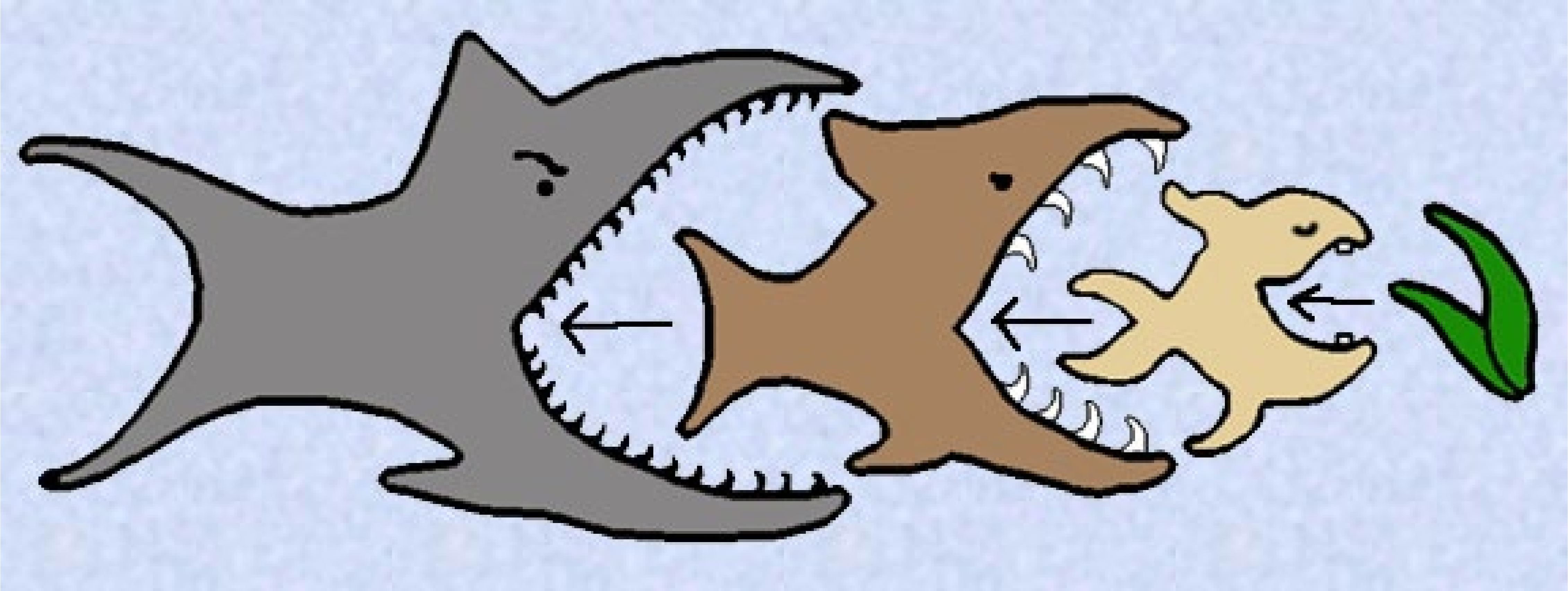
