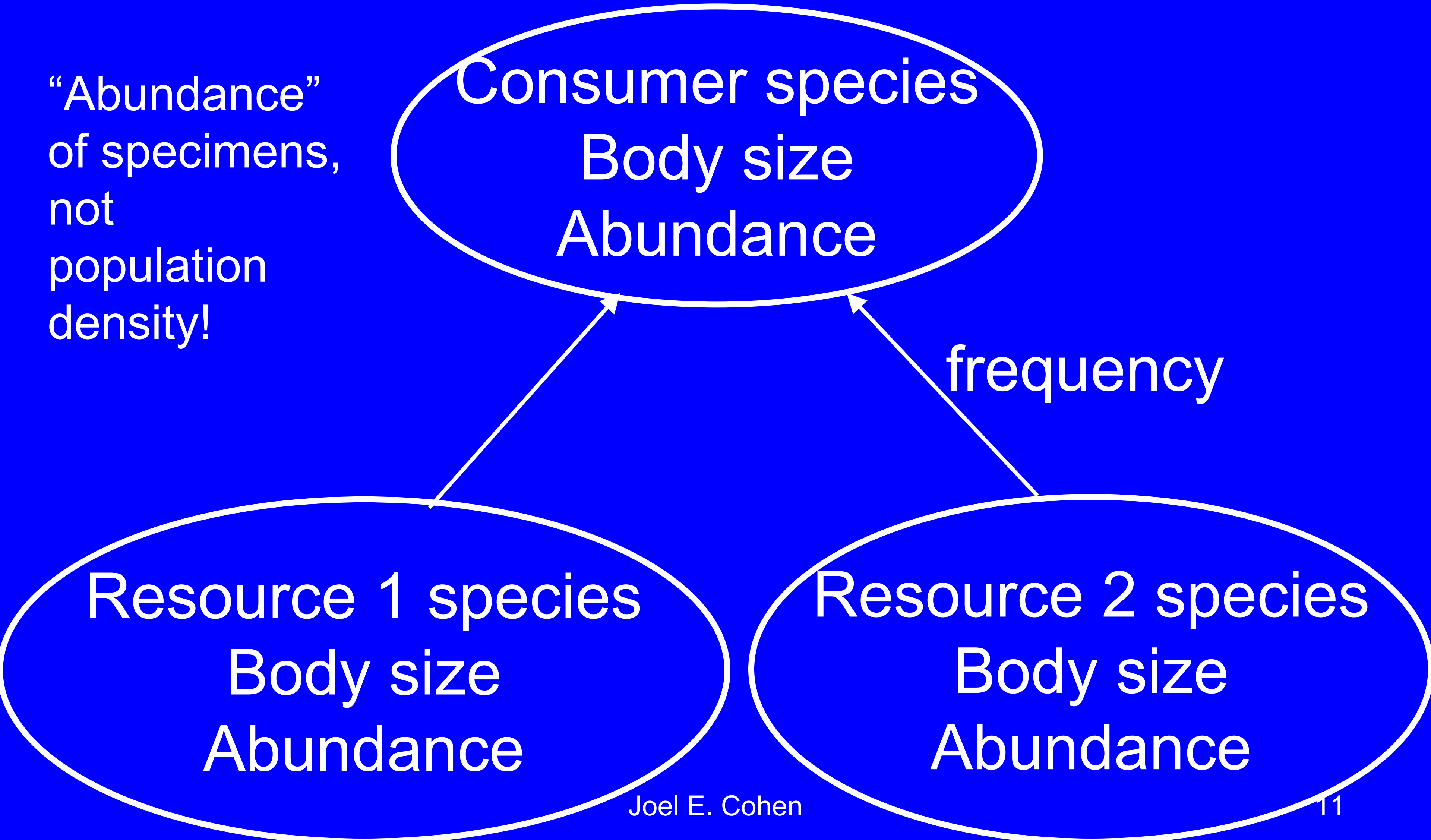
* For detailed tables of the food of the young of this family see the preceding paper on the food of the Acanthopteri.

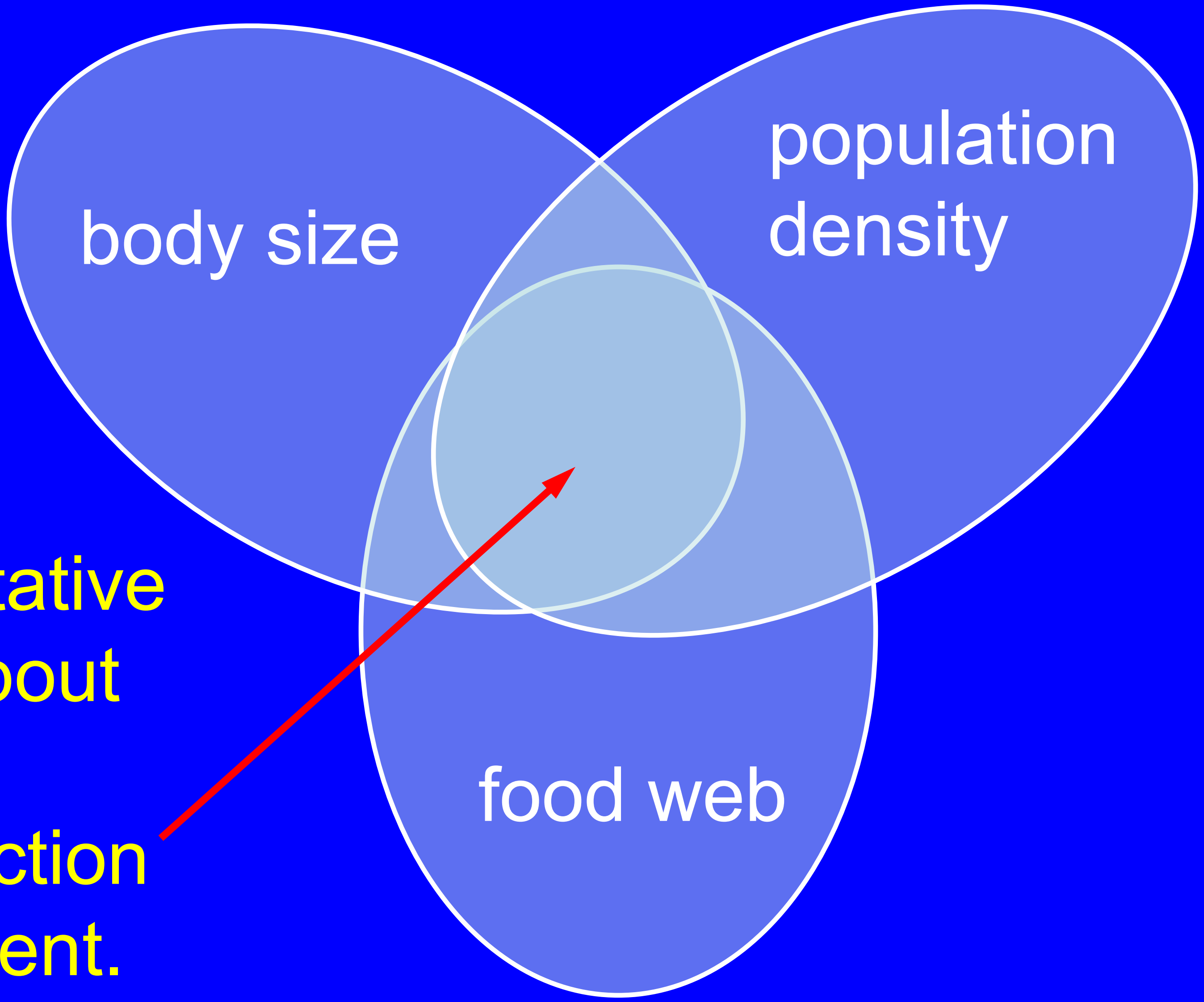
Camerano food web: feeding only



Forbes food web: species & trophic link characteristics

“Abundance” of specimens, not population density!



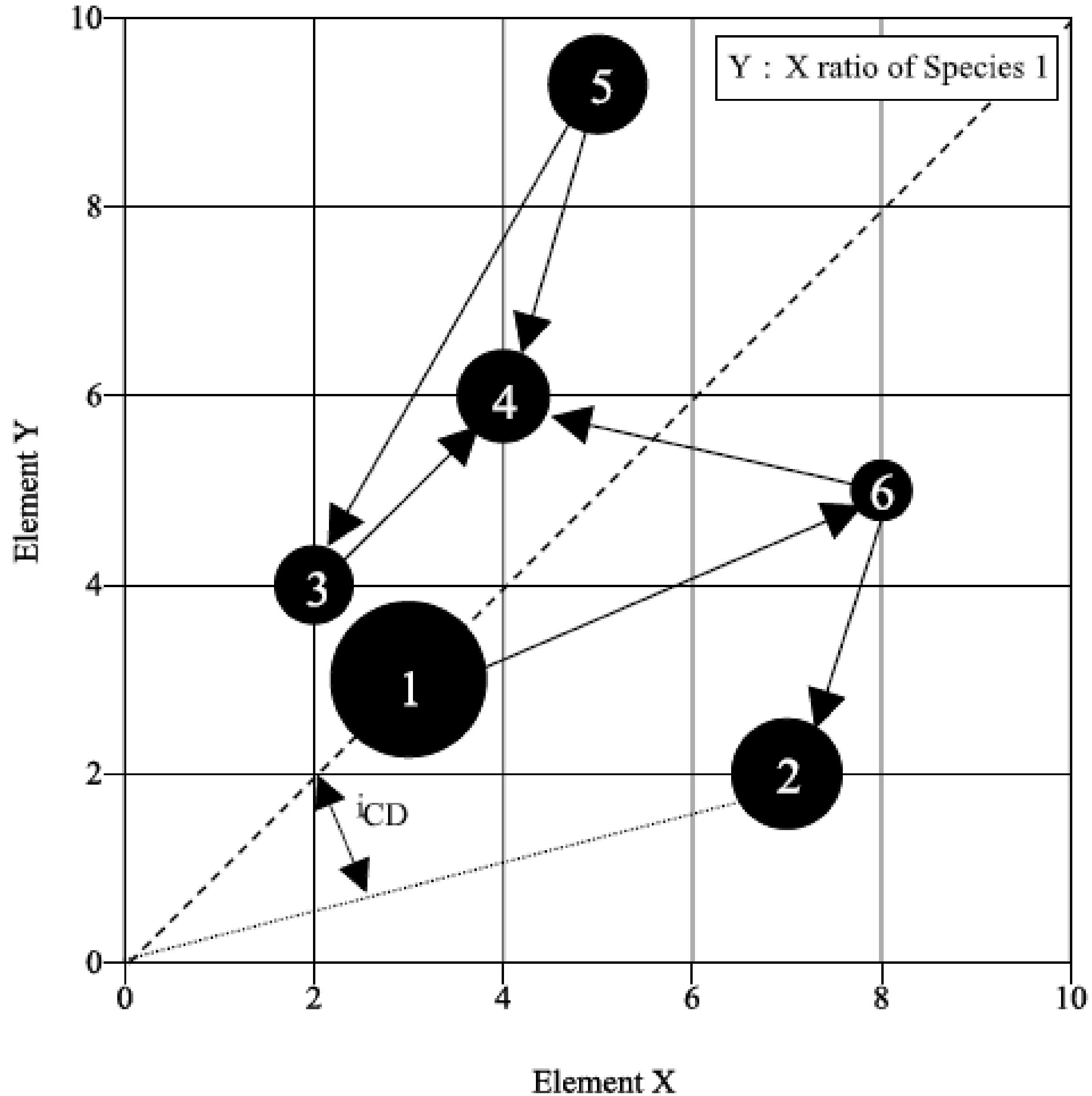


Quantitative data about the intersection are recent.

Trophochemical diagram

(Sterner 1995, from Woodward & Hildrew 2002)

Diameter of circle is concentration of 3d element. Arrows are trophic links.



A big idea has been added to thinking about food webs in the last 40 years.

While every food web is unique,

food webs display quantitative patterns individually & in ensembles.

These patterns can be understood.

Examples:

- intervality
- cascade model
- niche model (Williams & Martinez)
- scaling “laws”
- trophic cascade (Carpenter)
- interaction strength & stability (de Ruiter et al.)
- biomass spectrum

Patterns in M,N-webs

For each taxon (node), measure

M = average body mass per individual,

N = numerical abundance or population density per unit of habitat.

1. Allometry of N vs. M
2. Relation of consumer M to resource M
3. Tri-trophic interactions or 2-chains A→B→C

Allometric patterns in M,N-webs

Is log N roughly a linear function of log M?

If so, fit allometric function $N = aM^b$.

Then taxon biomass $B = M*N = aM^{b+1}$.

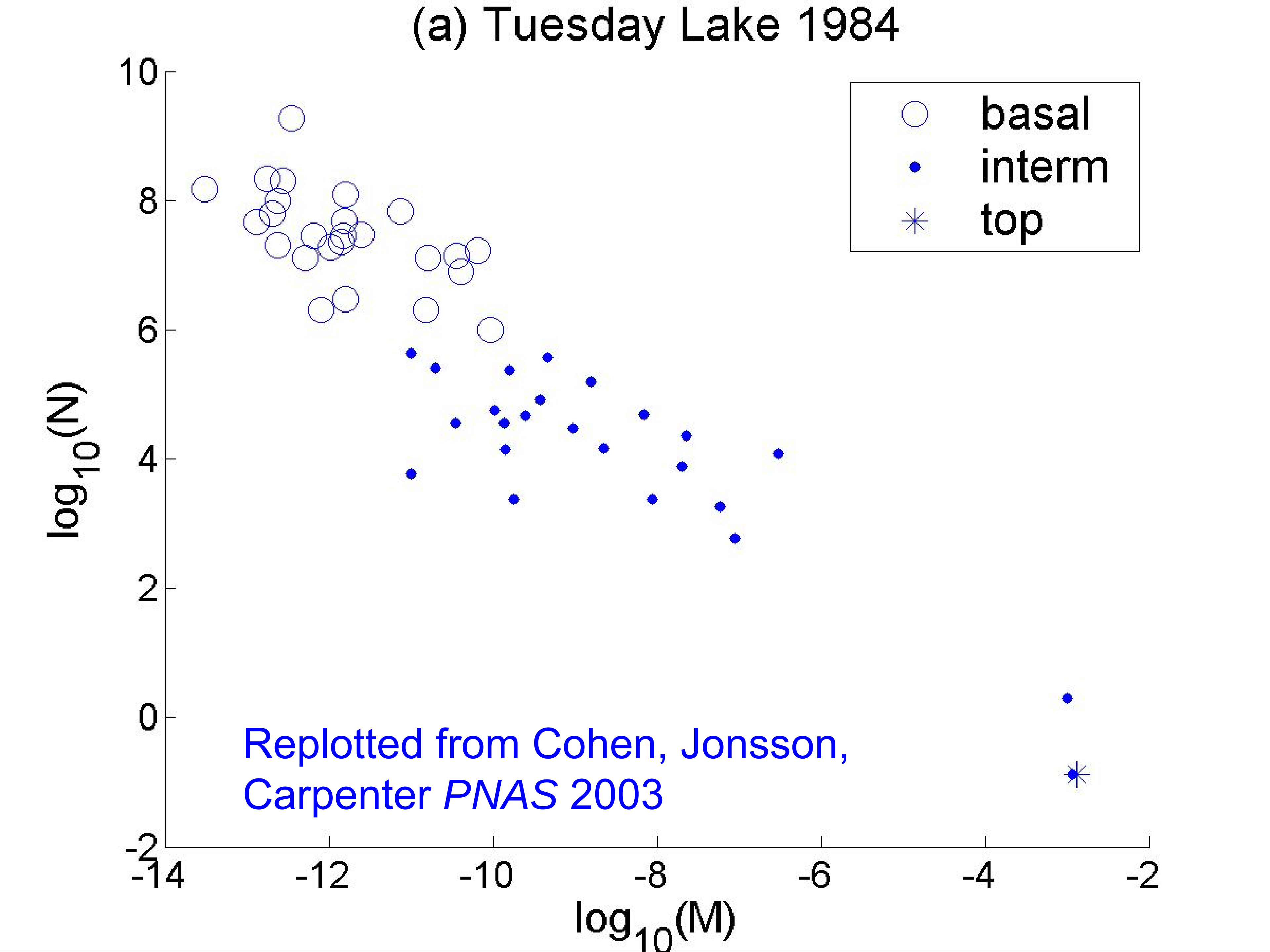
If $b > -1$, then taxon biomass increases with M.

