Food Webs in an ecological environment

Rigi-Workshop 2015 – Louis-Felix Bersier, University of Fribourg (CH)

1. A short history of the study of ecological networks
- From Camerano to MacArthur

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1. A short history of the study of ecological networks
- From Camerano to MacArthur (and May)

Definition of ecology

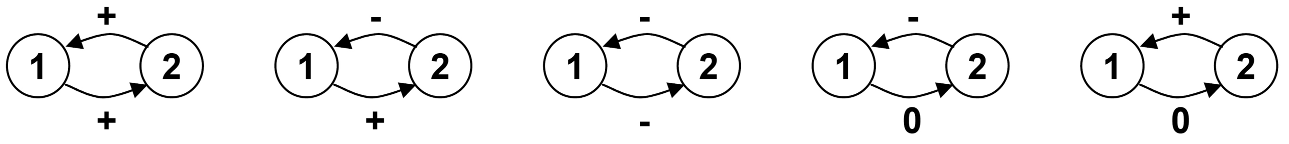
Original definition of “Ecology” by Haeckel (1866):

"By ecology we mean the body of knowledge concerning the economy of nature - the investigation of the total relations of the animal both to its inorganic and its organic environment; including, above all, its amical and inimical relations with those animals and plants with which it comes directly or indirectly into contact - in a word, ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence."

(source: http://www.uni-jena.de/-page-364-lang-en.html)

Types of biotic interactions

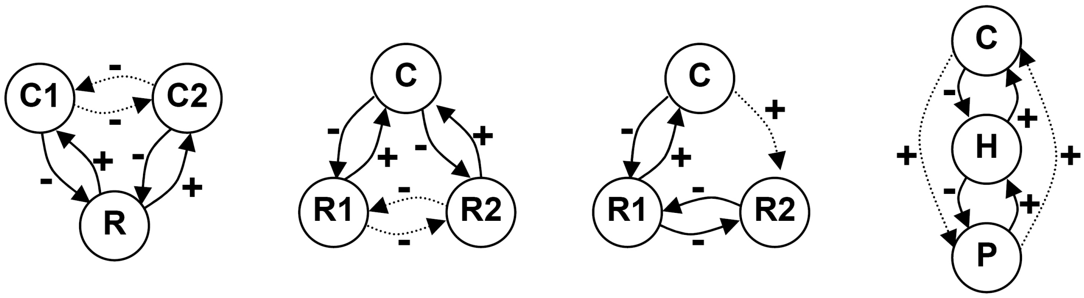
Direct :



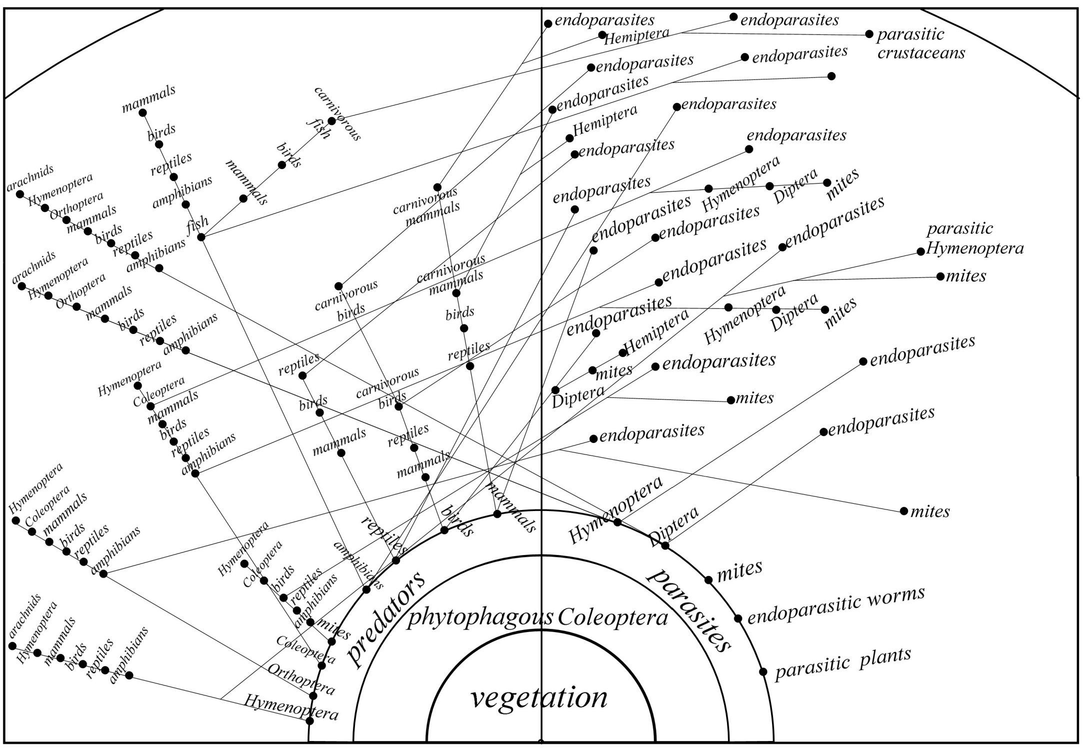
Mutualism | Predation | Competition | Amensalism | Commensalism

Indirect :

consumptive competition | apparent competition | keystone predation | trophic cascade



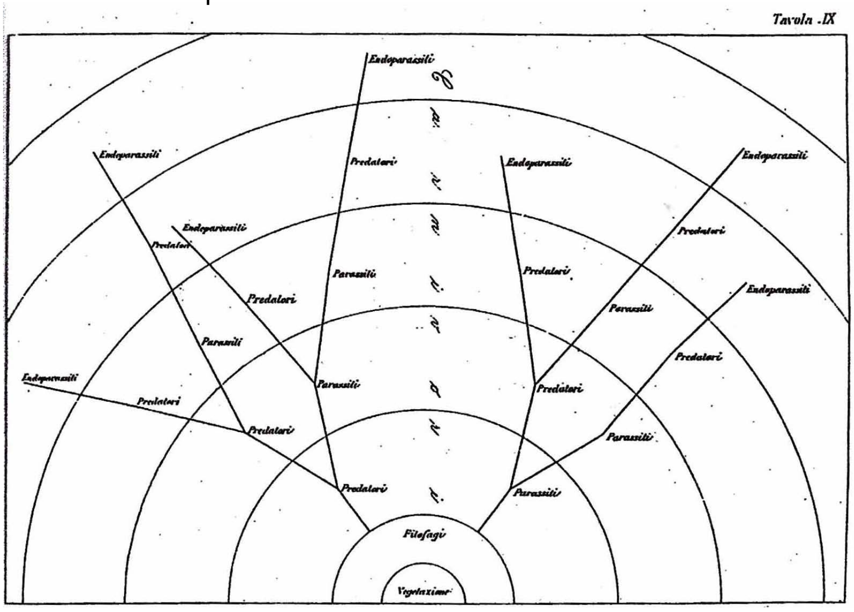
First graph of a food web : Camerano (1880)



Camerano, L. (1880) Dell'equilibrio dei viventi merce la reciproca distruzione. Atti della Reale Accademia delle Scienze di Torino, 15, 393-414. (For an English translation by Claudia M. Jacobi: Levin, S.A., ed. (1994) Frontiers in Mathematical Biology. Springer Verlag, Berlin, pp. 360-380).