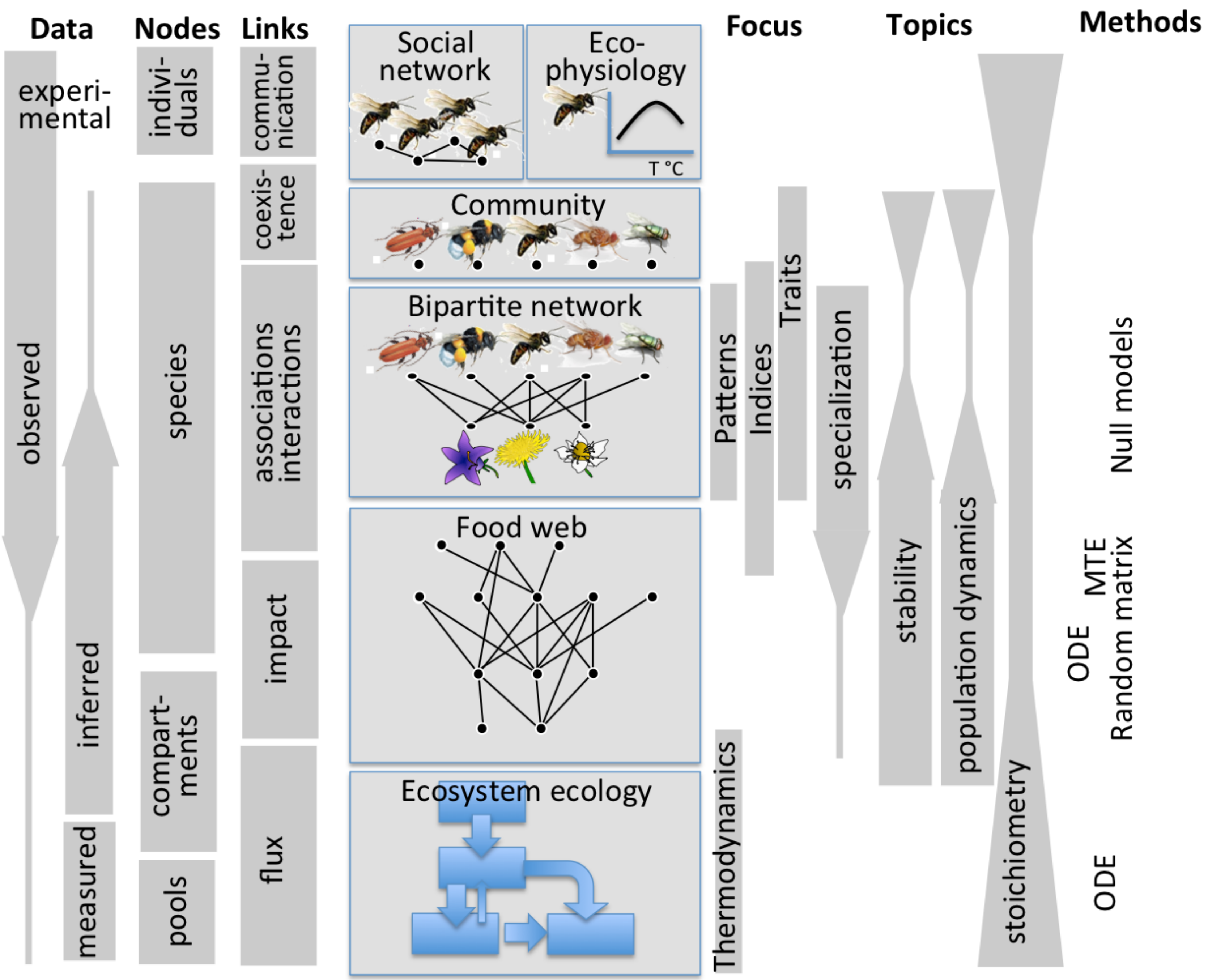
Food webs