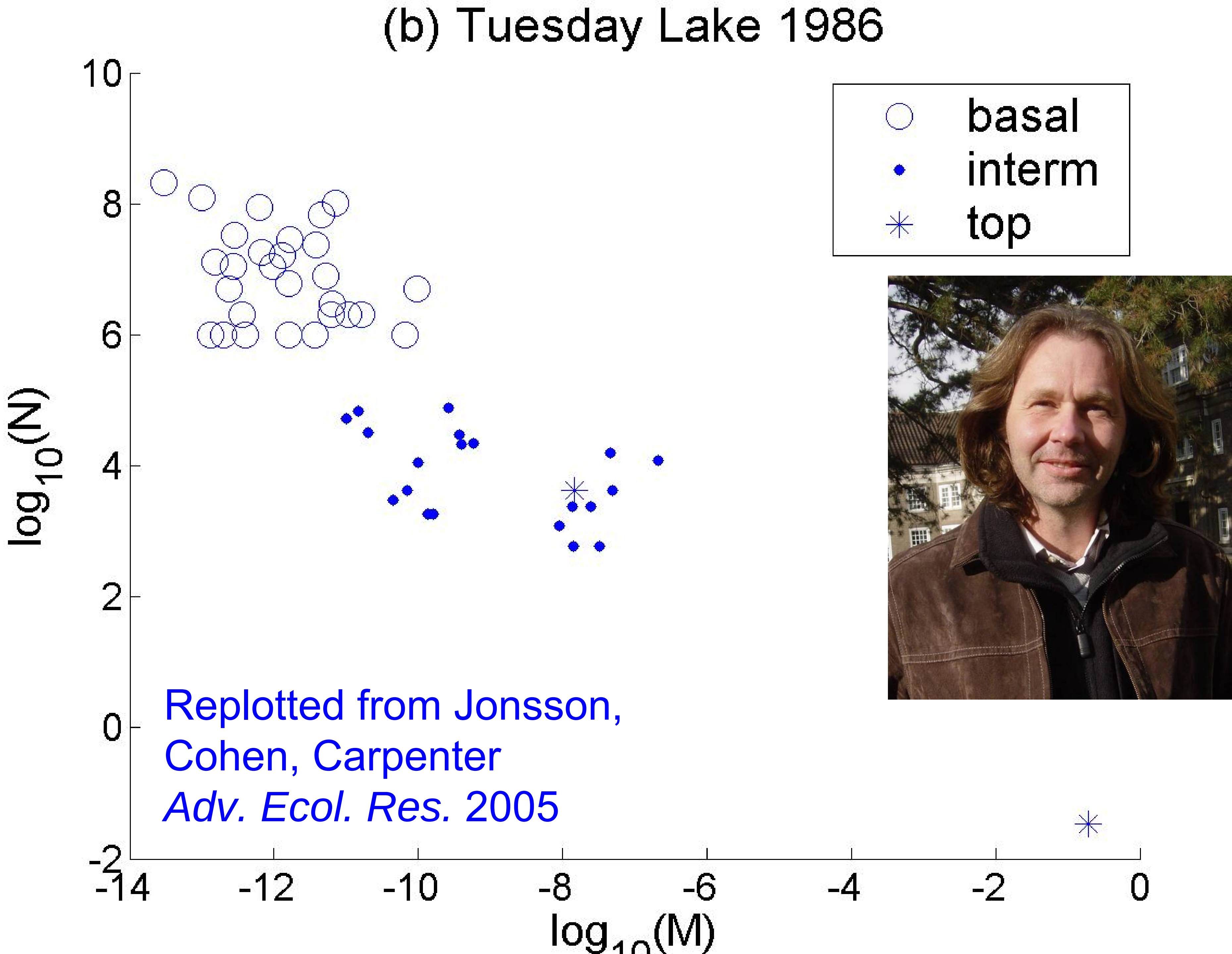
If $b < -1$, taxon biomass decreases with M.

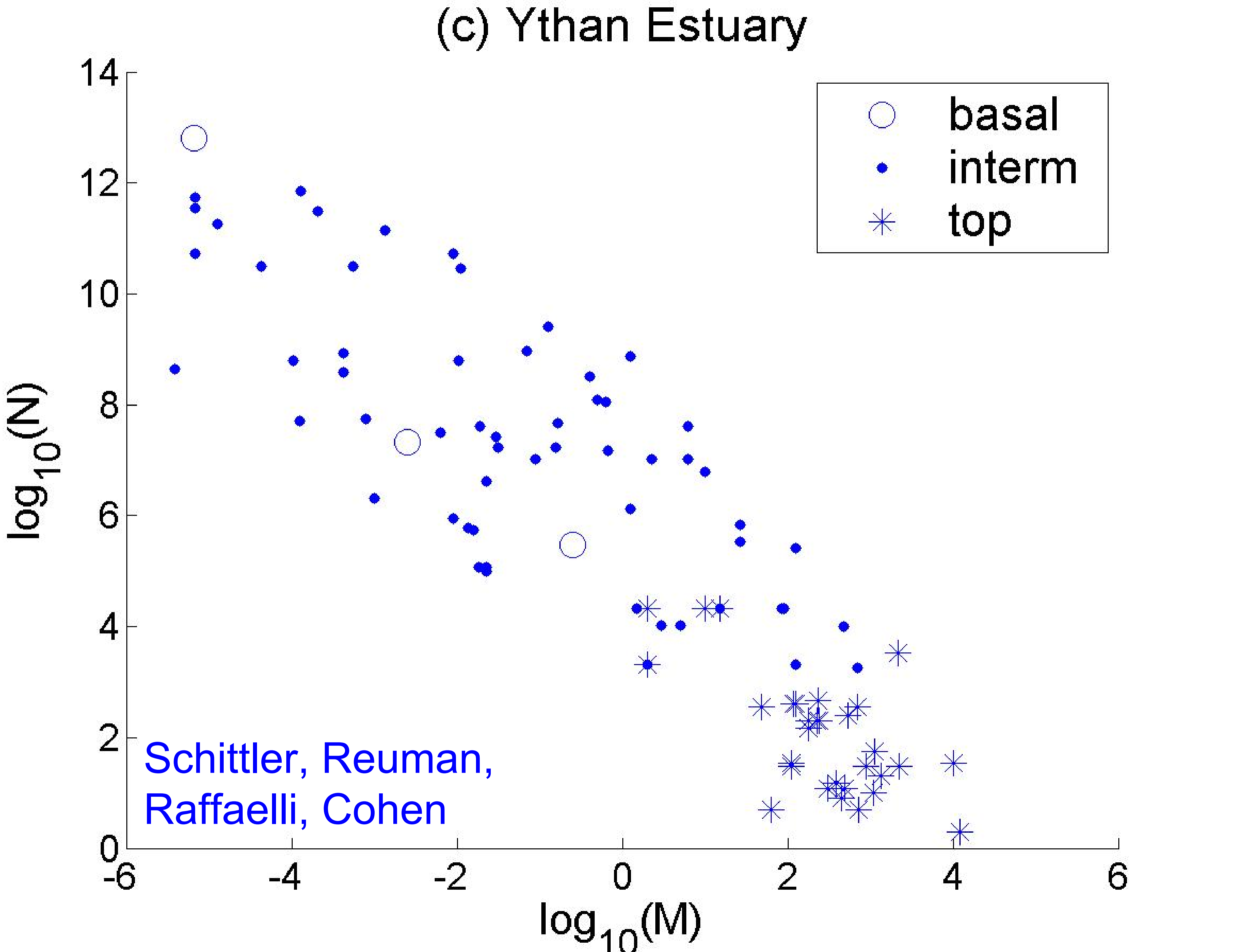
If $b = -1$, taxon biomass is independent of M.

Data: Tuesday Lake, Michigan

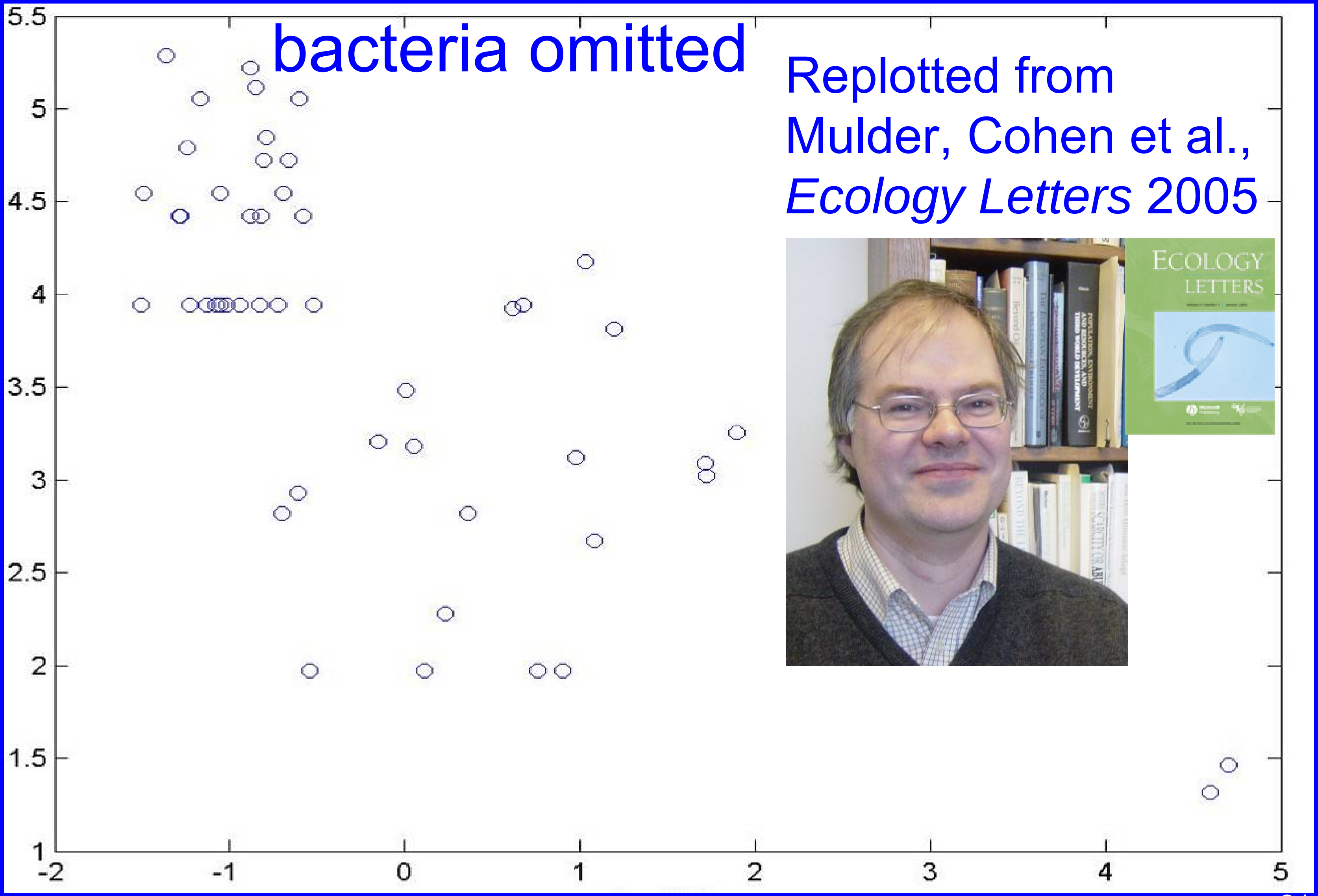
Stephen R. Carpenter, University of Wisconsin, Madison, Wisconsin, USA


(a) Tuesday Lake 1984
10
8
6
4
2
0
-2
-14
-12
-10
-8
-6
-4
-2
$\log_{10}(N)$
$\log_{10}(M)$
basal
interm
top
Replotted from Cohen, Jonsson,
Carpenter *PNAS* 2003


(b) Tuesday Lake 1986
basal
interm
top
$\log_{10}(N)$
$\log_{10}(M)$
10
8
6
4
2
0
-2
-14
-12
-10
-8
-6
-4
-2
0
Replotted from Jonsson,
Cohen, Carpenter
Adv. Ecol. Res. 2005


(c) Ythan Estuary
log10(N)
log10(M)
basal
interm
top
Schittler, Reuman, Raffaelli, Cohen
14
12
10
8
6
4
2
0
-6
-4
-2
0
2
4
6

Detrital soil, top 10 cm, identified to genus (except bacteria), organic farm, Netherlands



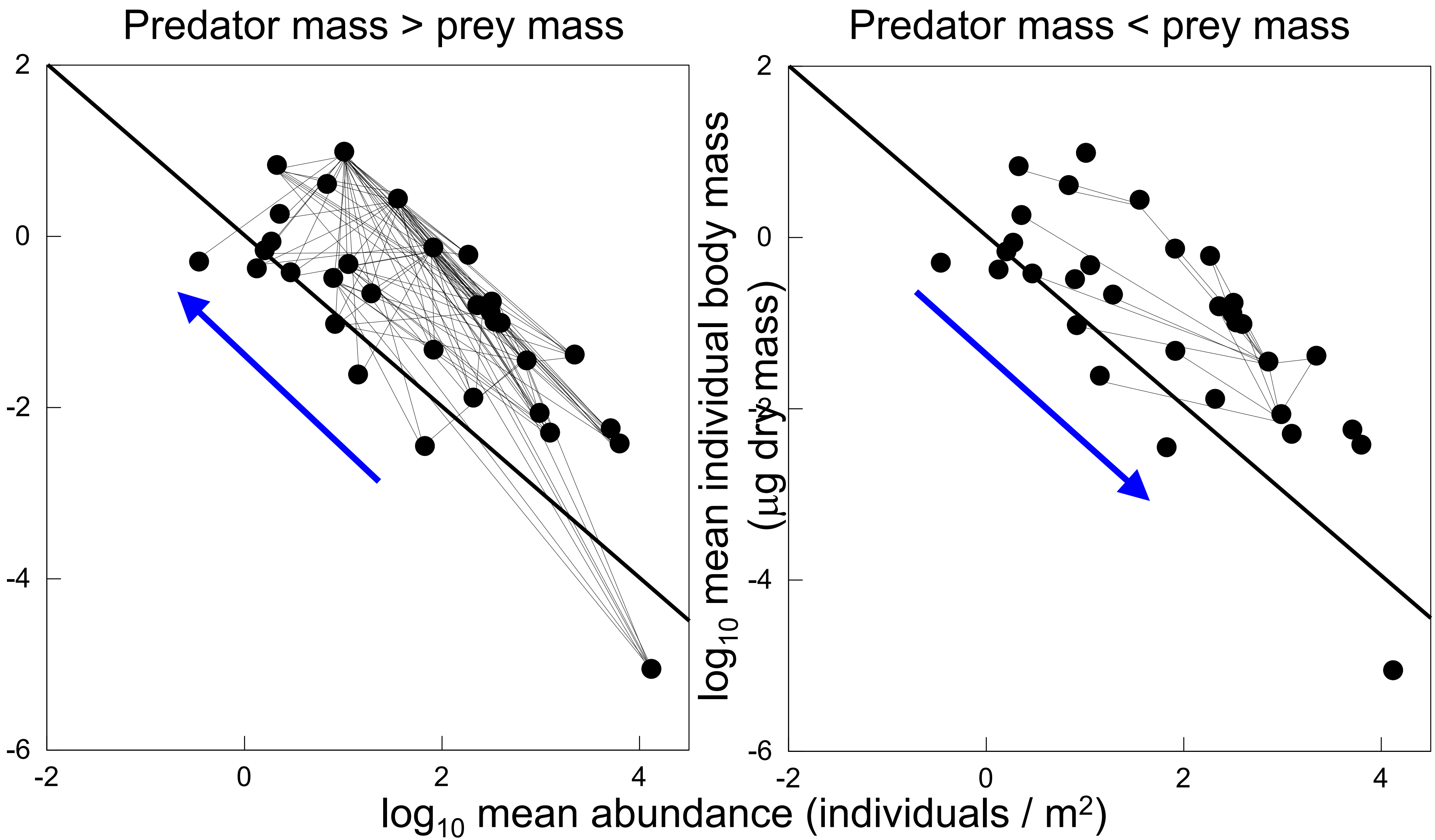
Broadstone Stream, UK

Guy Woodward

http://www.biology.qmul.ac.uk/research/staff/hildrew/guy.htm

Broadstone Stream, UK, benthic

Woodward, Speirs, Hildrew, *Adv. Ecol. Res.* 2005



What differs from Damuth 1981?

Damuth, Population density and body size in mammals, *Nature* 290:699-700,1981, found

population density = a*(body mass)$^{-3/4}$.

1. He included only herbivorous mammals.

We included all species, regardless of taxon.

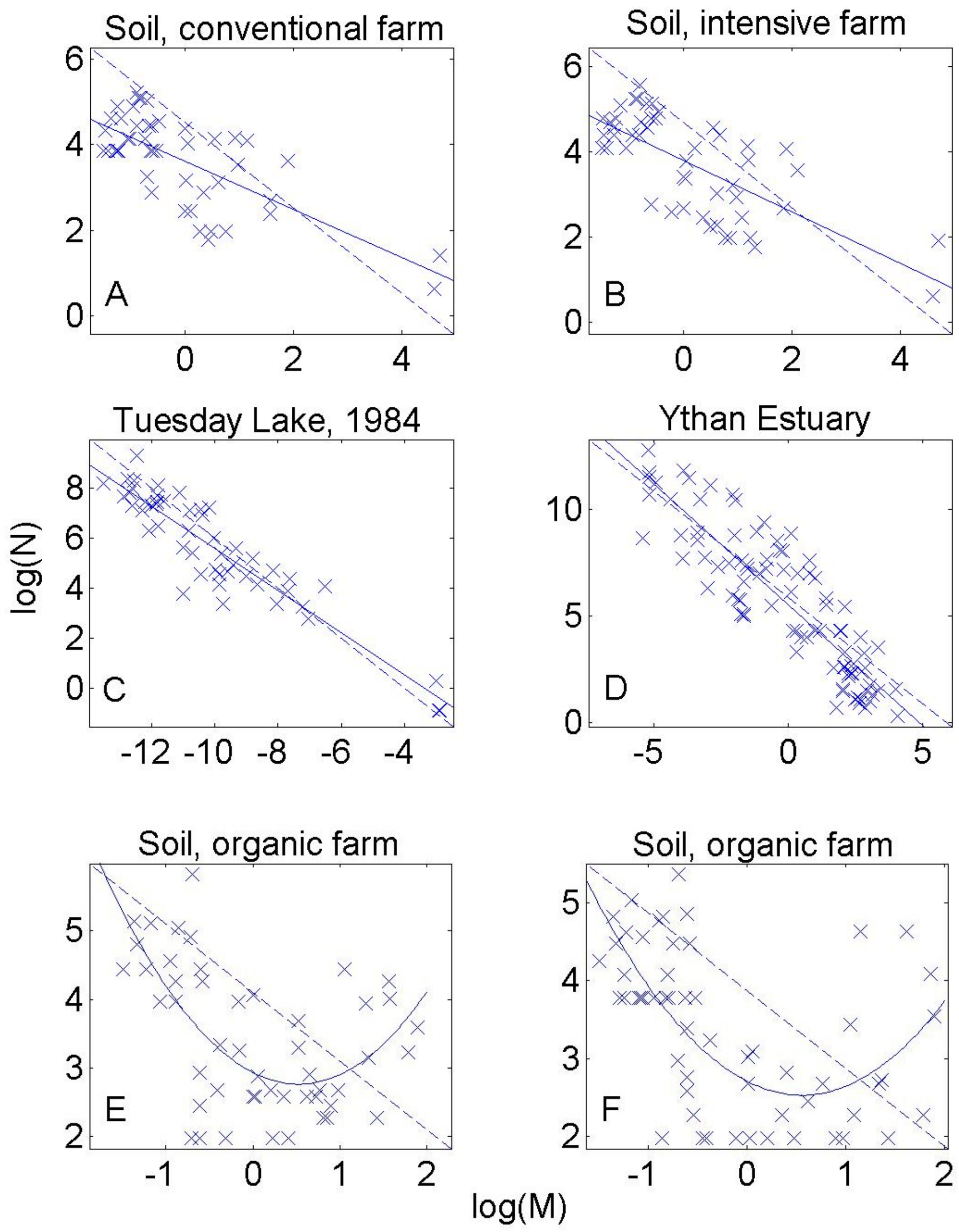
2. He included species from all over world.