Camerano (1880)

Generalized trophic network :



5 categories: vegetation, herbivors, parasites, endoparasites, predators

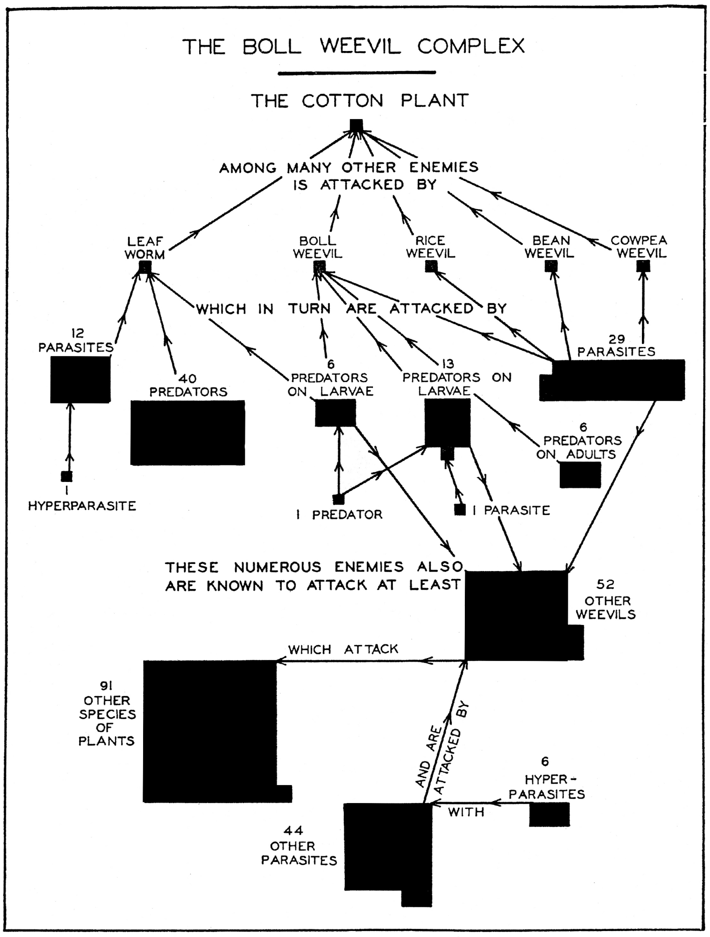
Camerano' view on community stability :

Rather, it is necessary to study each in relation to all other animals to see the general laws governing the equilibrium of animal and plant species…

From this it follows that no species, be it carnivore or herbivore, can develop beyond a certain limit which, if surpassed, would destroy the source of its own nourishment. Equilibrium, broken by the excessive growth of either kind of animal, would be again reestablished.

Pierce et al. (1912)

The food-web of the boll weevil, from Pierce et al. (1912). Direction of arrows is from consumer to prey; numbers and size of boxes refer to the number of species in the group.



Pierce, W.D., Cushman, R A. & Hood, C.E. (1912) The insect enemies of the cotton boll weevil. U.S. Department of Agriculture Bureau of Entomology Bulletin 100. 99pp.

Summerhayes and Elton (1923)

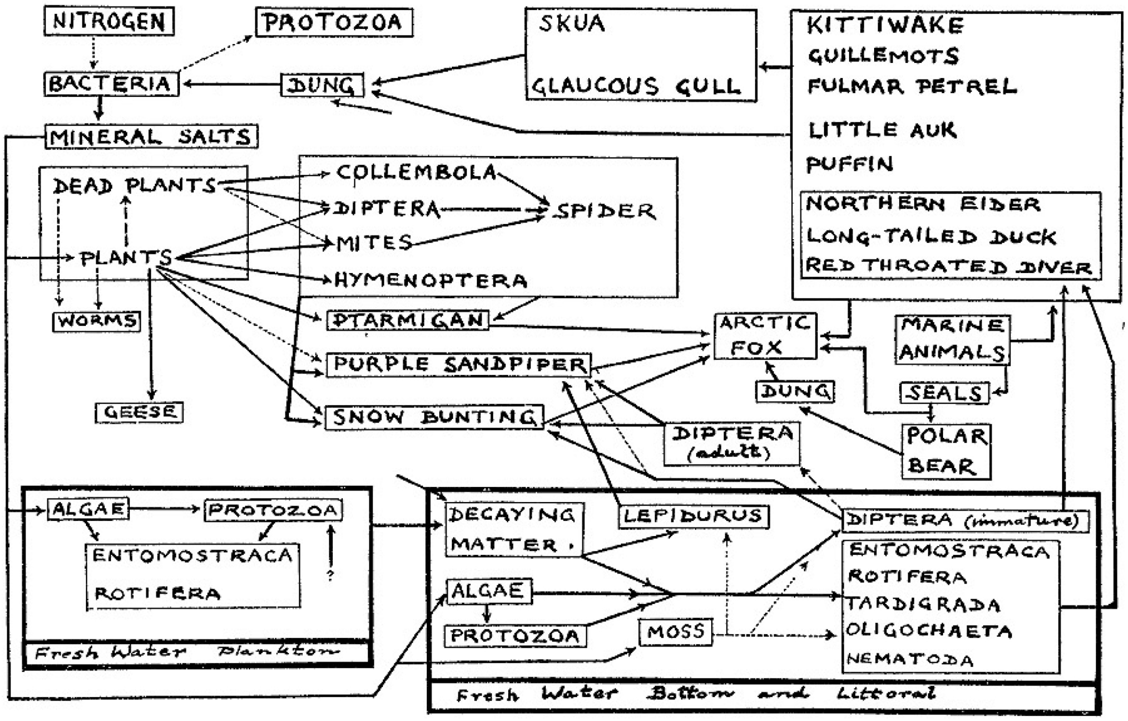


Diagram of the nitrogen cycle on Bear Island, from Summerhayes & Elton (1923). Dotted lines are links that were not observed but probable.

Summerhayes, V.S. & Elton, C.S. (1923) Contributions to the ecology of Spitsbergen and Bear Island. Journal of Ecology, 11, 214-286.

Lindemann

TABLE IV. *Productivities and progressive efficiencies in the Cedar Bog Lake and Lake Mendota food cycles, as g-cal/cm²/year*

	Cedar Bog Lake		Lake Mendota	
	Productivity	Efficiency	Productivity	Efficiency
Radiation	≦118,872		118,872	
Producers: Λ_1	111.3	0.10%	480*	0.40%
Primary consumers: Λ_2	14.8	13.3%	41.6	8.7%
Secondary consumers: Λ_3	3.1	22.3%	2.3†	5.5%
Tertiary consumers: Λ_4	—	—	0.3	13.0%

* Probably too high; see footnote of table III.
† Probably too low; see footnote of table III.