VOJTECH NOVOTNY: COMMUNITY ECOLOGY
LECTURE NO 4, University of S. Bohemia

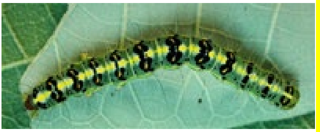


ODE ordinary differential equations, MTE metabolic theory of ecology

Dormann & Bruthgen in "Food Webs: Science for Impact", Moore et al Eds

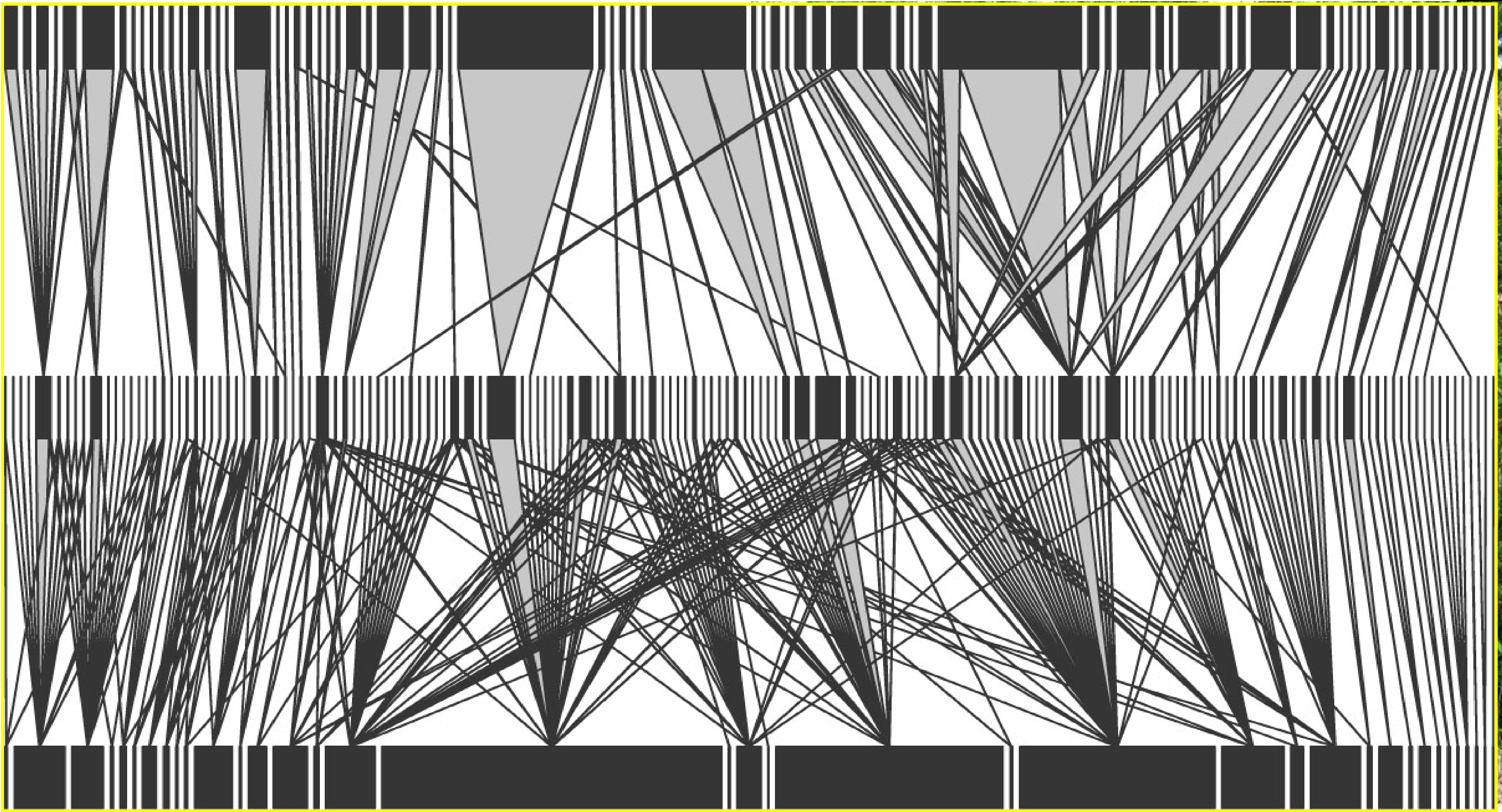
Tripartite food webs

1,523
parasitoids
from 166 spp.



11,621
caterpillars
from 267 spp.

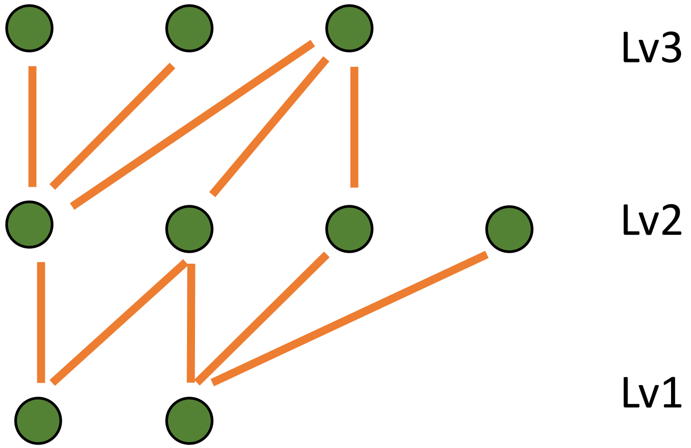
38 tree spp.