We included species in one local food web at a time.

3. He found one exponent, -3/4.

We found different exponents, depending on site.

Linear relation is common but not universal.



Allometry of body size and abundance in 166 food webs. Reuman, Mulder et al. *Adv. Ecol. Res.*

2008-04-05

Food webs in a landscape

Data structure: ensemble of webs with M, N for nodes & community attributes

146 soil food webs from The Netherlands: data from Christian Mulder, RIVM.

Top-down control? Or bottom-up control? Or how much of each?

To what extent do above-ground characteristics (biotic & abiotic) influence below-ground food web & community structure, & vice versa?

Attributes of below-ground food web

- Total animal biomass
  - Omitting bacteria, fungi, detritus
- Slope of abundance-mass allometric line
  - In regression of log(N) as a function of log(M)
- Faunal diversity
  - Number of genera

Best predictor of below-ground food web properties is above-ground ecosystem type.

1) Forests (mostly Scots pine plantations) were least disturbed, most nutrient limited.

2-6) Pastures & farms (organic, conventional, intensive, super-intensive) were recently fertilized.

7) Winter farms were most disturbed by human & environmental factors, not recently fertilized.

At most 1 or 2 additional characteristics were selected as predictors by stepwise general linear regression.

Slope of log N v. log M reflects community structure.

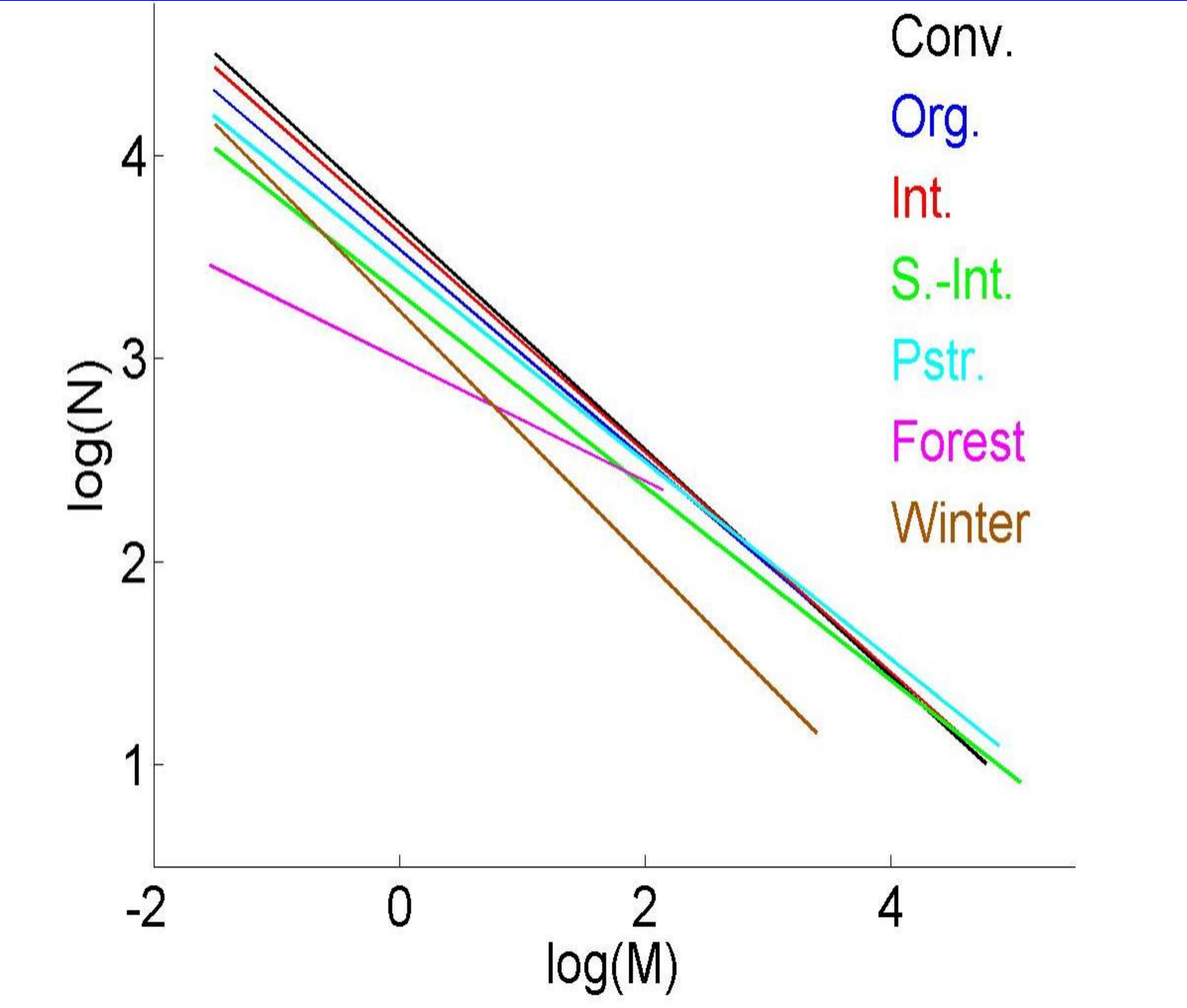
Reuman, Cohen, Mulder, Human and environmental factors influence soil faunal abundance-mass allometry and structure. *Adv. in Ecol. Res.*

In 146 Dutch sites, above-ground ecosystem type explains 52% of variation in slope.

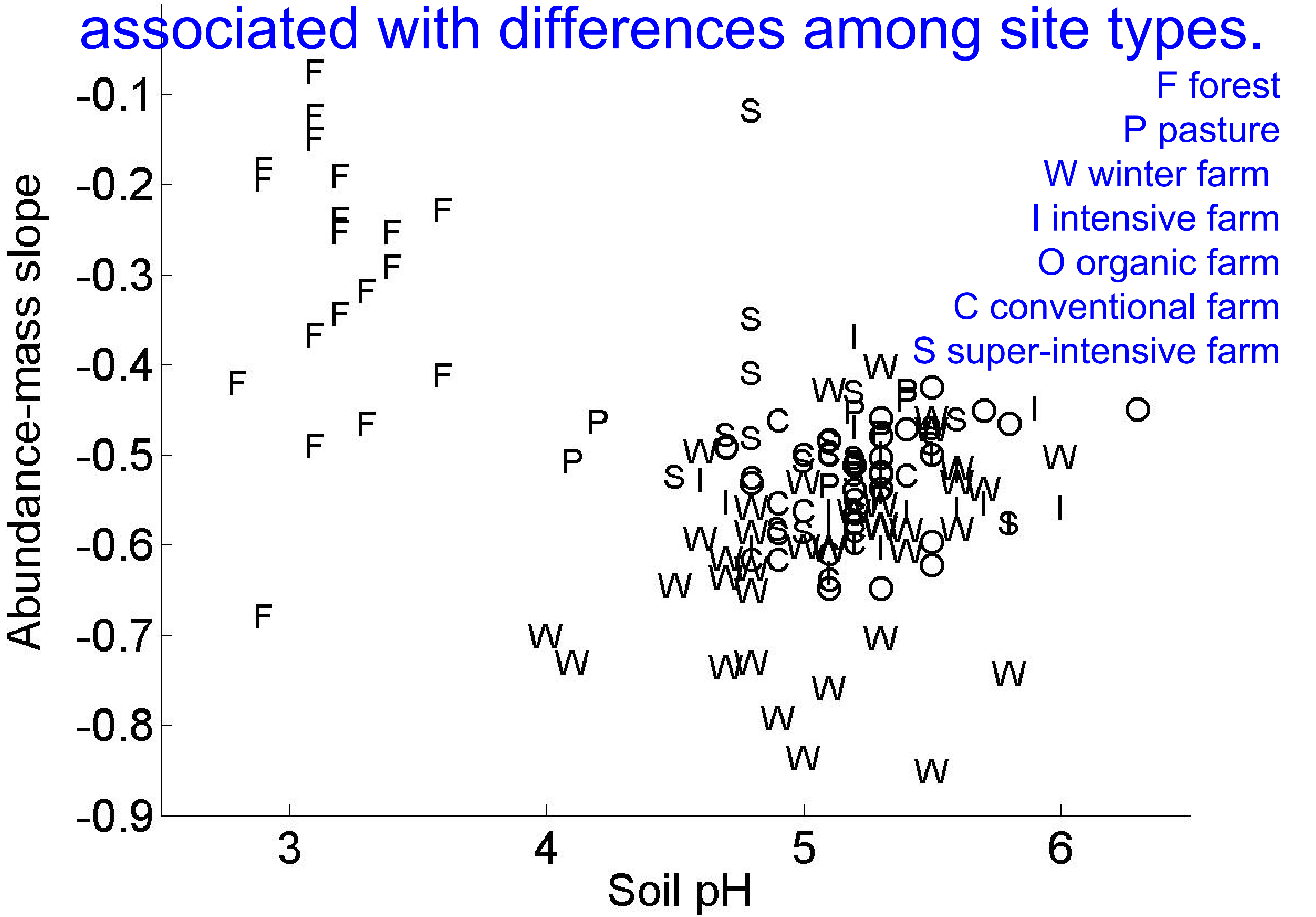
Adding soil bacterial biomass explains total of 58% of variation in slope, & no other variables significantly affect slope.

Above-ground ecosystem type dominates, but a below-ground variable also matters.

Slopes in Dutch soil food webs vary with ecosystem type (human land use).

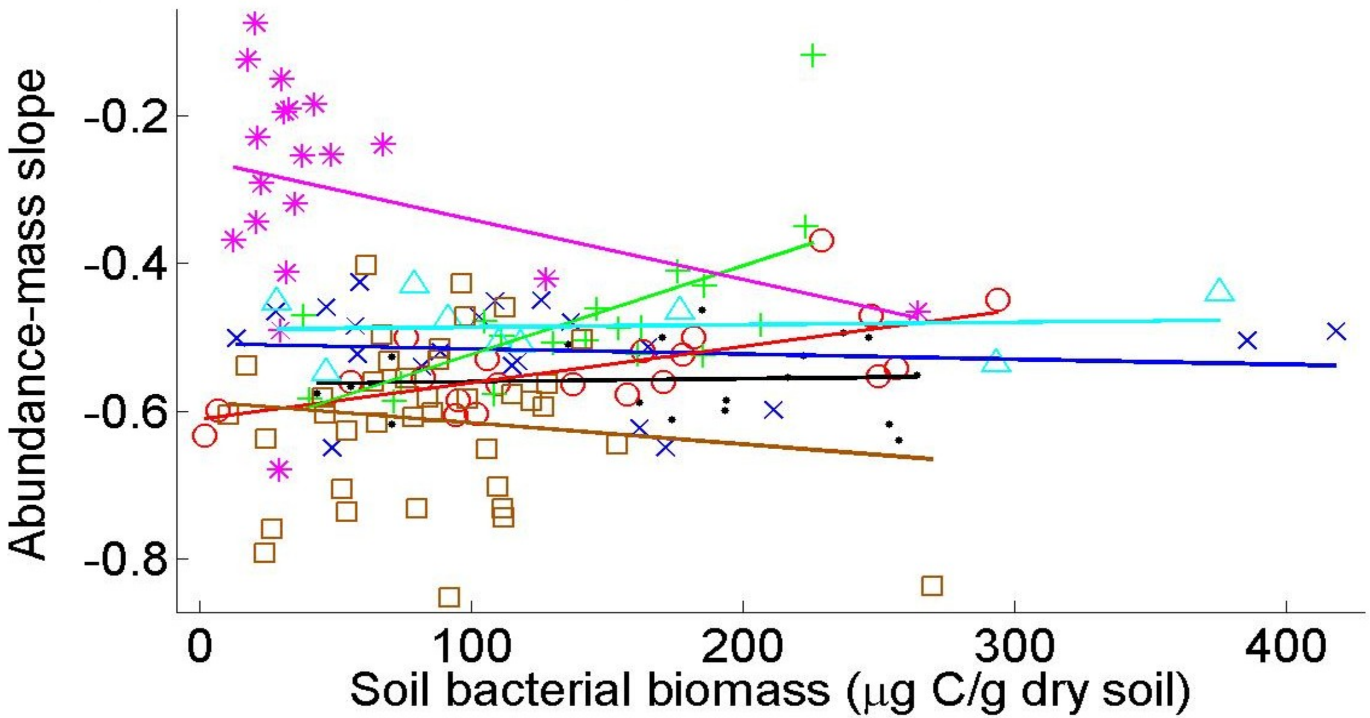


Abundance-mass slope decreases with soil pH associated with differences among site types.

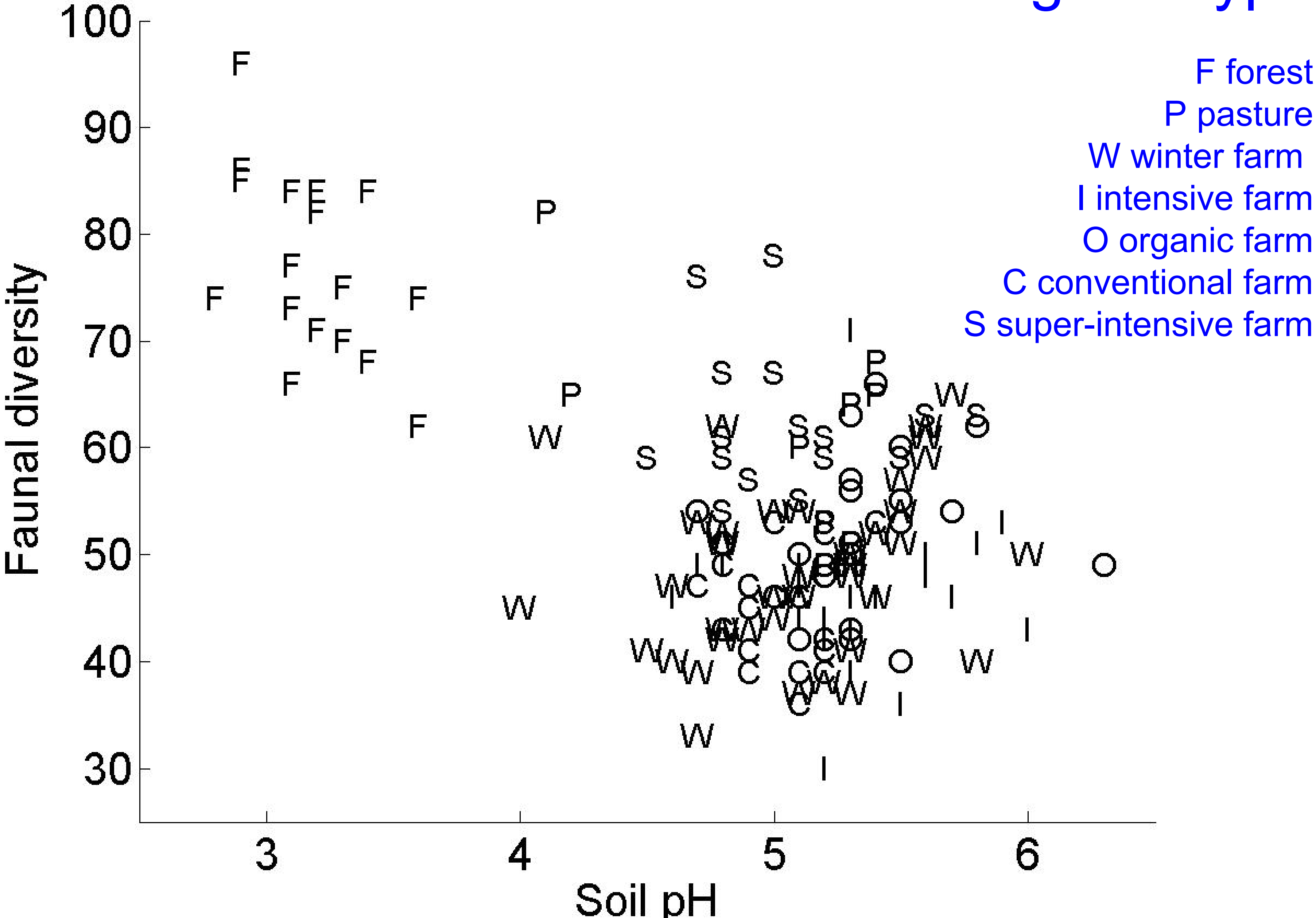


Slope increases with soil bacterial biomass only in super-intensive farms

ET		Slope	99% Conf.		Intercept	99% Conf.	
Conv.	•	3.86e-5	-7.01e-4	7.79e-4	-0.563	-0.7	-0.427
Org.	×	-7.02e-5	-5.76e-4	4.35e-4	-0.508	-0.591	-0.426
Int.	○	4.91e-4	-1.58e-4	1.14e-3	-0.61	-0.716	-0.505
S.-Int.	+	1.20e-3	2.17e-4	2.18e-3	-0.643	-0.79	-0.496
Pstr.	△	3.18e-5	-6.84e-4	7.48e-4	-0.489	-0.62	-0.358
Forest	*	-8.05e-4	-1.76e-3	1.54e-4	-0.26	-0.332	-0.189
Winter	□	-2.88e-4	-1.12e-3	5.42e-4	-0.587	-0.668	-0.506

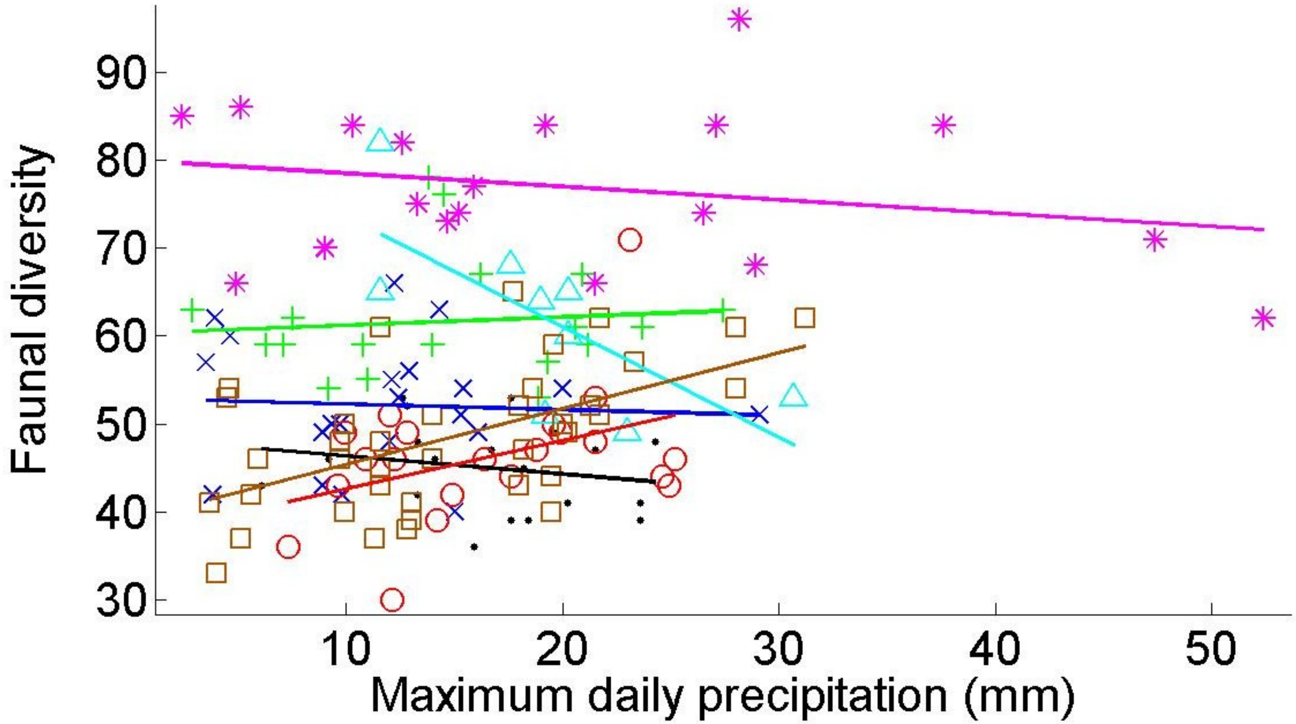


Number of faunal taxa decreases with soil pH associated with differences among site types.