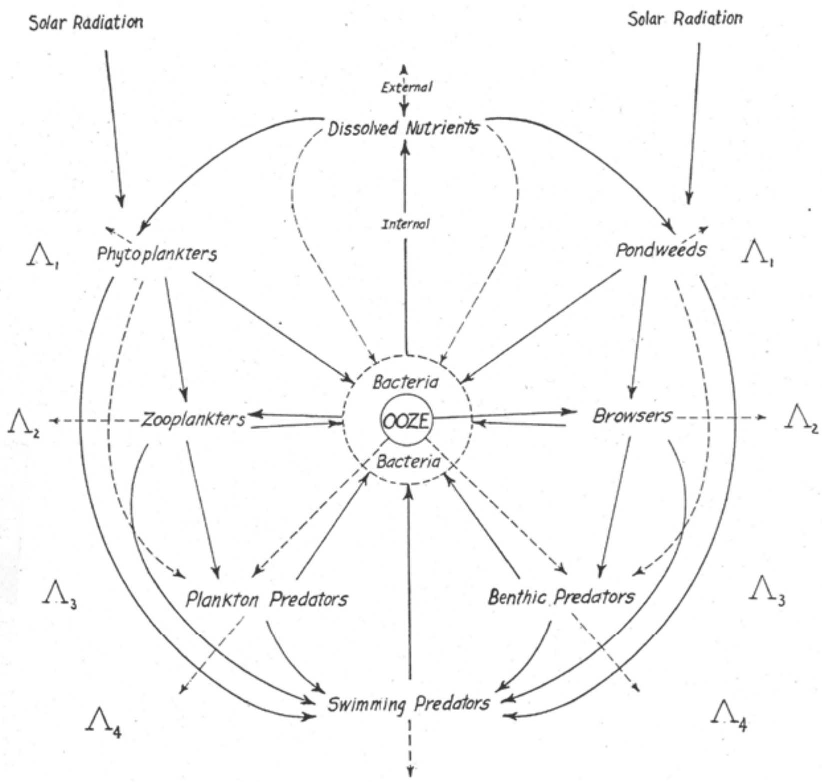


FIG. 1. Generalized lacustrine food-cycle relationships (after Lindeman, '41b).

Lindeman, R.L. (1942) The trophic-dynamic aspect of ecology. Ecology, 23, 399-417.

Late 19th Century: Early thoughts on equilibrium

Forbes 1880:

It is a general truth, that those animals and plants are least likely to oscillate widely which are preyed upon by the greatest number of species, of the most varied habitat. Then the occasional diminution of a single enemy will not greatly affect them, as any consequent excess of their own numbers will be largely cut down by their other enemies, and especially as, in most cases, the backward oscillations of one set of enemies will be neutralized by the forward oscillations of another set. But by the operations of natural selection, most animals are compelled to maintain a varied food habit, --so that if one element fails, others may be available.

Forbes (1880) On some interactions of organisms. Illinois Lab. Of Nat. Hist. Bull. 1(3):3-17

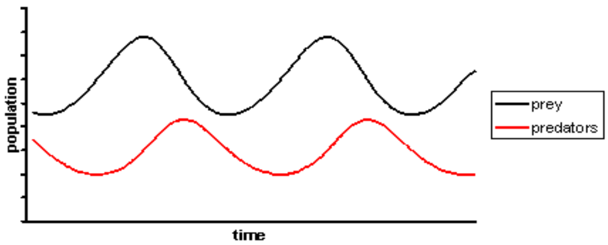
Early 20th Century: Lotka & Volterra

Alfred J. Lotka (1925) & Vito Volterra (1926)

A pair of first order, non-linear differential equations, representing the change in numbers of a predator y and prey x over time t due to their interaction.

$$\frac{dx}{dt} = \alpha x - \beta xy \qquad \frac{dy}{dt} = \delta xy - \gamma y$$

α is the intrinsic exponential growth of prey
β is the rate of predation of y on x, which is proportional to rate at which y and x meet
δ is the "growth rate" of the predator through the conversion of prey into newborns
γ is the natural death rate of the predator (exponential decay)



Lotka (1925) Elements of physical biology. Williams and Wilkins, Baltimore
Volterra (1925) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem R Accad Naz dei Lincei 2:31-113

1920s to 50s: Complexity begets stability

Odum (1953) Fundamentals of Ecology. Saunders.

MacArthur (1955) Fluctuation of animal populations and a measure of community stability. Ecology 36: 533-536.

"…a large number of paths through each species is necessary to reduce the effects of overpopulation of one species…"

> There are several properties of this stability which are interesting.
>
> 1. Stability increases as the number of links increases.
>
> 2. If the number of prey species for each species remains constant, an increase in number of species in the community will increase the stability.

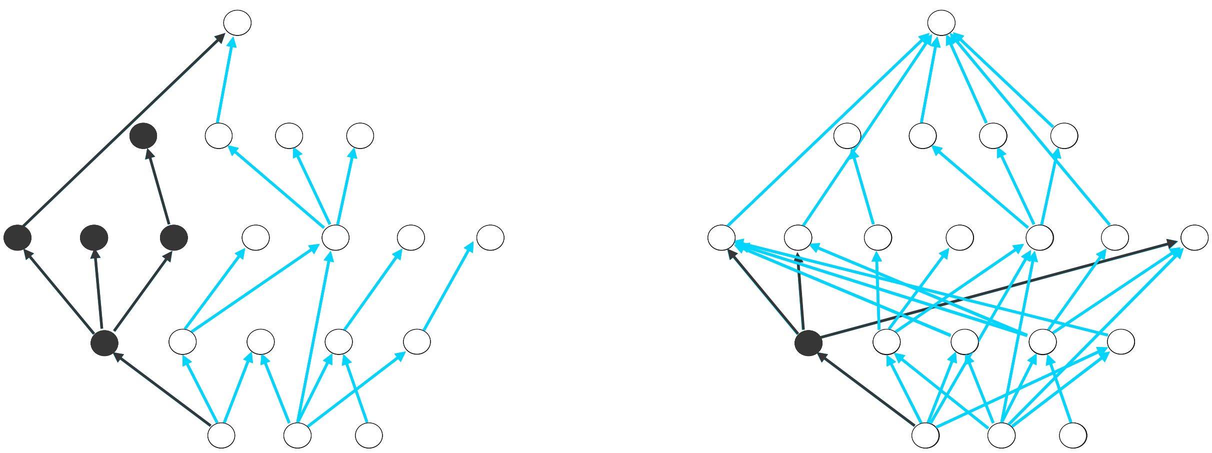
Elton (1958) Ecology of Invasions by Animal and Plants. Chapman and Hall.

List of arguments supporting the "complexity begets stability" dogma, among them: 2 species Lotka-Volterra systems are inherently unstable and show large fluctuations.

Hutchinson (1959) Homage to Santa Rosalia, or why are there so many kinds of animals?The American Naturalist 93: 145-159.