Lowland secondary rainforest vegetation in Papua New Guinea

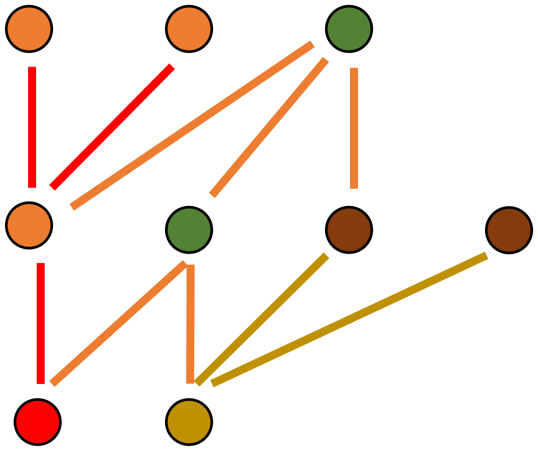
Jan Hrcek et al. 2013 *Oecologia* **173**: 521

Food-web attribute	Biological meaning
Taxa richness (S)	Number of taxa (nodes) in the food web.
Number of trophic links (L)	Number of directed feeding links (edges) between taxa.
Linkage density (= L/S)	Number of links per taxon. A measure of mean dietary specialisation across the food web [90].
Connectance (C) (= L/{S^2})	Proportion of potential trophic links that do occur. An indication of degree of inter-connectivity in a food web, typically 0.05–0.30 [91,92].
Generality (G)	The mean number of prey per consumer [93].
Vulnerability (V)	Mean number of consumers per prey [93].
Food chain	A distinct path within the food-web matrix from any taxon down to a basal taxon (a taxon which feeds on no other taxa) [18].
Mean chain length (mean FCL)	Average number of links found in a food chain across a food web [94]. Food-chain length appears to be reduced by disturbance and increased by higher energy supply and increased ecosystem size [21–23].
Maximum chain length (max FCL)	The maximum number of links found in any food chain in a food web [94].
Number of basal taxa (b)	The number of taxa which do not consume any other taxa, by definition autotrophs.
Number of intermediate taxa (i)	The number of taxa which are both consumed by, and consume, other taxa.
Number of top taxa (t)	The number of taxa which are not consumed by any other taxa.
Prey:predator (= {b + i}/{t + i})	A measure of food-web 'shape'; high values are more triangular, low values are more 'square' in shape. When <1 the food web has an inverted structure that might indicate instability. Note criticisms of this attribute [95] and its sensitivity to the common practice of aggregating of low trophic level taxa.
Robustness	The minimum level of secondary extinction that occurs in response to a particular perturbation (species removal) [96].