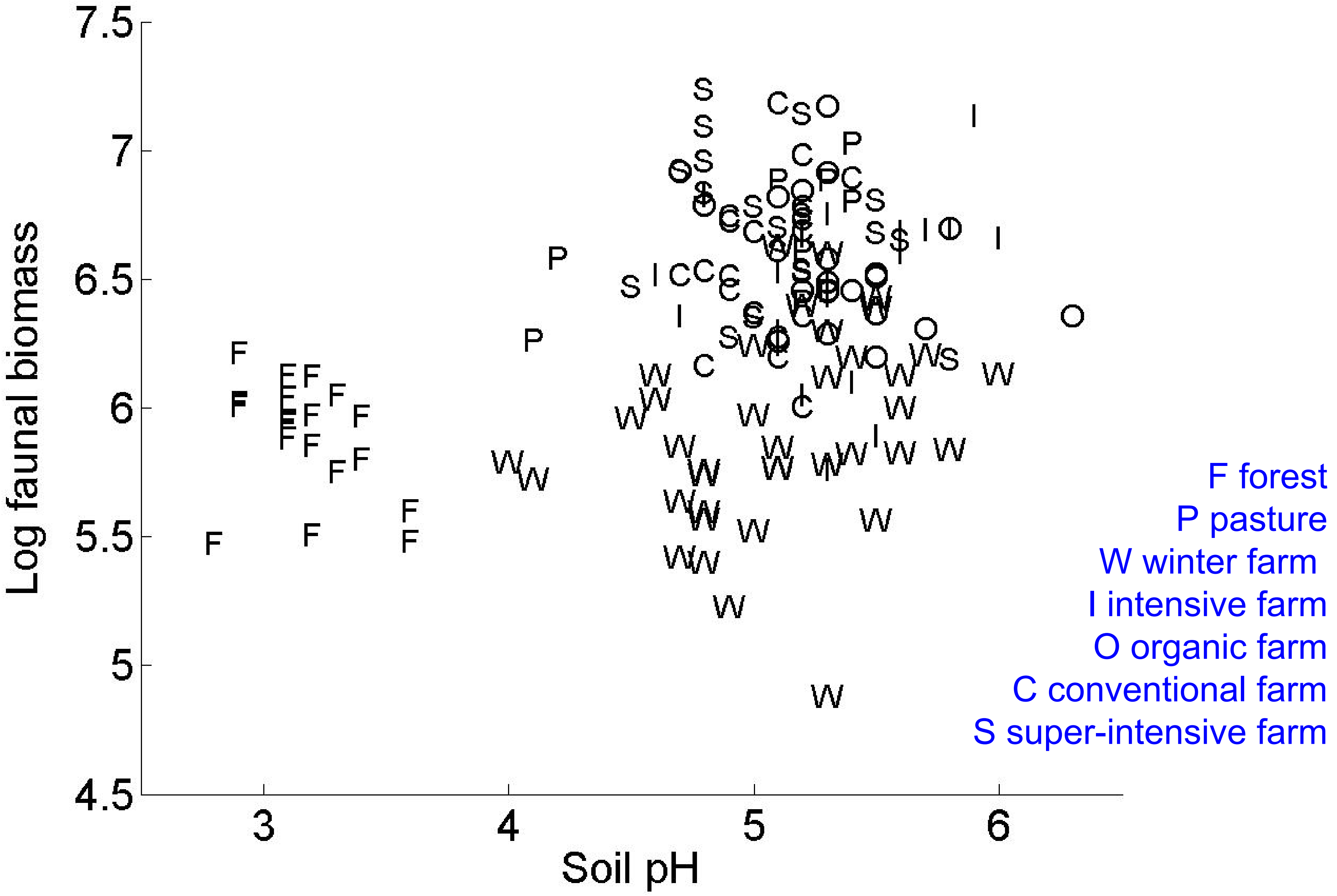


More rain increases number of faunal taxa in winter farms, decreases it in pastures.

ET		Slope	99% Conf.		Intercept	99% Conf.	
Conv.	·	-0.205	-1.09	0.68	48.4	32.9	63.8
Org.	×	-0.0631	-0.757	0.631	52.9	43.7	62.1
Int.	○	0.553	-0.188	1.29	37.1	24.1	50.1
S.-Int.	+	0.0947	-0.544	0.734	60.3	50.2	70.4
Pstr.	△	-1.26	-2.39	-0.13	86.1	63.5	109
Forest	*	-0.152	-0.465	0.161	80	72.3	87.7
Winter	□	0.636	0.21	1.06	39	32.1	46



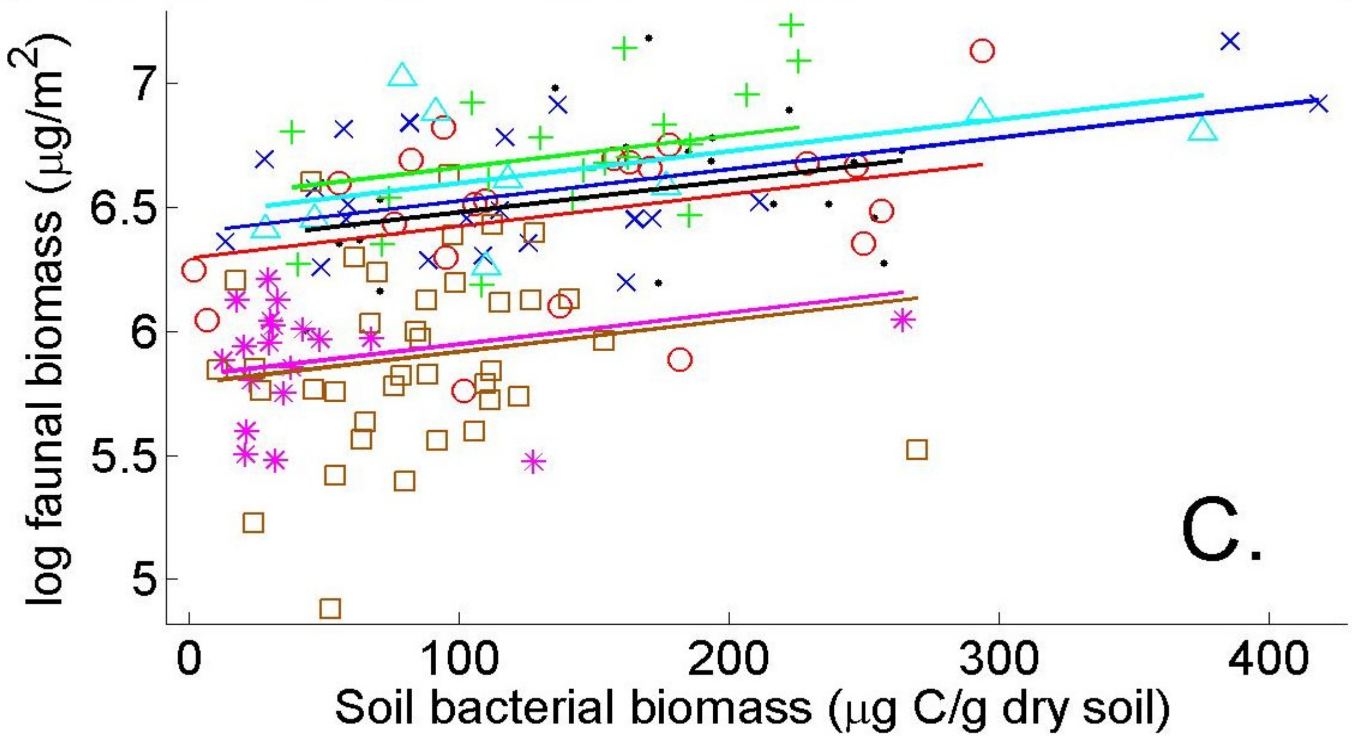
Total faunal biomass varies little with soil pH, but differs among site types.



Total faunal biomass increases with soil bacterial biomass.

ET		Intercept	99% Conf.		Slope	99% Conf.	
Conv.	·	6.352	6.121	6.583	0.001	0.0004	0.002
Org.	×	6.398	6.195	6.601			
Int.	○	6.296	6.086	6.506			
S.-Int.	+	6.533	6.318	6.748			
Pstr.	△	6.470	6.182	6.757			
Forest	✳	5.819	5.638	6.001			
Winter	□	5.789	5.643	5.935			

same slope, different intercepts



Size matters, but that's not all that matters!

Human use of land, associated
with ecosystem type (& pH)

Rainfall

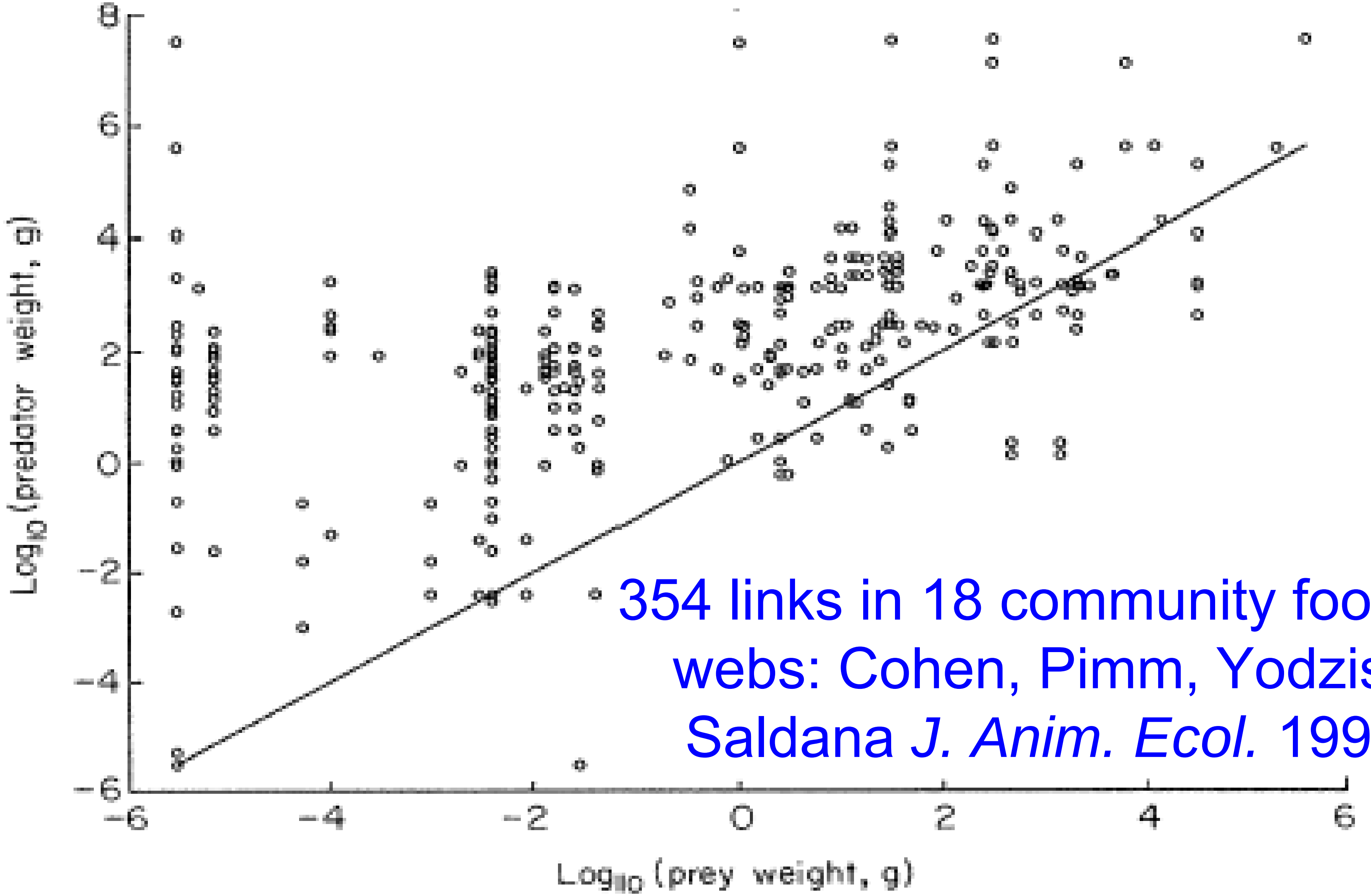
Soil bacterial biomass

Consumer-resource body size allometry in M,N-webs

Are patterns affected by units over which body masses are averaged?

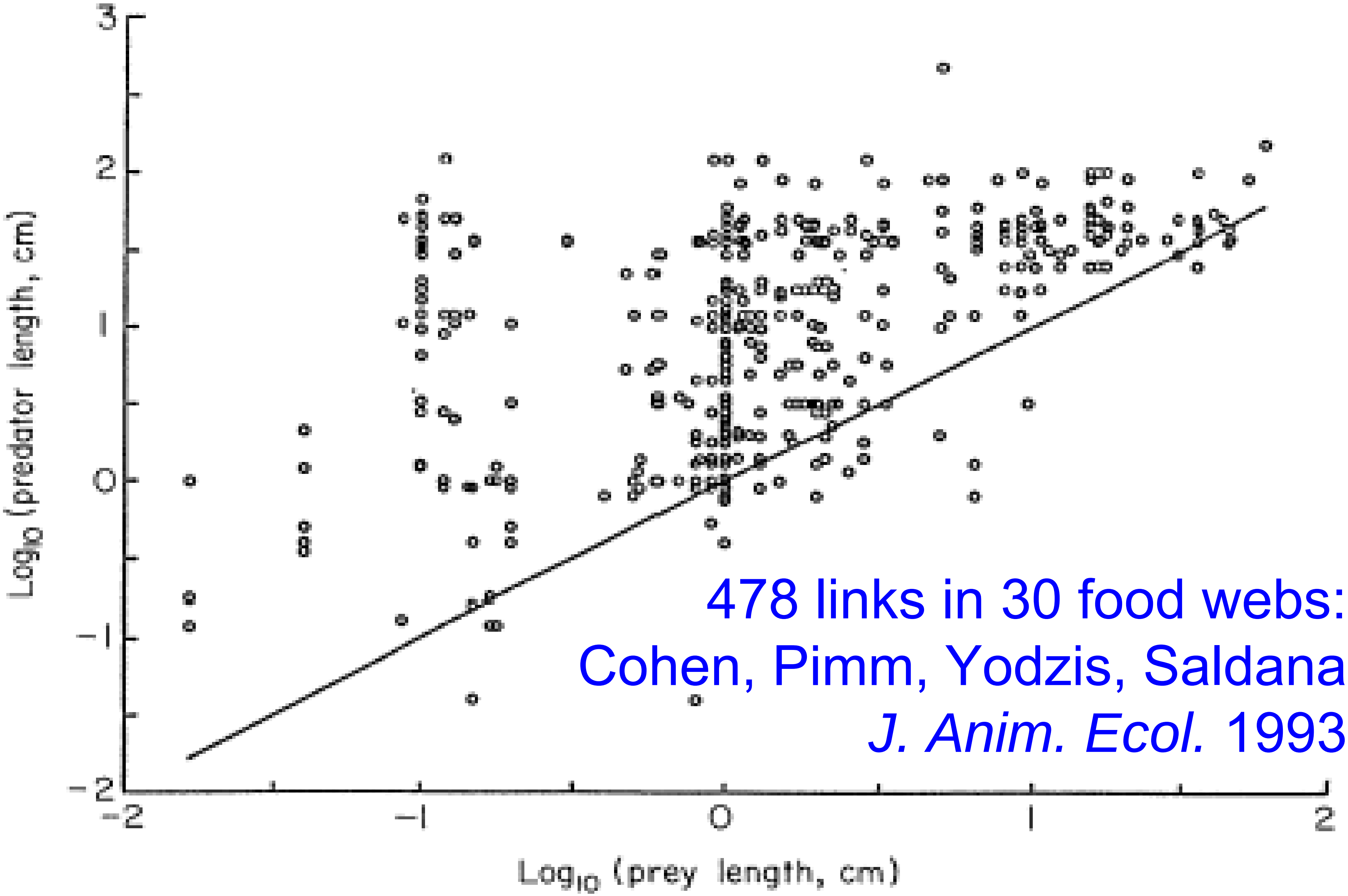
- taxon
- link
- individual

Predators weigh more than prey.