> Modern ecological theory therefore appears to answer our initial question at least partially by saying that there is a great diversity of organisms because communities of many diversified organisms are better able to persist than are communities of fewer less diversified organisms. Even though the

MacArthur (1955) : more complex → more stable



MacArthur (1955) Fluctuation of animal populations and a measure of community stability. Ecology 36: 533-536.

Early 1970s: Complexity inhibits stability

May and Wigner Stability Criterion: **$i\,(SC)^{1/2} < 1$**

Local stability analyses of randomly structured, competitive community matrices indicate that the will be stable if:

i (interaction strength), or
S (diversity- number of species), or
C (connectance- probability that two species interact)

do not exceed critical values (following Ashby & Gardner 1970)

Implications:

→Increased links or species tend to increase destabilizing positive feedback loops

→If we assume i is constant, for communities with increasing S to be stable, C must decrease accordingly (or vice-versa)

→Mathematically speaking, increasing diversity (S) and complexity (C) destabilizes idealized communities, contrary to earlier ecological intuition

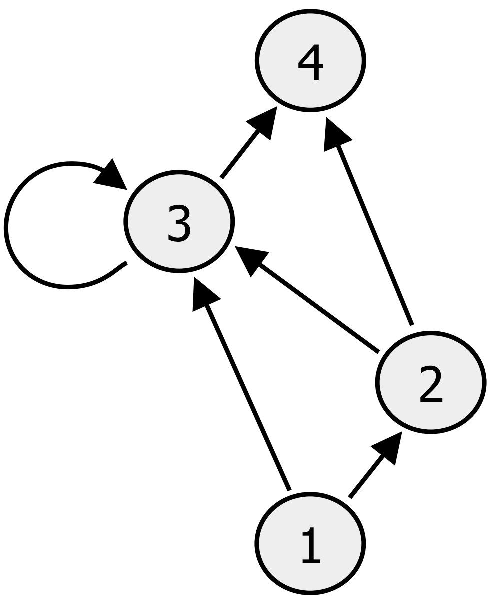
Conclusion:

In short, there is no comfortable theorem assuring that increasing diversity and complexity beget enhanced community stability; rather, as a mathematical generality the opposite is true. The task, therefore, is to elucidate the devious strategies which make for stability in enduring natural systems.

May RM (1972) Will a large complex system be stable? Nature 238:413-414.
May RM (1973) Stability and Complexity in Model Ecosystems. Princeton University Press

2. The search for regularities in the structure of food-webs

Food-web graph and food-web matrix



Predators (j)

prey(i)	1	2	3	4
1	0	1	1	0
2	0	0	1	1
3	0	0	1	1
4	0	0	0	0

Qualitative food-web properties

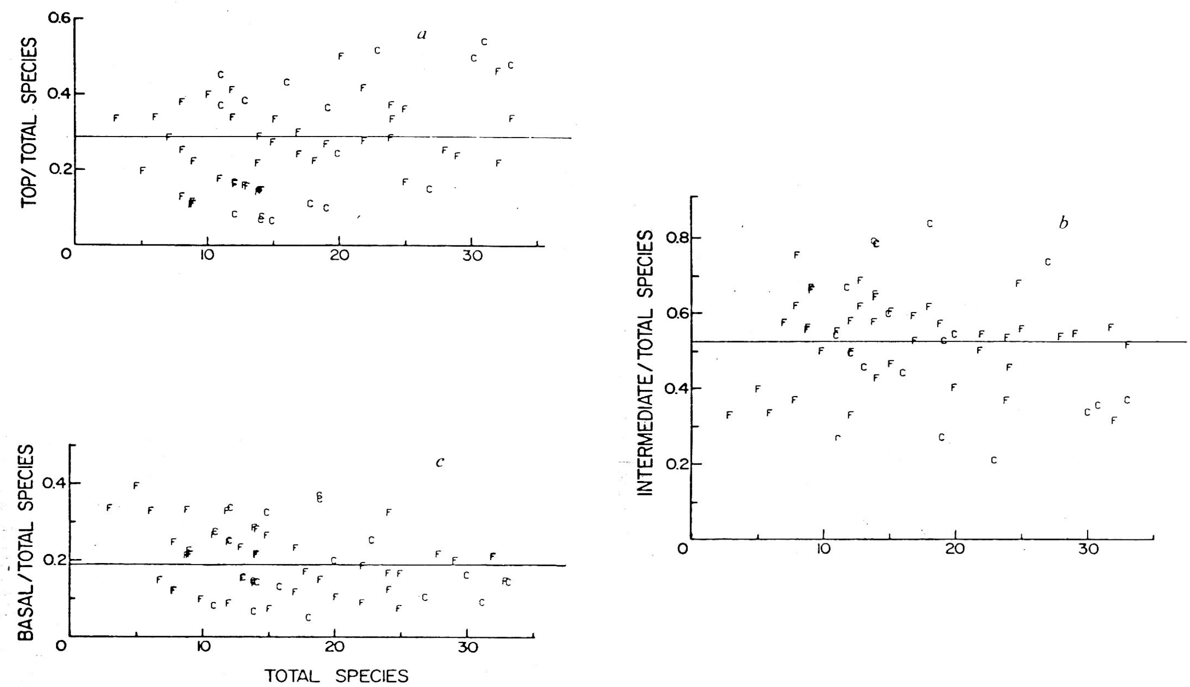
predators (j)

prey(i)

0	1	1	0
0	0	0	1
0	1	1	1
0	0	0	0

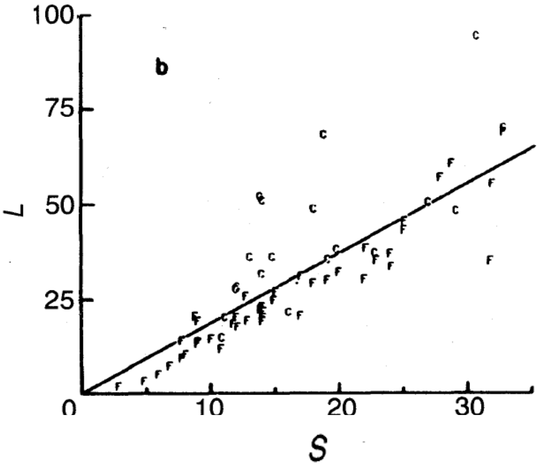
- directed connectance:
  $C = 6/16 = 0.375$
- proportion of top, intermediate, basal species:
  $\%T = 0.25$
- ratio of prey to predators
- vulnerability and generality
- SD of vuln. and SD of gen.
- Average (max) path (chain) length
- Proportion of omnivorous species
- Proportion of species in loops
- Diet discontinuity

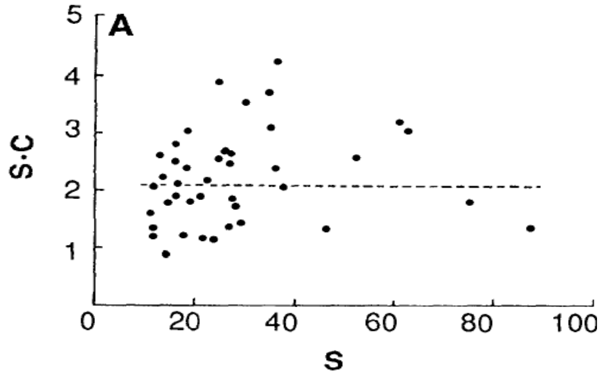
"Scaling laws"