S = 9 L = 10

Robustness = 2.5



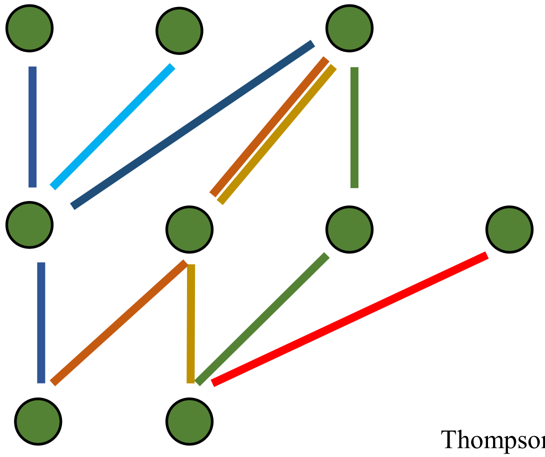
L/S = 10/9 = 1.1 C = $10/9^2$ = 0.12

G = (1+1+1+1+1+2+3)/7= 1.4

V = (2+3+3+1+1+0)/6 = 1.7

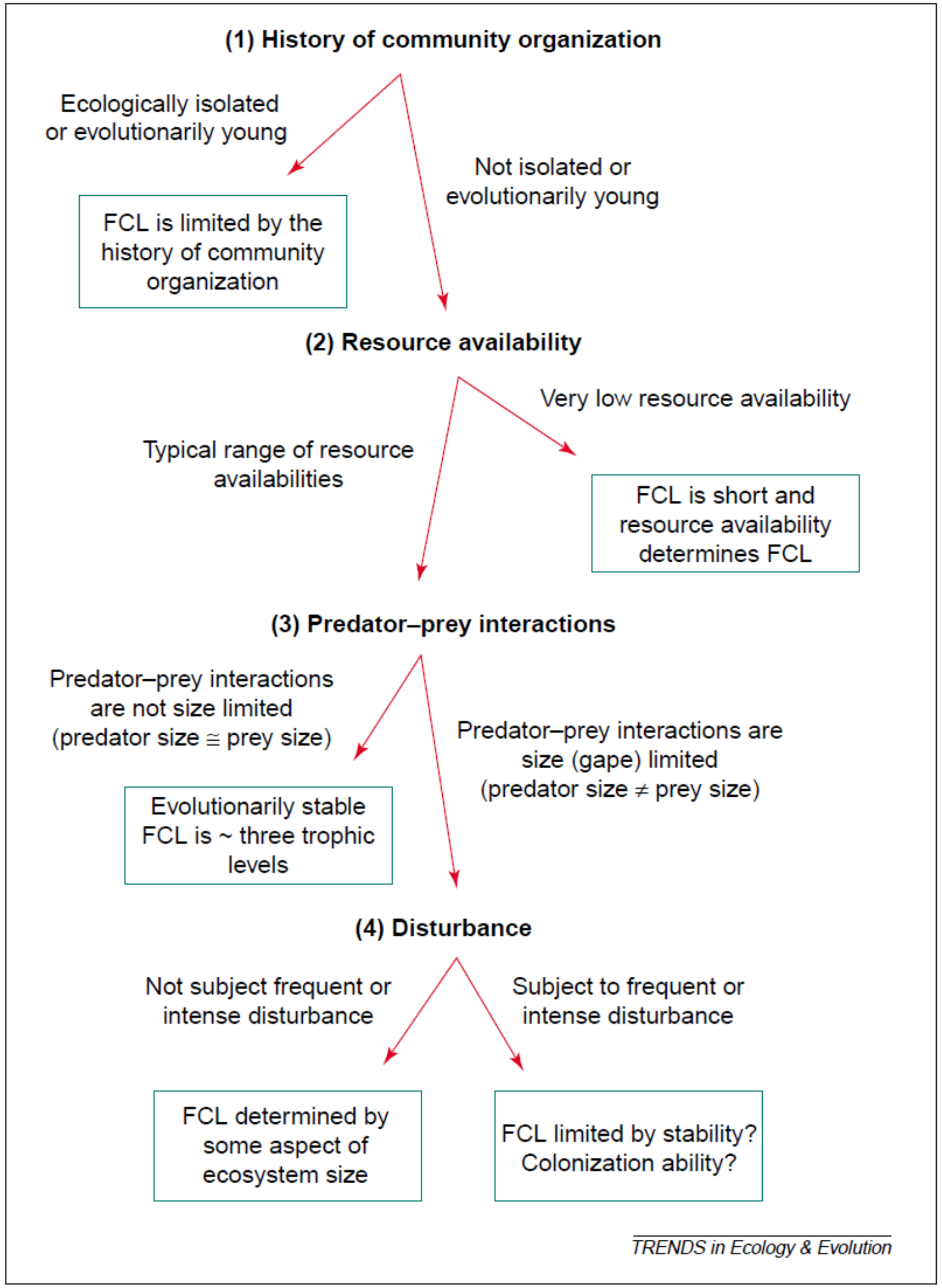
FCL = (2+2+2+2+2+2+1)/7 = 1.9 FCL_{max} = 2