354 links in 18 community food webs: Cohen, Pimm, Yodzis, Saldana *J. Anim. Ecol.* 1993

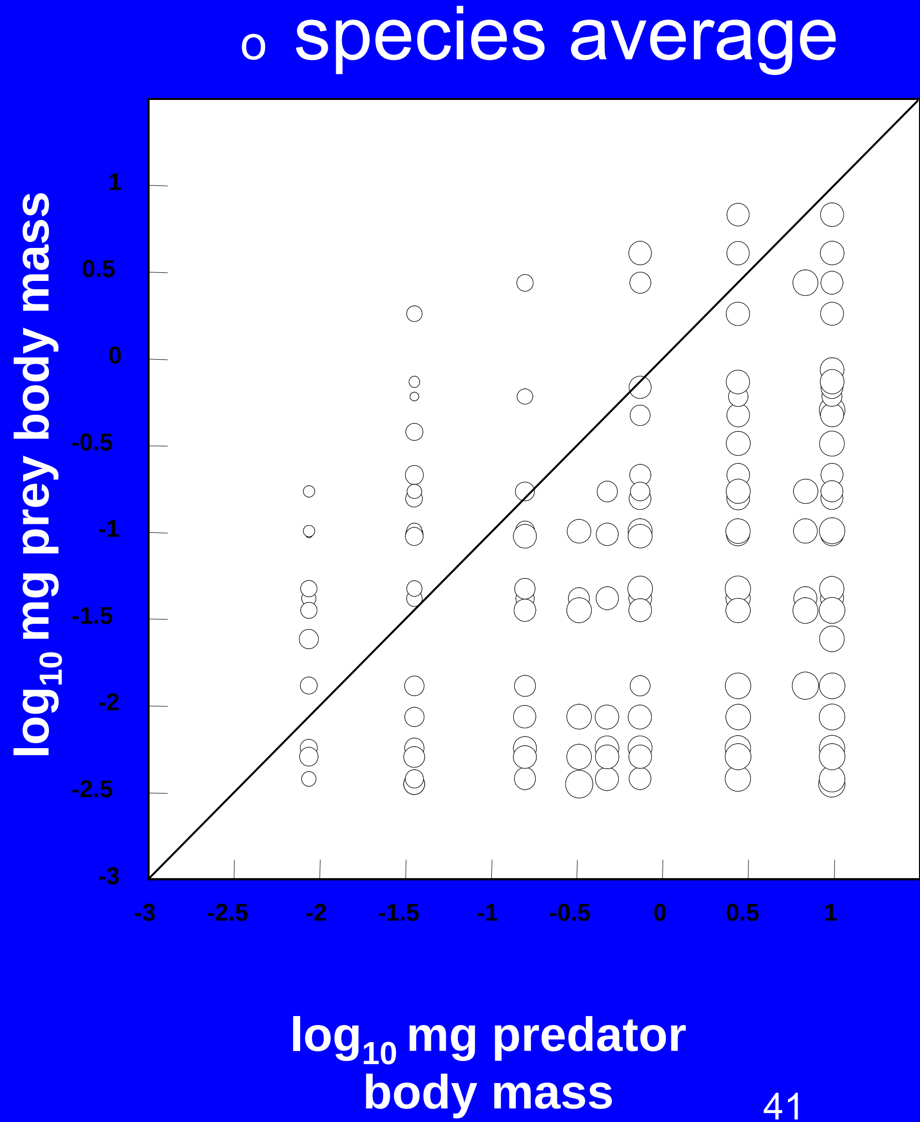
Predators weigh more than prey.



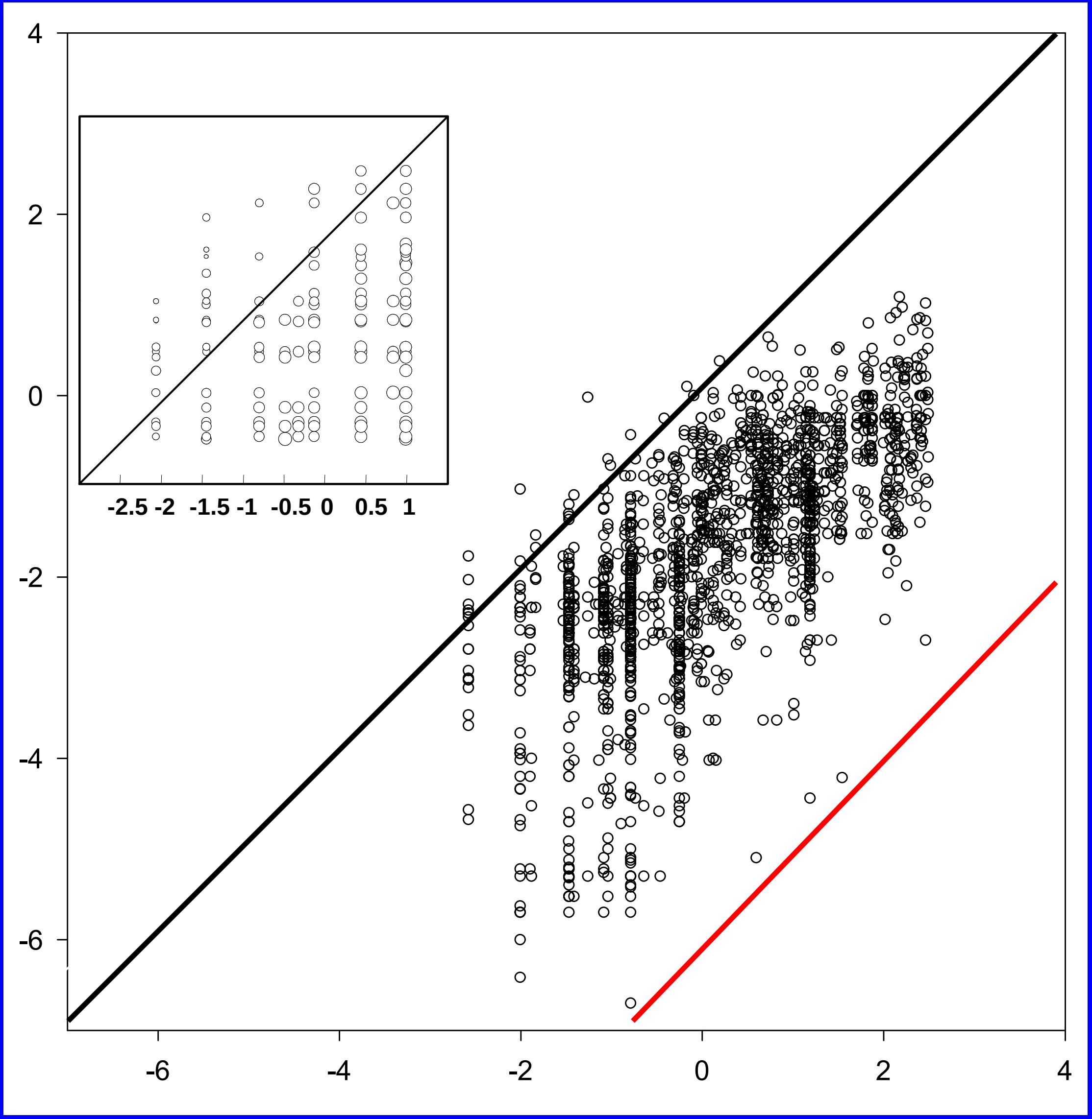
478 links in 30 food webs:
Cohen, Pimm, Yodzis, Saldana
J. Anim. Ecol. 1993

Broadstone Stream UK benthic invertebrates

Guy Woodward



Species-average (inset) & ~1800 individual links



Log prey body-mass (mg)

Log predator body-mass (mg)

Broadstone Stream (Guy Woodward)

Aphelinus varipes female ovipositing into aphid host, *Diuraphis noxia*

Christine Mueller

12 aphid species, 37 wasp species

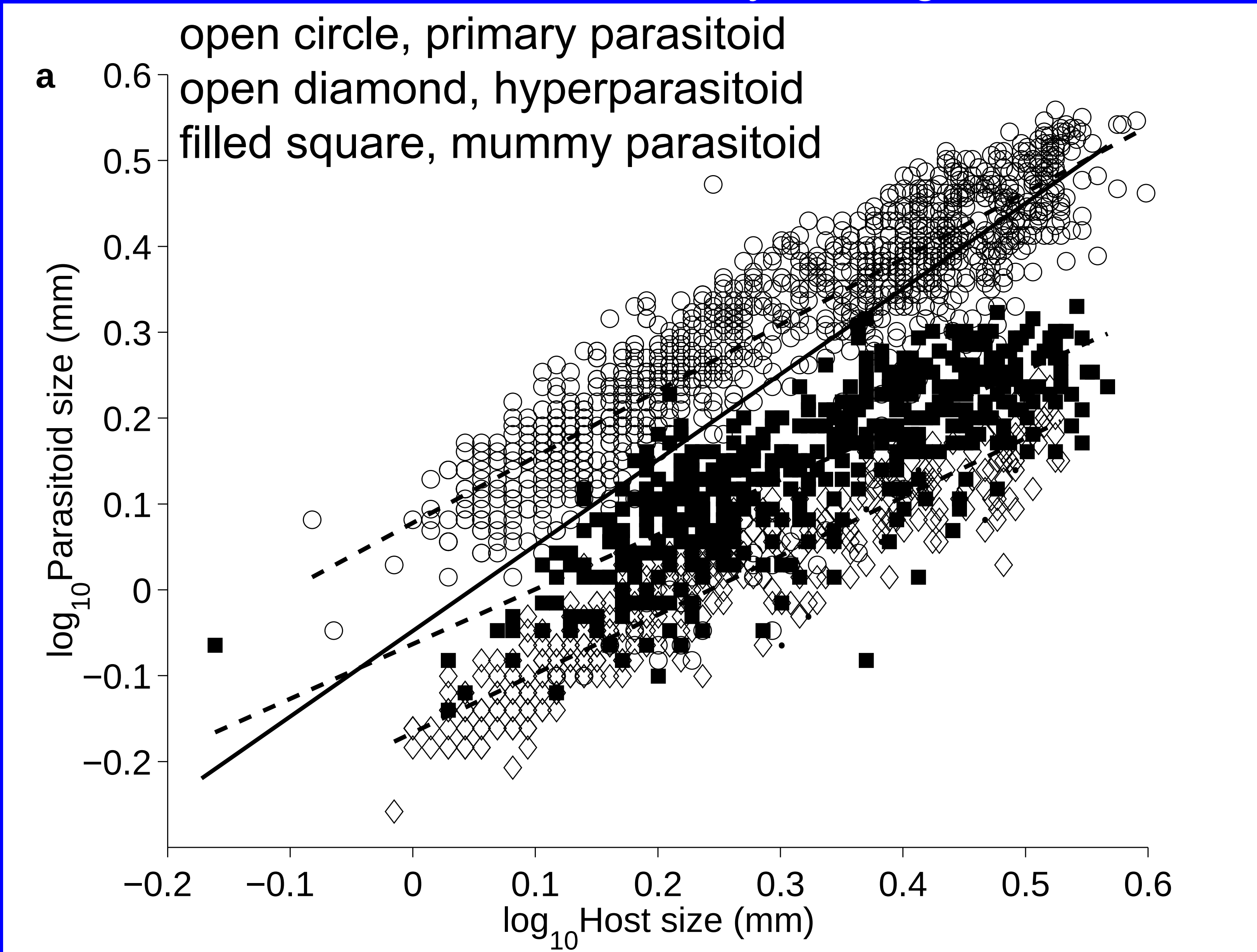
Rush Meadow is a damp abandoned field in Silwood Park, UK.
It has an area of 18 000 m^2 and is surrounded by woodland.

Parasitoid wasps lay eggs in aphids.

- Primary parasitoid wasp lays egg in living, unparasitized aphid.
- Secondary parasitoid wasp lays egg in previously parasitized aphid.
  - Hyperparasitoid wasp attacks previously parasitized aphid while aphid is alive.
  - Mummy parasitoid wasp attacks previously parasitized aphid after aphid dies.

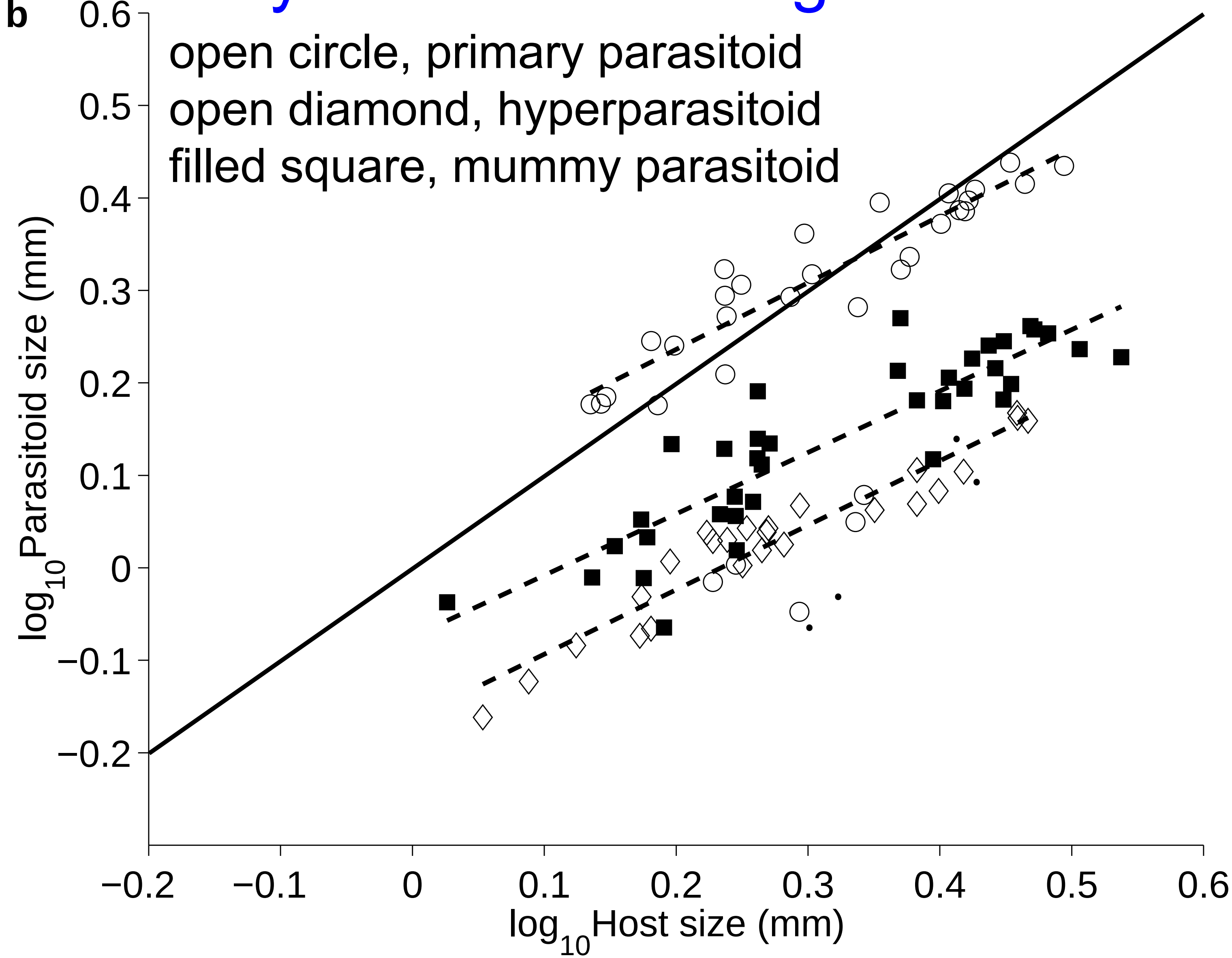
2,151 individual aphid-wasp couples

Cohen, Jonsson, Mueller, Godfray, Savage *PNAS* 2005



Aphid-wasp links

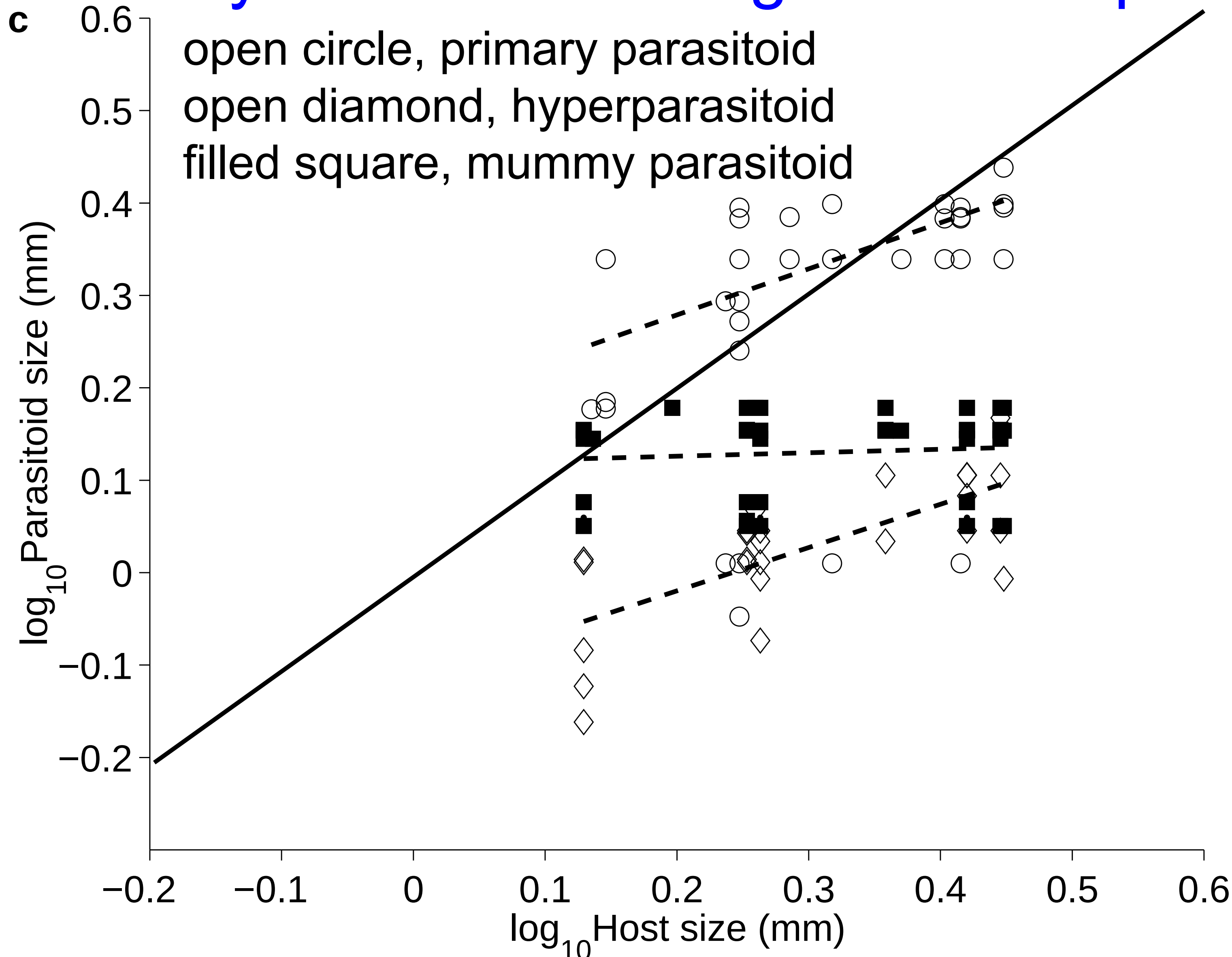
Body sizes are averaged within links.