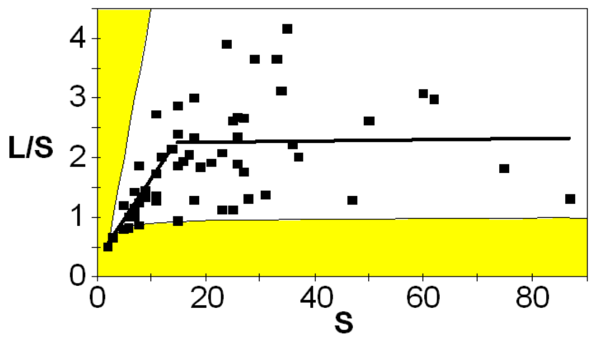


Cohen and Briand 1984

“Scaling laws”





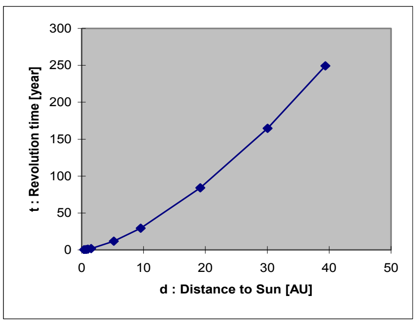


Cohen et al. 1990; Sugihara, Schoenly, & Trombla 1989; Bersier and Sugihara 1997

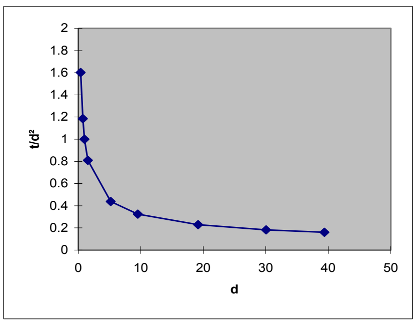
The importance of invariant properties

Keppler's third law

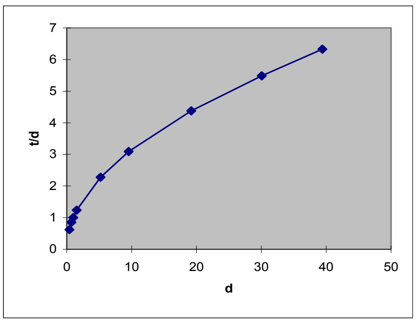
	Mean distance to Sun [u.a.] d	Revolution time [y] t
Mercury	0.3871	0.24
Venus	0.7233	0.62
Earth	1	1
Mars	1.5237	1.88
Jupiter	5.2028	11.86
Saturne	9.5388	29.46
Uranus	19.182	84.02
Neptune	30.058	164.79
Pluto	39.4	249.17



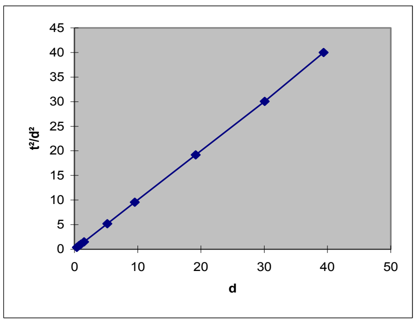
d	t/d²
0.3871	1.601639973
0.7233	1.185099348
1	1
1.5237	0.809764837
5.2028	0.4381375
9.5388	0.32377645
19.182	0.228346786
30.058	0.182394061
39.4	0.160510449



d	t/d
0.3871	0.619994833
0.7233	0.857182359
1	1
1.5237	1.233838682
5.2028	2.279541785
9.5388	3.088438797
19.182	4.380148055
30.058	5.482400692
39.4	6.324111675

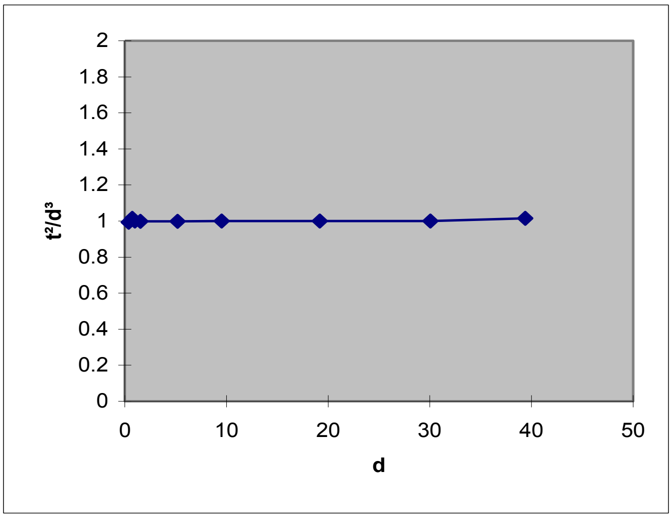


d	t²/d²
0.3871	0.384393593
0.7233	0.734761596
1	1
1.5237	1.522357894
5.2028	5.19631075
9.5388	9.538454205
19.182	19.18569699
30.058	30.05671735
39.4	39.99438848