b,i,t = 2,4,3 Prey:predator (2+4)/(4+3) = 0.9



Thompson et al. 2012, TREE 7, 689

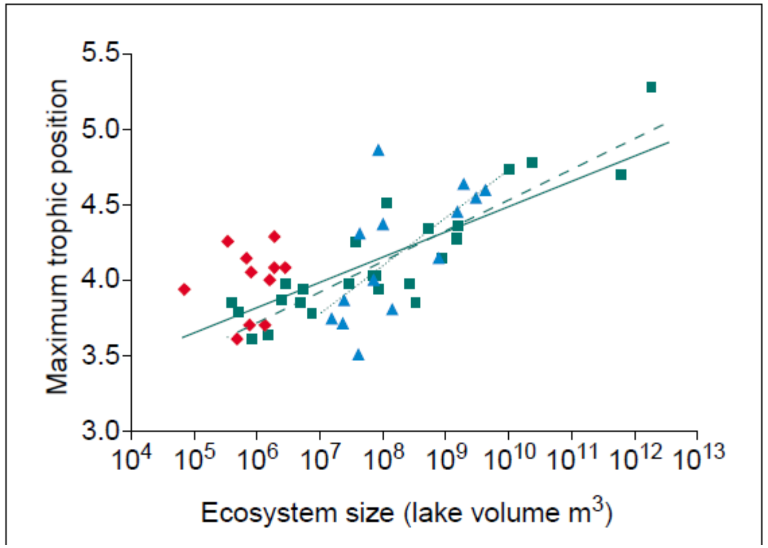
Why are trophic chains limited to 3-4 trophic levels?



Energy flow hypothesis: 90% of energy lost in every trophic transfer [but more prodictive environments do not have longer chains]

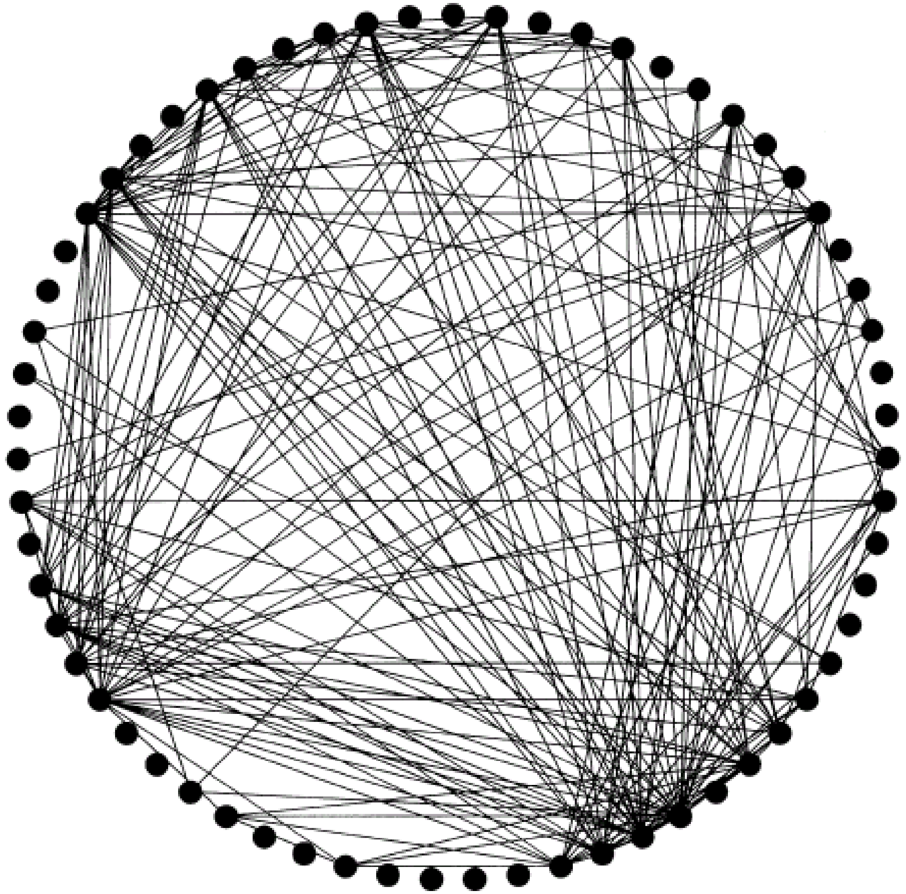
Stability hypothesis: trophic chains integrate population variability of all their component species so that long chains can become unstable, with the extinction of the top species

Design constraints hypothesis: it is difficult to come with a predator capable of feeding on the existing top predators [have to be big, therefore low population density] or parasitising the existing hyperparasites