Cohen, Jonsson, Mueller, Godfray, Savage PNAS 2005

Aphid-wasp links

Body sizes are averaged within species

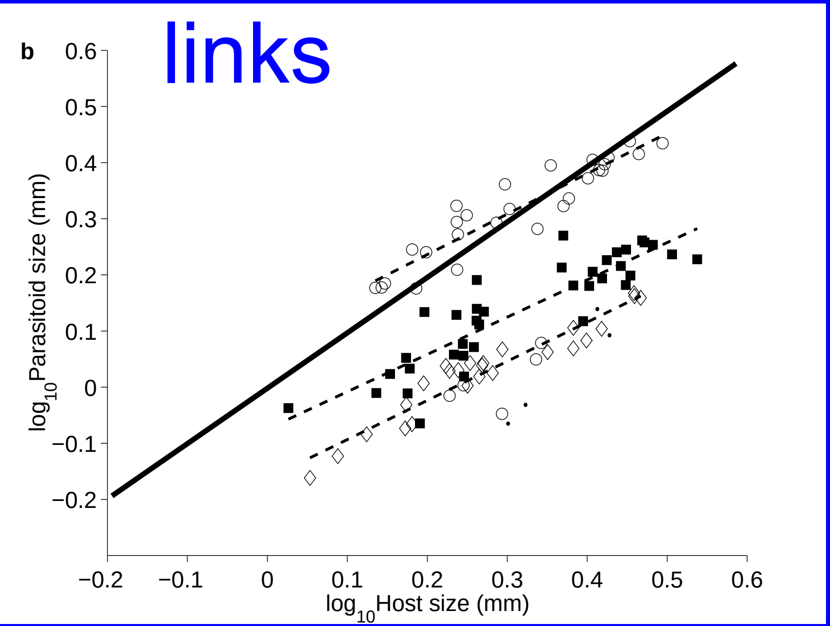


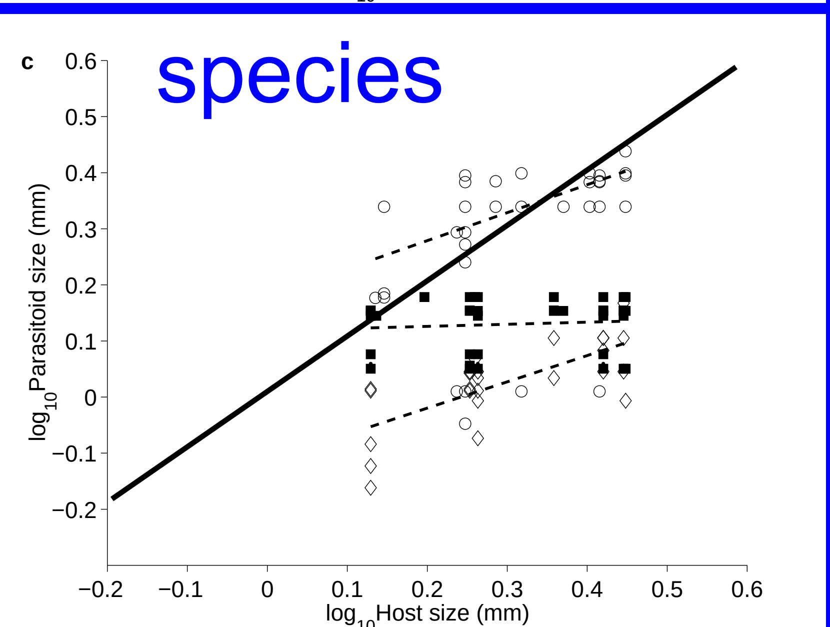
Cohen, Jonsson, Mueller, Godfray, Savage PNAS 2005

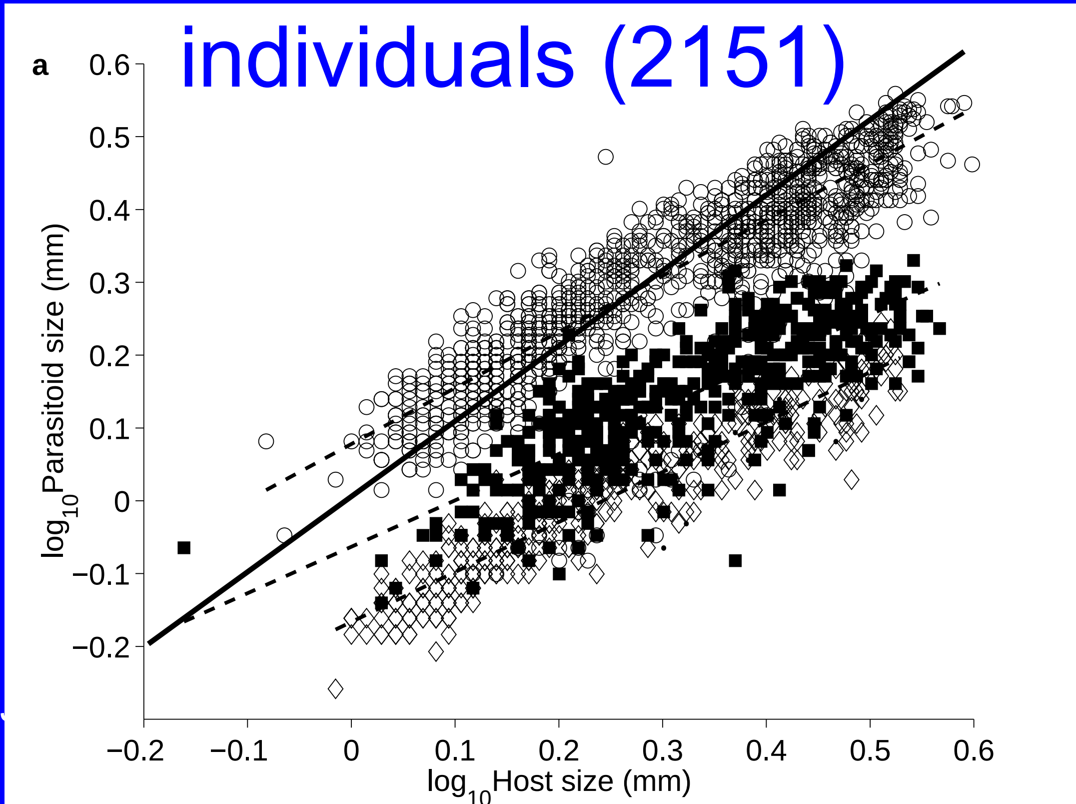
Aphid-wasp links

Cohen, Jonsson, Mueller, Godfray, Savage *PNAS* 2005

open circle, primary parasitoid
open diamond, hyperparasitoid
filled square, mummy parasitoid







Parasitoid wasps on aphid hosts

A=individuals, B=link averages, C=species averages

Relationship		*b* (±95%c.I.)	*r*
$\log(PP)=a+b*\log(H)$	A	0.769±0.018	0.9239
	B	0.721±0.115	0.9326
	C	0.506±0.192	0.7349
$\log(HP)=a+b*\log(H)$	A	0.686±0.026	0.9339
	B	0.697±0.091	0.9571
	C	0.469±0.198	0.7140
$\log(MP)=a+b*\log(H)$	A	0.637±0.041	0.8026
	B	0.664±0.120	0.8854
	C	0.037±0.143	0.0892

PP=primary parasitoid, HP=hyperparasitoid, MP=mummy parasitoid, H=aphid host, log=$\log_{10}$

Cohen, Jonsson, Mueller, Godfray, Savage *PNAS* 2005

Size matters, but that's not all!

The type of parasitoid (primary, hyper-, or mummy parasitoid) & species identity of the plant, aphid, or parasitoid affected the relationship between parasitoid body size & final aphid host body size.

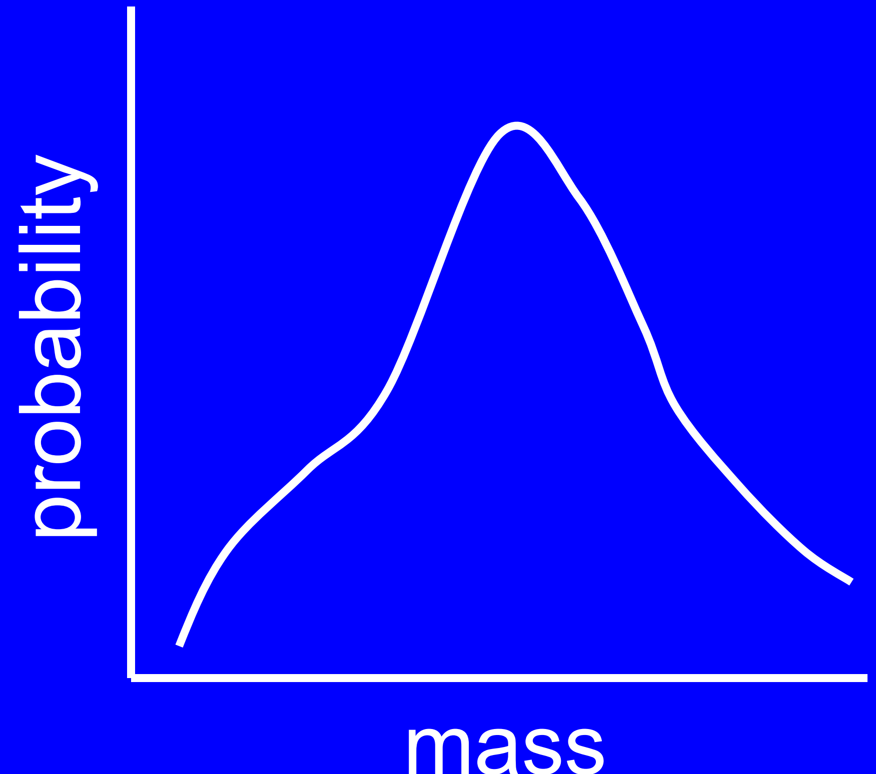
Parasitoid type & species identity mattered most for the relationship between parasitoid & aphid body size.

Plant & aphid species identities were important through association with different parasitoid species & because different aphid species had different body sizes.

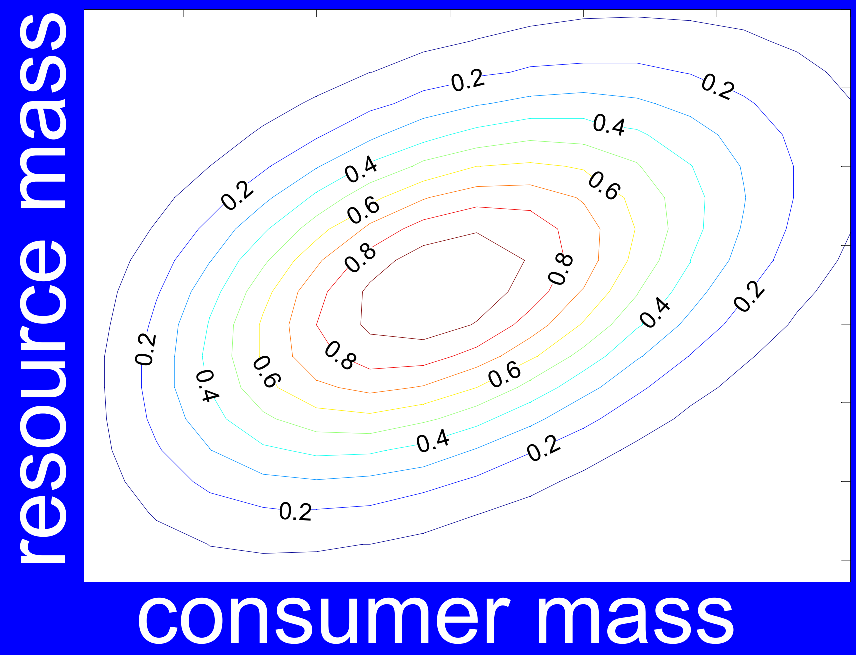
New data structure: beyond the trophic link, beyond the M,N web

Replace average body mass M of each taxon with frequency distribution of mass of all individuals in the taxon.

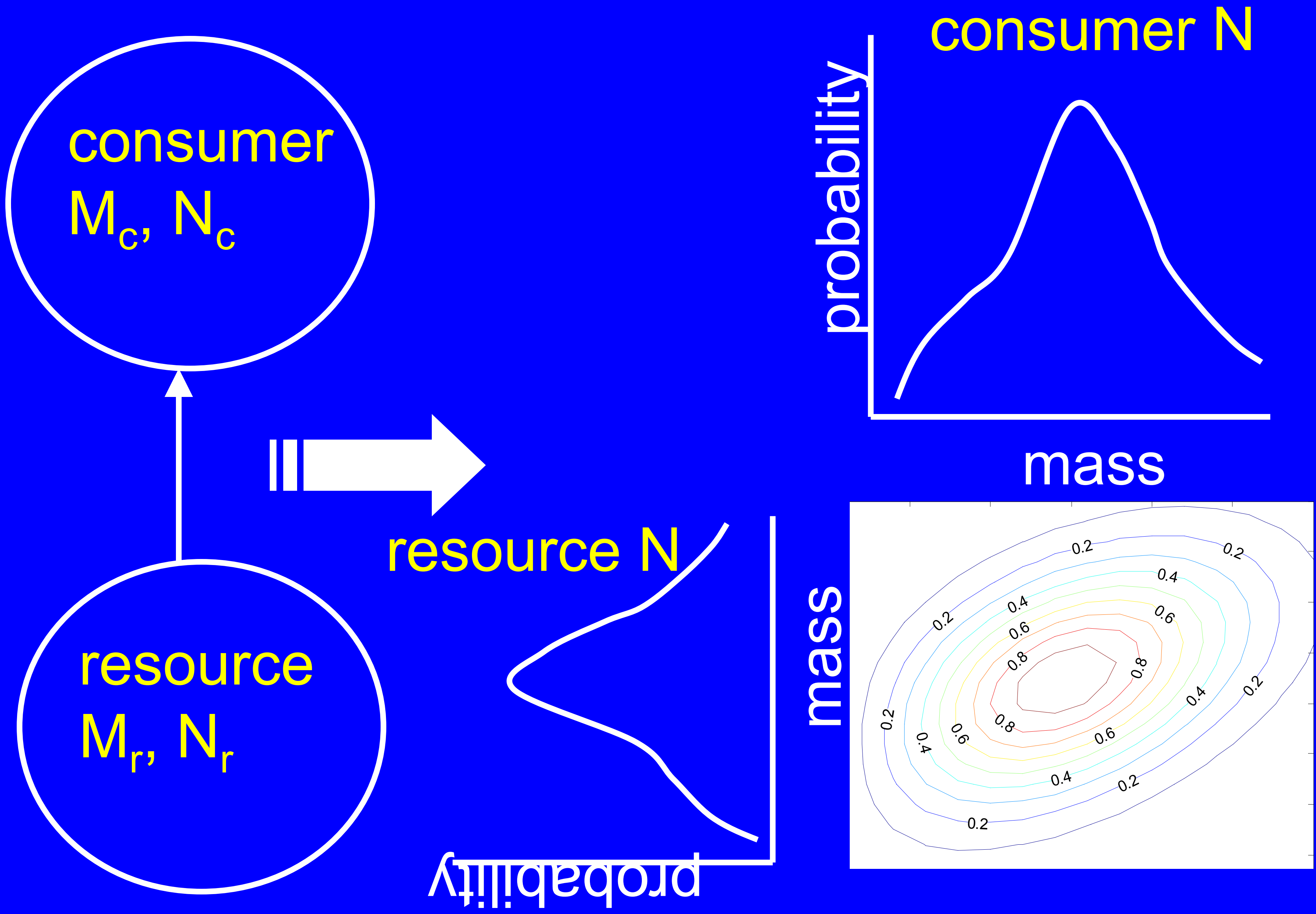
de Roos & Persson 2005



Replace link from resource to consumer with bivariate conditional probability function: $f(M_c, M_r)$ is conditional probability of feeding event by consumer individual of mass M_c on resource individual of mass M_r, per consumer individual of mass M_c & resource individual of mass M_r.