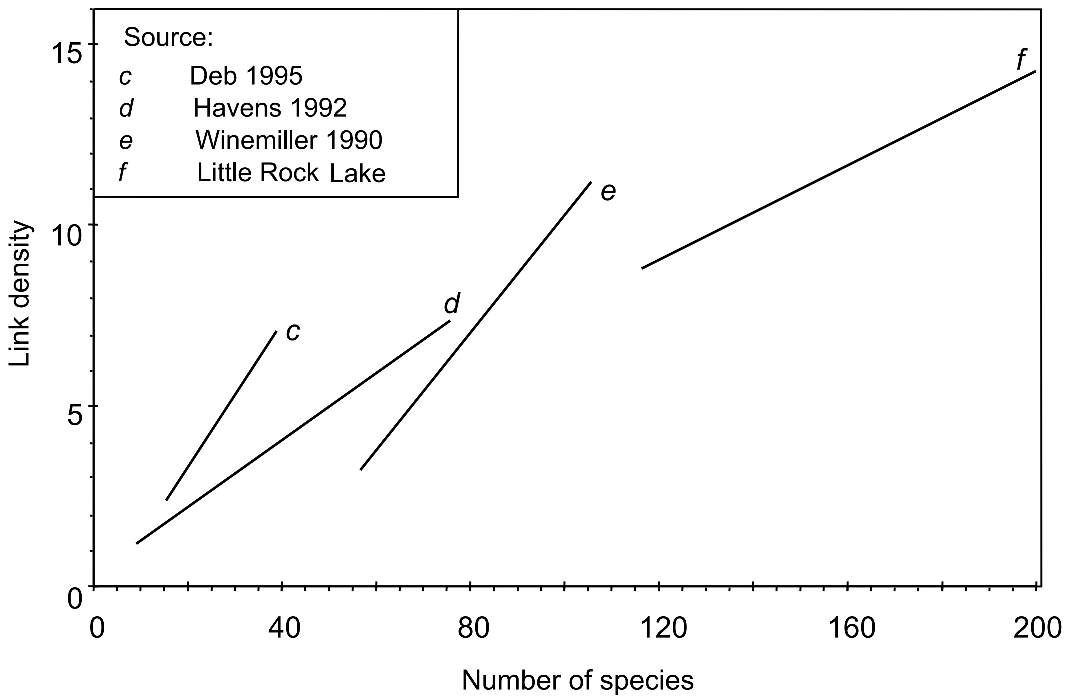


The importance of invariant properties

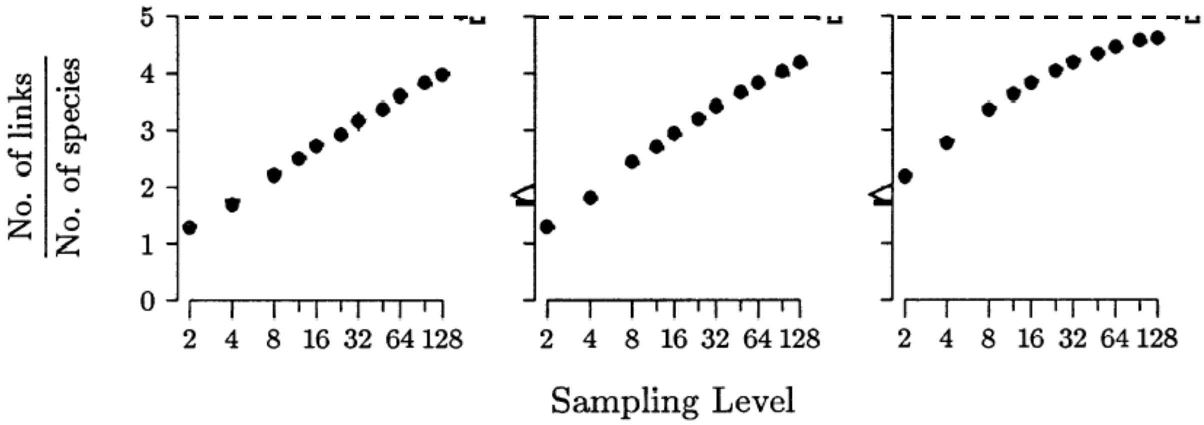
d	t^2/d^3
0.3871	0.993008508
0.7233	1.015846255
1	1
1.5237	0.999119179
5.2028	0.998752739
9.5388	0.999963749
19.182	1.000192732
30.058	0.999957327
39.4	1.015086002



Scaling laws are not confirmed in high-quality datasets

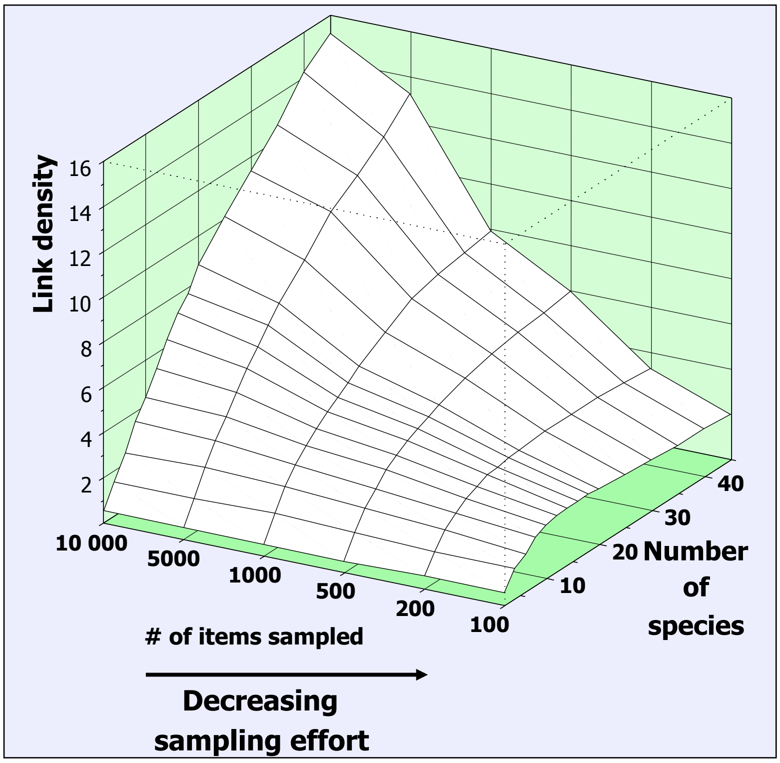


Caveat : Sensibility to sampling effort



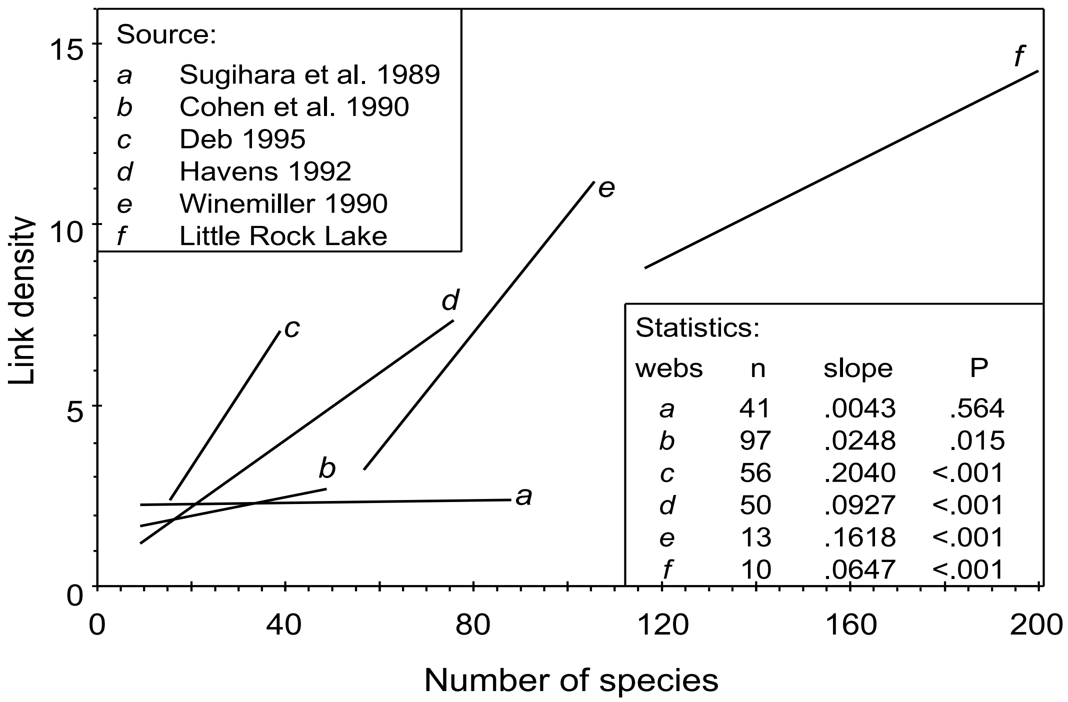
- Goldwasser & Roughgarden (1997)