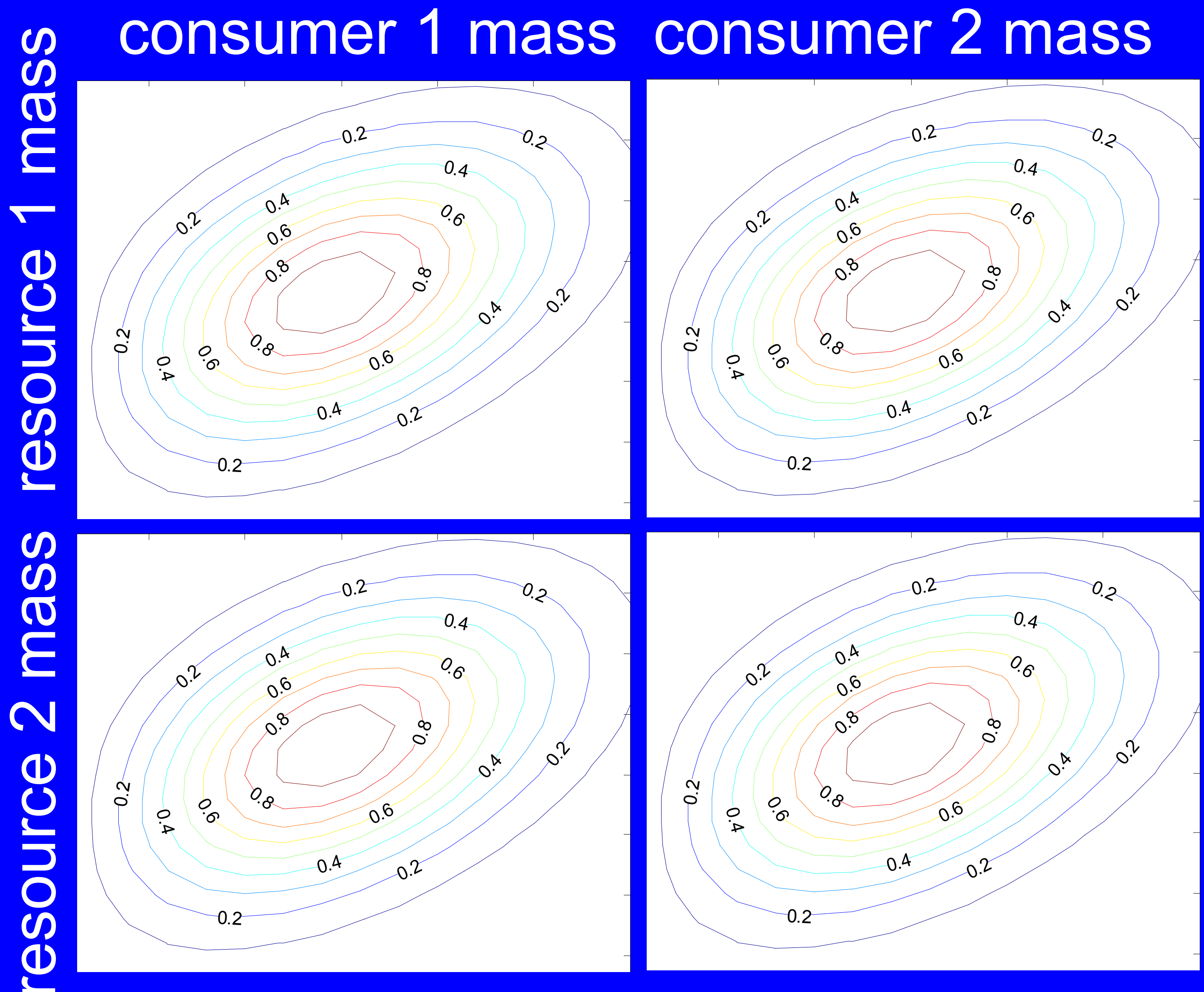


Consumer & resource taxa need not be distinct (cannibalism).

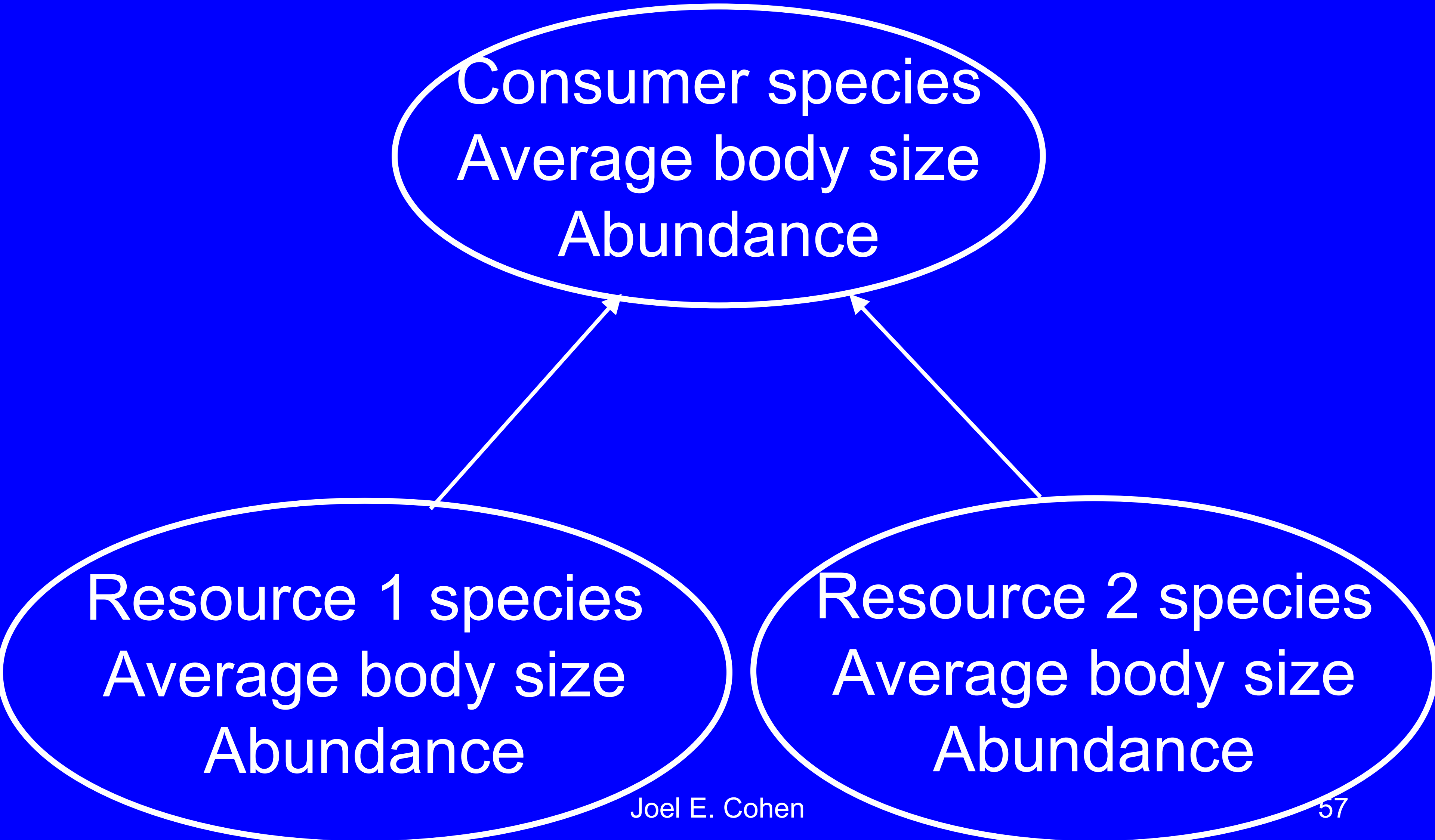

consumer N
consumer
M_c, N_c
probability
mass
resource N
resource
M_r, N_r
mass
probability

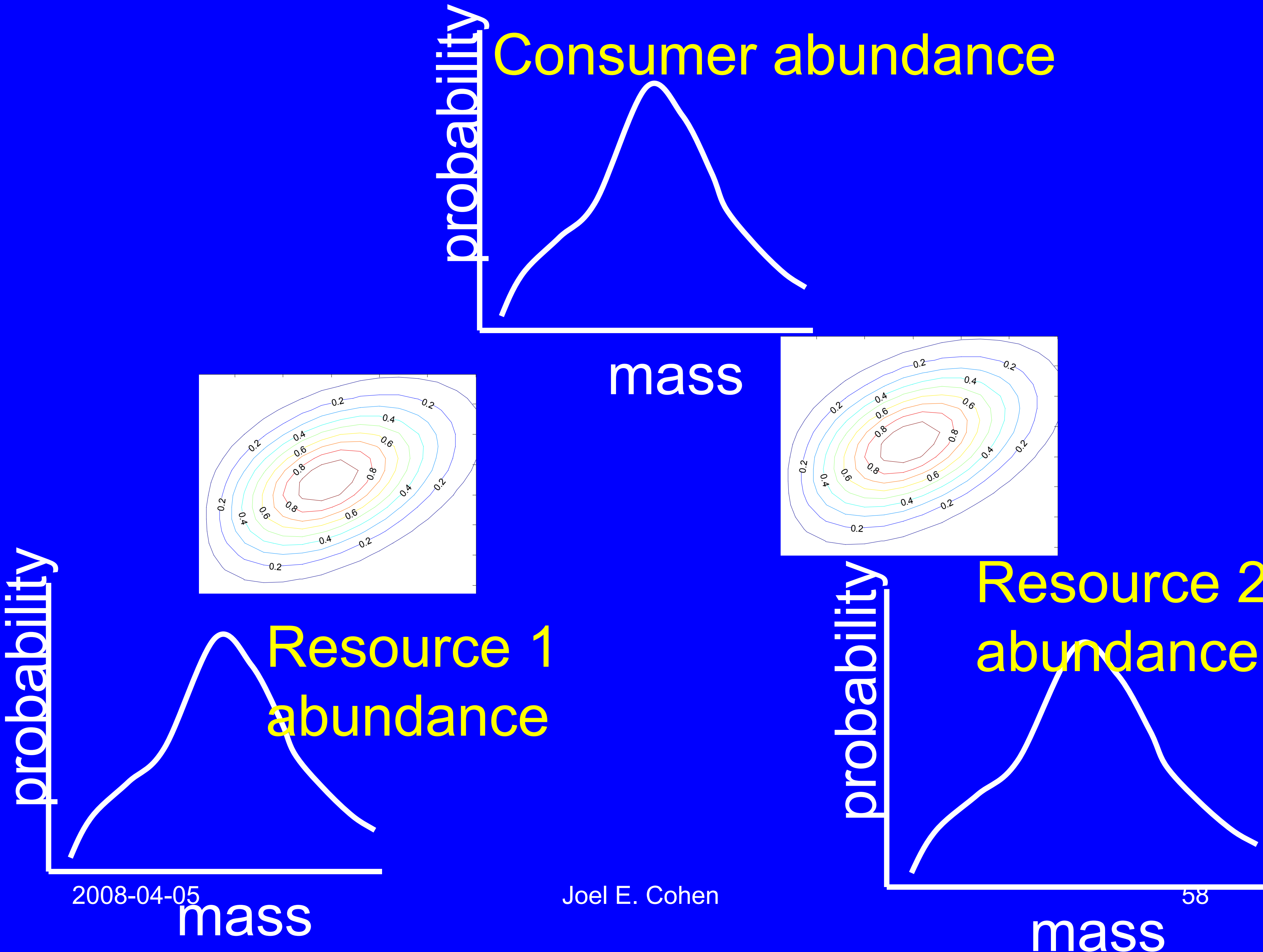
Do taxa matter, or only size?

Does the conditional probability distribution of feeding events depend on taxon identities? Or only on body masses?



Forbes food web:
species & trophic link characteristics



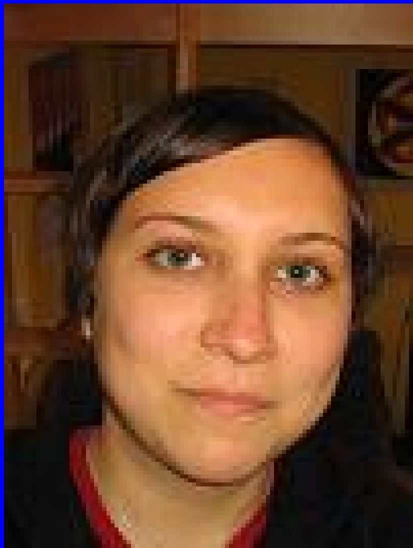

Consumer abundance
probability
mass
Resource 1
abundance
probability
mass
Resource 2
abundance
probability
mass
0.2
0.4
0.6
0.8

Tri-trophic interactions or 2-chains A (resource) →B (intermediate) → C (consumer) in webs with M, N

Do properties of links explain properties of 2-chains?

Do properties of 2-chains explain properties of longer food chains?

Daniella Schittler



Schittler, Reuman, Raffaelli, Cohen

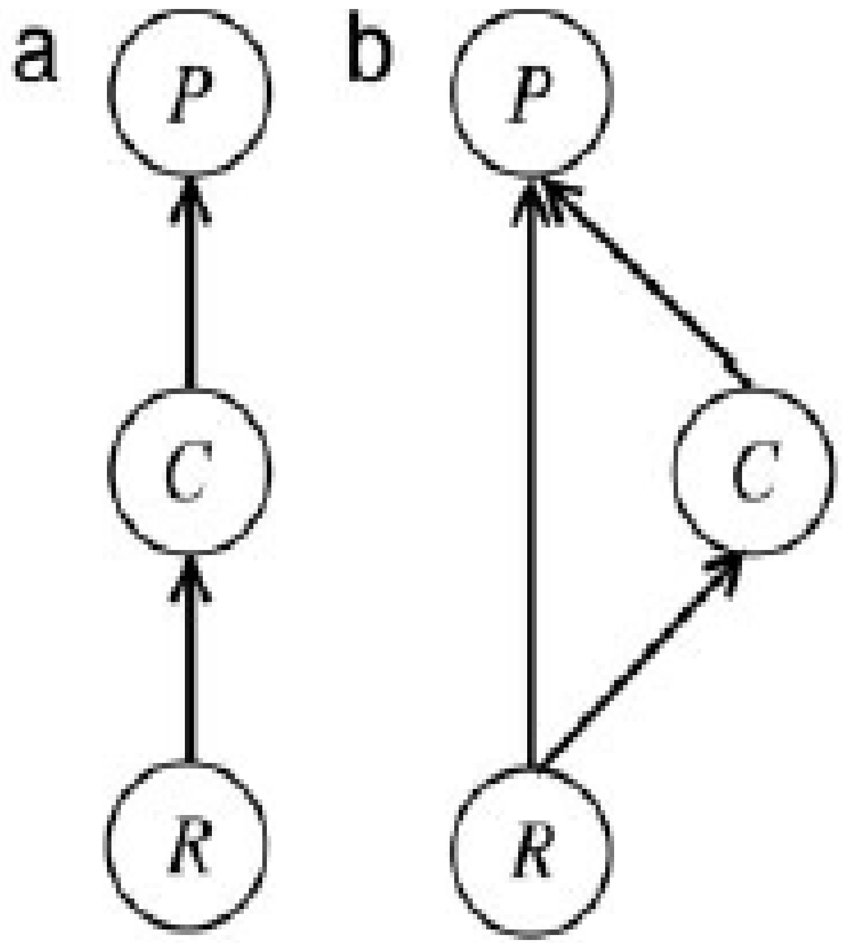
2008-04-05

Body size rules links & 2-chains.

links:	Tu 1984	Tu 1986	Ythan
all links	264	236	379
MR<MC	262 (99%)	232 (98%)	368 (97%)
MR=MC	0 (0%)	0 (0%)	2 (1%)
MR>MC	2 (1%)	4 (2%)	9 (2%)

2-chains:	Tu 1984	Tu 1986	Ythan
all 2-chains	1042	651	1371
MR≤MI≤MC	1000 (96%)	577 (87%)	1232 (90%)
MR≤MC<MI	29 (3%)	59 (9%)	65 (5%)
MI<MR≤MC	12 (1%)	10 (2%)	68 (5%)
MI≤MC<MR	0 (0%)	1 (0+%)	3 (0+%)
MC<MR<MI	1 (0+%)	3 (0+%)	0 (0%)
MC<MI<MR	0 (0%)	1 (0+%)	3 (0+%)

“…in a large Caribbean marine food web



…, the cooccurrence of strong interactions on two consecutive levels of food chains occurs less frequently than expected by chance.”

Bascompte, Melián, Sala *PNAS* 2005

Length of links

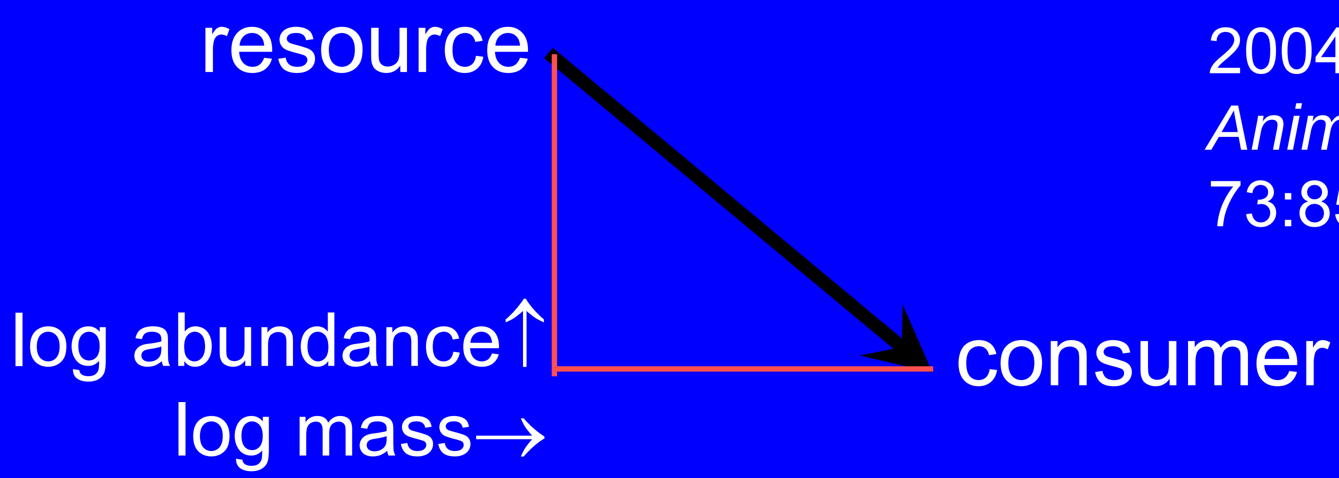
Length = orders of magnitude of mass ratio
+ orders of magnitude of abundance ratio

$$l_1 = |\log(M_c) - \log(M_r)| + |\log(N_c) - \log(N_r)|$$

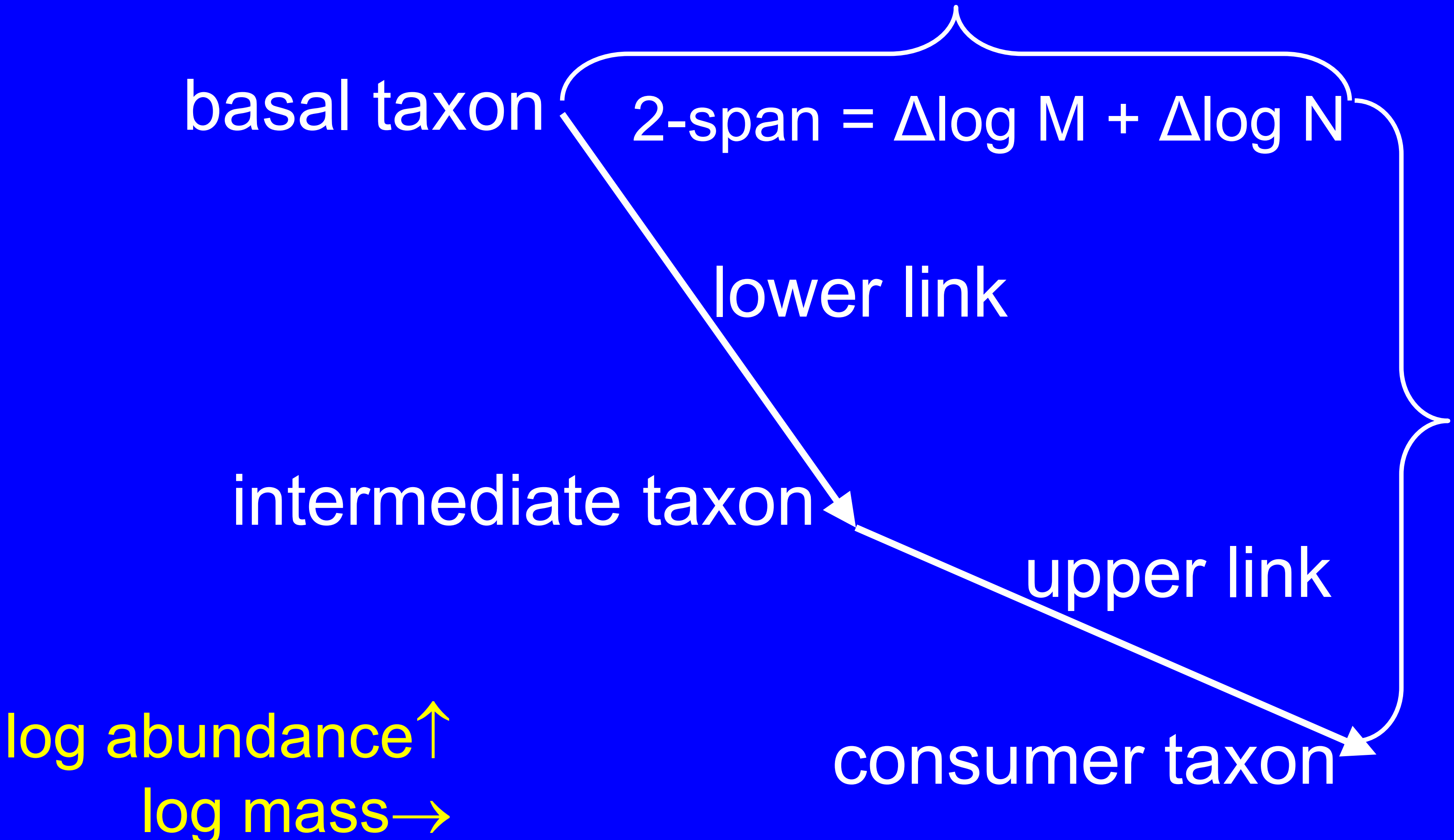
$$l_1 = |\log(M_c / M_r)| + |\log(N_c / N_r)|$$

All logarithms to base 10.

Reuman & Cohen 2004 *Journal of Animal Ecology* 73:852-866.



Names for 2-chains



Are links in 2-chains chosen at random from all links? No. Upper & lower links in 2-chains are shorter than average links.

	Tu'84	Tu'86	Ythan
mean link length	6.29	5.89	7.29
2×mean link length	12.59	11.79	14.58
mean $L_{upper}+L_{lower}$	11.35	9.11	11.21
mean L_{upper}	5.40	3.42	5.06
mean L_{lower}	5.95	5.69	6.15
mean 2-span	10.97	8.65	10.51

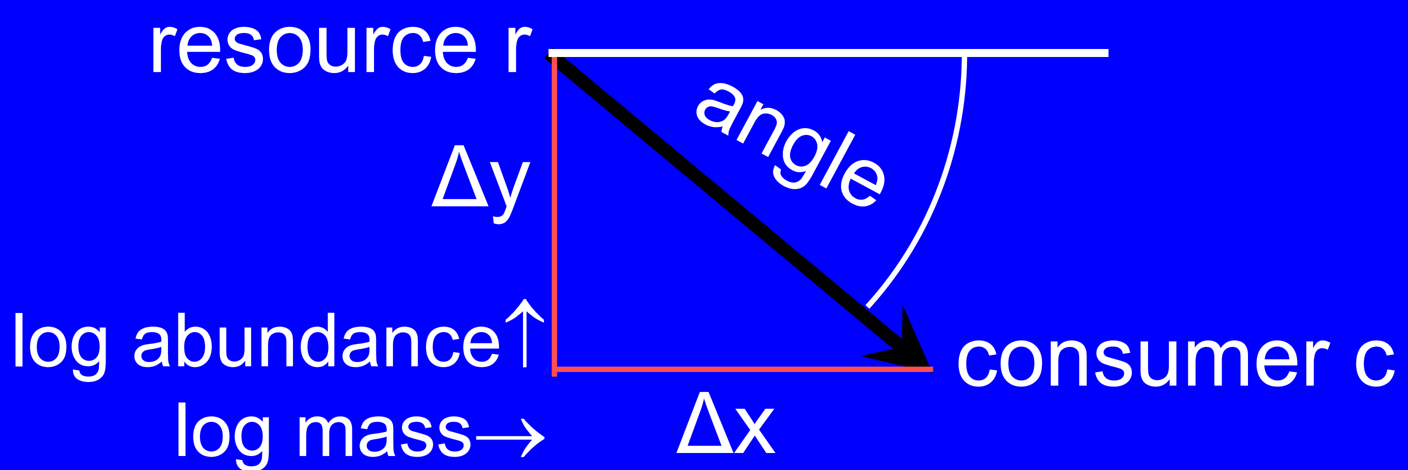
Angle & slope of links

Angle is measured in degrees from positive x-axis (log body mass).

Slope = $\Delta y/\Delta x$ = $\log(N_c / N_r) / \log(M_c / M_r)$.

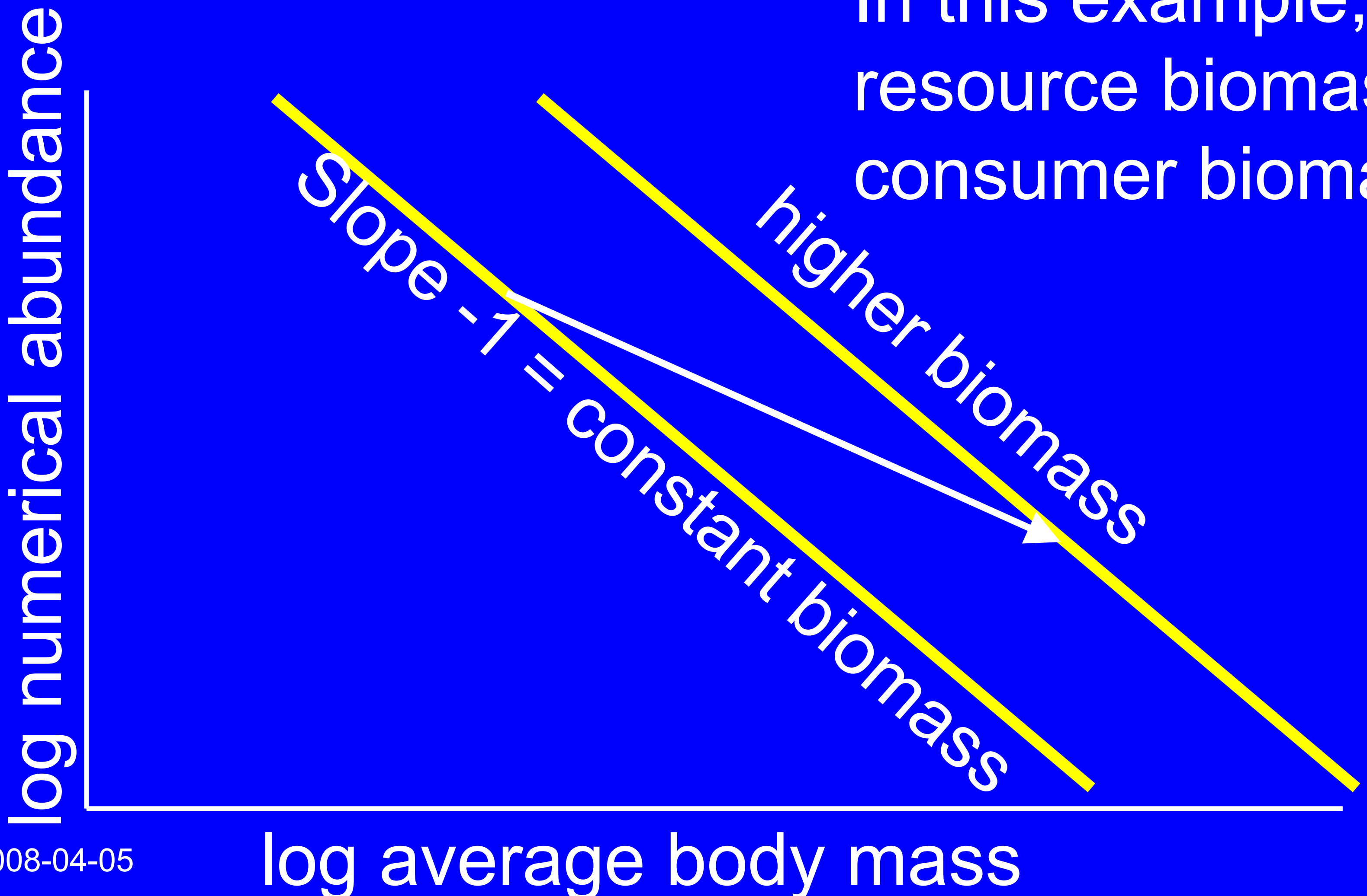
Angle = -45 degrees ←→ slope = -1.

Angle = -36.9 degrees ←→ slope = -3/4.



Biomass = body mass x abundance. Link slope reveals biomass change.

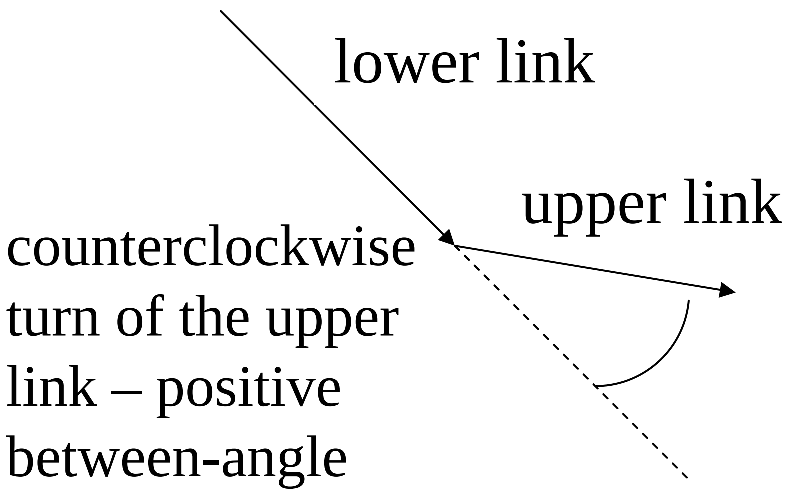
In this example, resource biomass < consumer biomass.

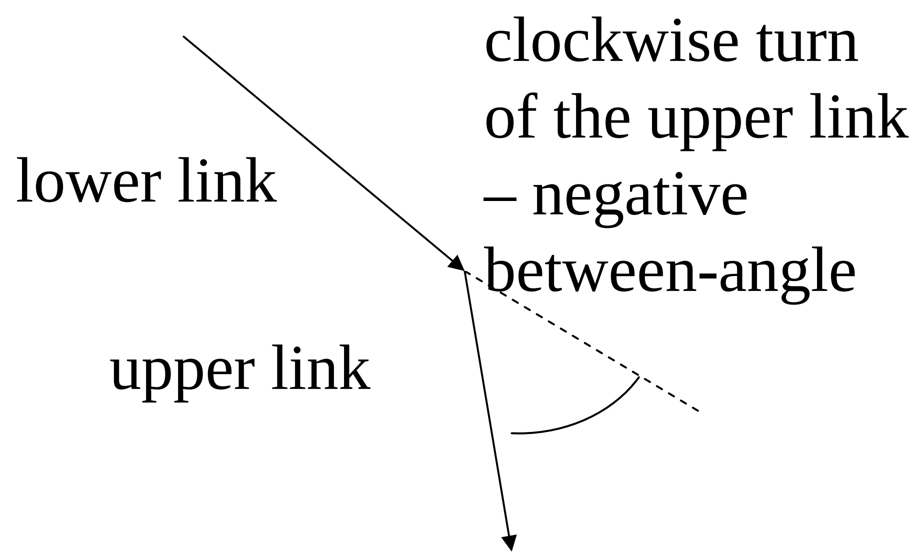


Angle or slope of a link reveals rate of change in biomass, population productivity & population consumption from resource to consumer.

- If population productivity & population consumption scale as NM^b, $0<b<1$, e.g. $b=3/4$,
- then in a link with slope $> -b$, population productivity & population consumption of the resource taxon < population productivity & population consumption of the consumer taxon; & vice versa.

Between-angle of 2 chains



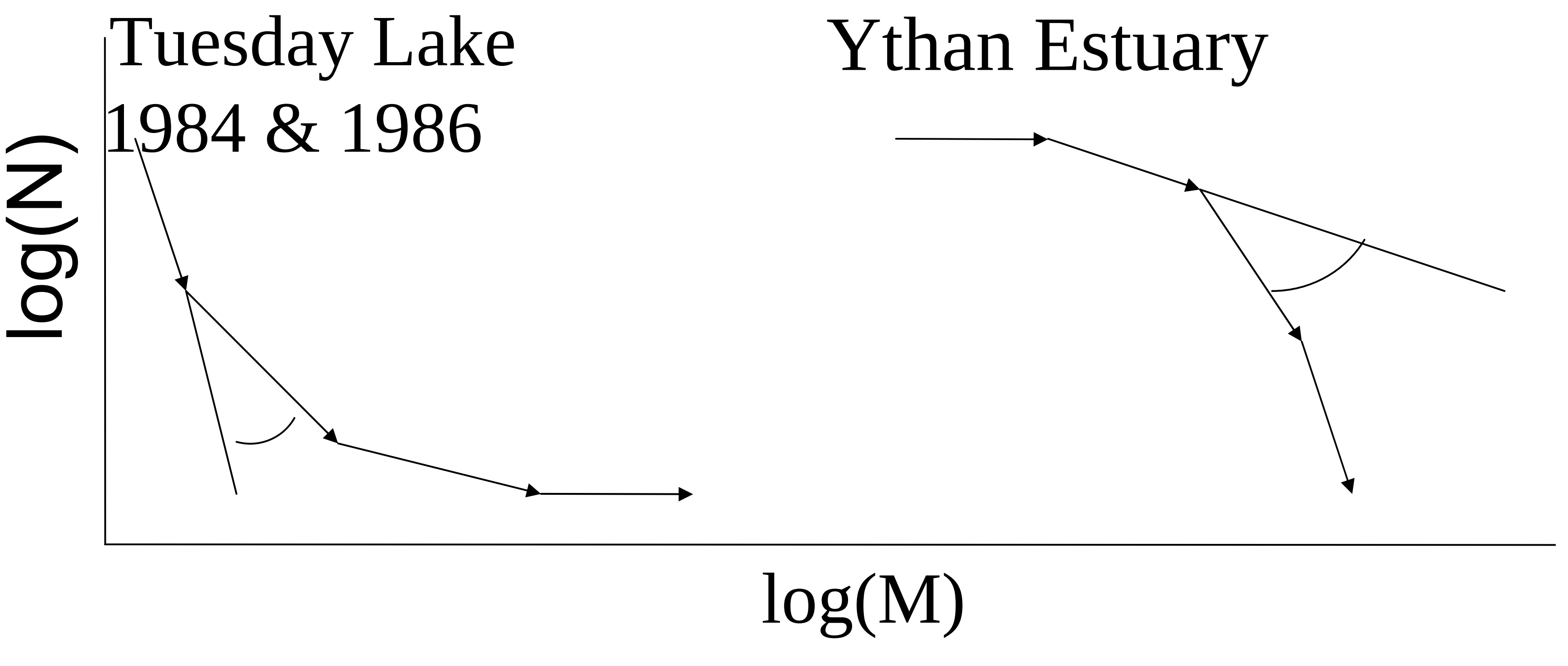


Between-angle is rate of change in rate of change in biomass, population productivity & population consumption from resource to intermediate taxon to consumer: acceleration of biomass, population productivity & population consumption.

Are between-angles of 2-chains same as those of random triples of taxa ordered by size? No. Webs differ from one another & from random ordered triples.

	Tu'84	Tu'86	Ythan
mean between-angle	16	30	-32
std. dev.	52	63	62
mean between-angle of random ordered triples	-3	-4	-2

Biomass accelerates up food chains in Tuesday Lake, decelerates in Ythan Estuary.



Single links are not enough!

2-chains have emergent properties not predicted by properties of single links.

2-chains are not enough!

Tri-trophic interactions do not account for emergent properties of longer food chains.

In Tuesday Lake, typical chains extended over most of the community’s range of log(M) and log(N), whereas in the Ythan Estuary, typical chains covered only 60% to 77% of the community’s range of log(M) & log(N).

New structure emerges at each level.

Tri-trophic interactions have properties not readily derived from properties of trophic links.

Longer chains have properties not readily derived from properties of trophic links or tri-trophic interactions.

At each higher level of structure, new properties emerged that differed from ecosystem to ecosystem.

Future food web data structures

Dynamic community models: a Leslie matrix for every taxon, with parameters influenced by trophic interactions

Ecological stoichiometry for every taxon

Genetics of reproduction, survival, migration, consumption, resistance to consumption

Community-level attributes associated with each food web

Thank you! Questions?

cohen@rockefeller.edu

Canadian lynx & snowshoe hare

http://homestudy.ihea.com/wildlifeID/rudolfos_usenet_animal_pict.jpg