Sampling effort affects perceived food-web structure

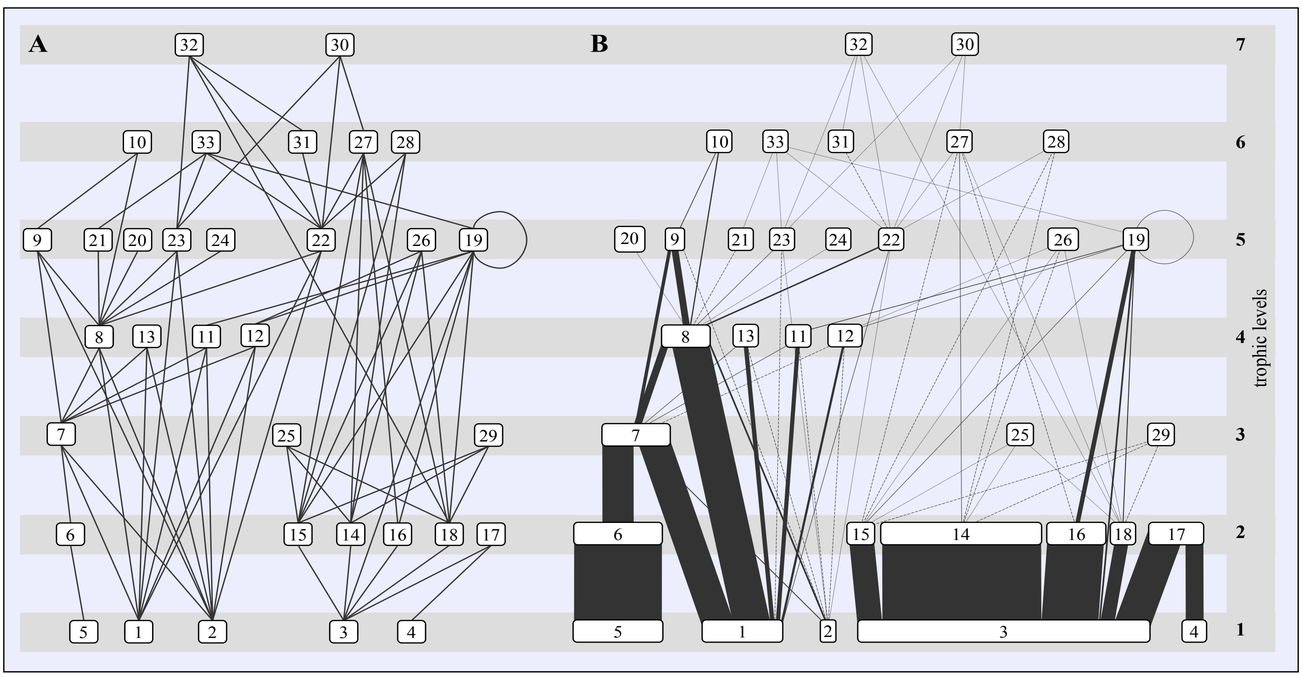


[Bersier et al. 1999]

This reconciles first and more recent studies



Qualitative vs. quantitative food webs



Data: [Baird & Ulanowicz 1989]

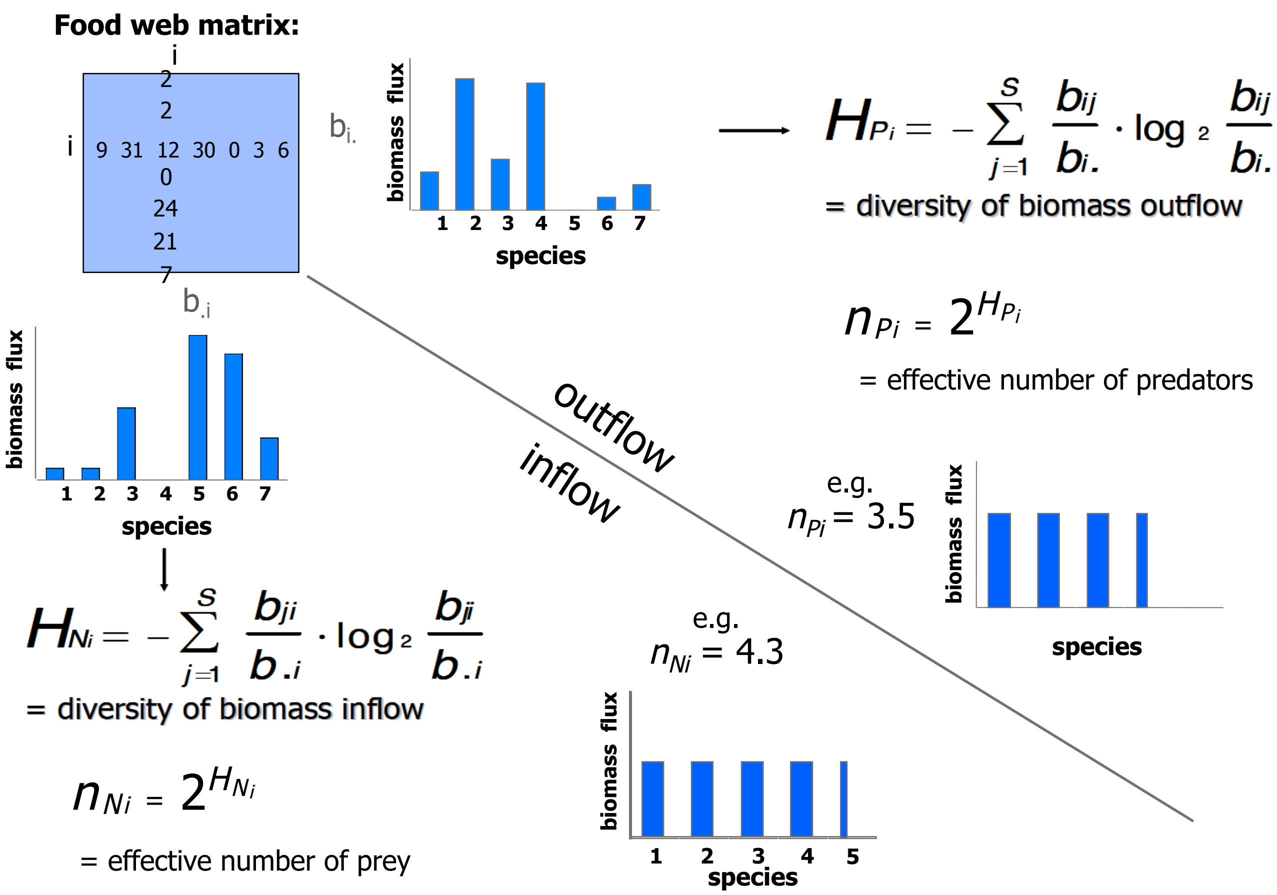
Developing a quantitative counterpart of qualitative descriptors

- qualitative link density = L/S

- quantitative link density = ???

  idea: base calculations on the Shannon and Wiener index of diversity

$$H_s = -\sum_{i=1}^{S} p_i \cdot \log_2 p_i$$



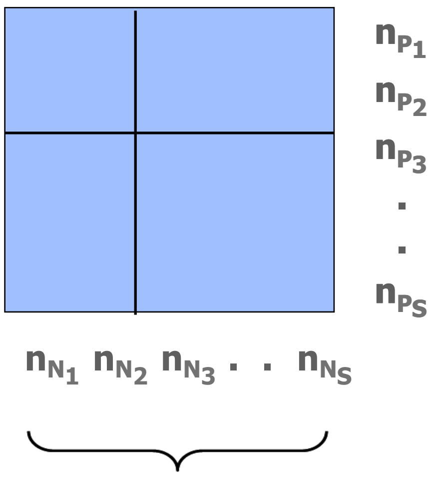
Food web matrix:

					$b_{i\cdot}$
0	1	1	0	1	3
0	0	1	1	0	2
0	1	0	1	0	2
0	0	0	1	1	2
0	0	0	0	0	0

average of $b_{i\cdot}$ values:

$$\sum_{i=1}^{S} \frac{1}{S} \cdot b_{i\cdot} = LD$$

Food web matrix:



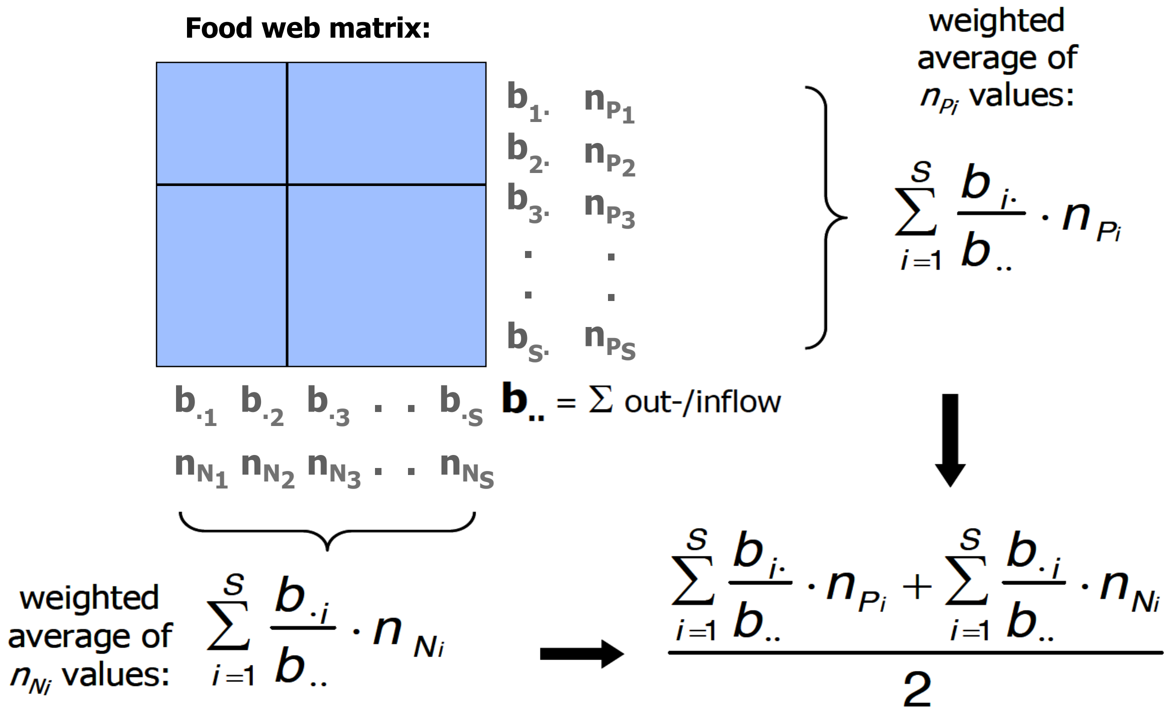
average of n_{P_i} values:

$$\sum_{i=1}^{S} \frac{1}{S} \cdot n_{P_i}$$

average of n_{N_i} values:

$$\sum_{i=1}^{S} \frac{1}{S} \cdot n_{N_i}$$

$$\rightarrow \frac{\sum_{i=1}^{S} \frac{1}{S} \cdot n_{P_i} + \sum_{i=1}^{S} \frac{1}{S} \cdot n_{N_i}}{2}$$



quantitative descriptors of link density

$$\frac{1}{2}\left(\sum_{i=1}^{S} \frac{1}{S} \cdot n_{P_i} + \sum_{i=1}^{S} \frac{1}{S} \cdot n_{N_i}\right)$$

= unweighted version

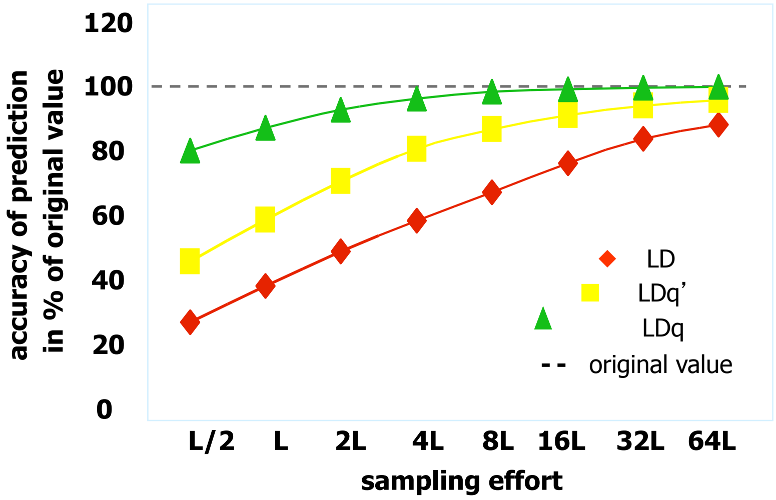
(each species is given the same weight)

$$\frac{1}{2}\left(\sum_{i=1}^{S} \frac{b_{i\cdot}}{b_{\cdot\cdot}} \cdot n_{P_i} + \sum_{i=1}^{S} \frac{b_{\cdot i}}{b_{\cdot\cdot}} \cdot n_{N_i}\right)$$

= weighted version

(the total amount of in- and outflow is considered)

Robustness of quantitative link density



food web data from:

- Baird & Ulanowicz (1989),
- Ulanowicz (unpublished),
- Goldwasser & Roughgarden (1993)

results:

❑ LDq' and LDq are more robust than LD against variable sampling effort.

❑ LDq' and LDq more adequately incorporate the information inherent to quantitative food webs, and are thus more suitable to reveal general trends in food-web structure.

Scaling of qualitative (diamond) and quantitative (triangles) links