D. M. Post 2002. TREE 17: 269

Leaf-miner species (dots) connected by shared parasitoids: qualitative and quantitative description of reality



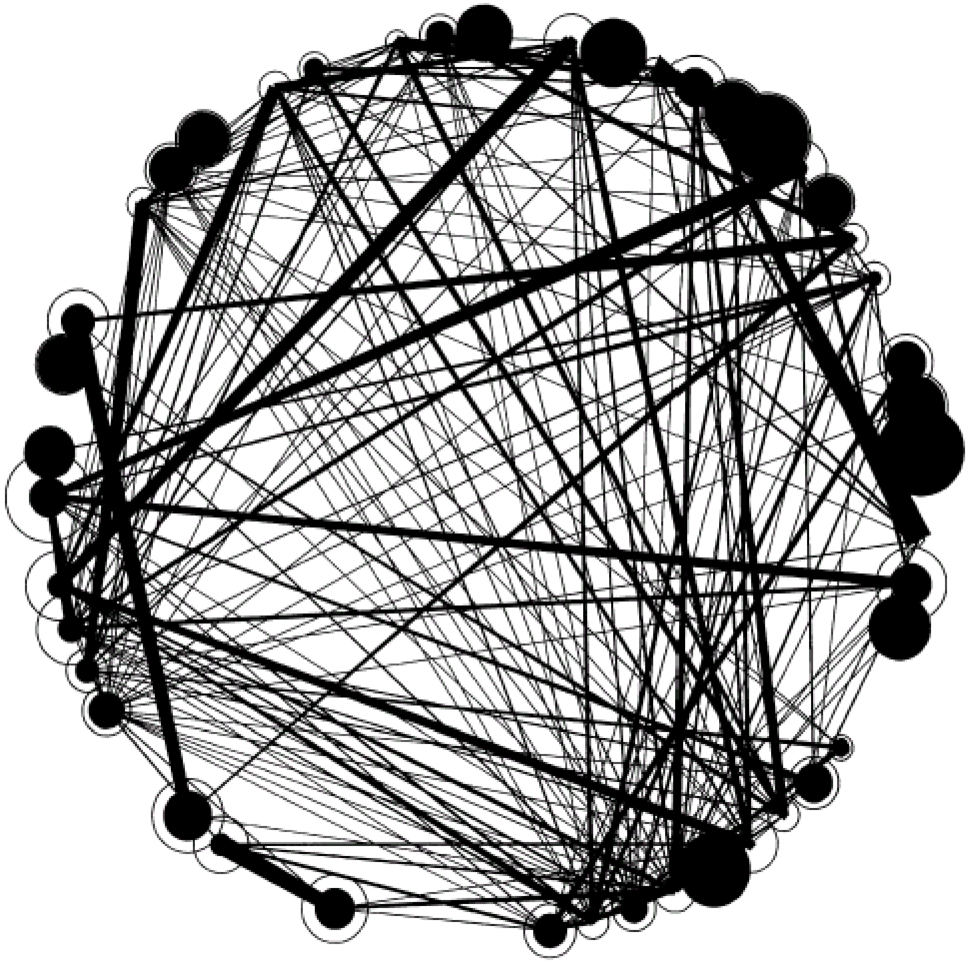


Figure 3. Parasitoid o
described more fully i
vertices arranged in a
different miner host sp
connecting two species
they share a parasitoid

Figure 4. Quantitative parasitoid overlap graph. As figure 3, but now the size of the vertex indicates the number of parasitoids reared from that host (hence the vertex is missing if no parasitoids were reared). The extent to which a vertex is coloured black indicates the degree to which a species acts as host for its own parasitoids (see definition in text). The links show shared parasitoids, and the width of the connecting line between hosts i and j at species i indicates the importance of species j as a source of parasitoids that attack species i (note that links between two species may be asymmetrical).

As
63
t

Bipartite network metrics: weighted links

Interaction strength

Interaction strength of species j on species i (b_{ij}) can be defined by the proportion of interactions between i and j (a_{ij}) of the total interactions recorded for i; thus $b_{ij} = a_{ij}/\Sigma_{j=1}^{J} a_{ij}$. For mutualistic networks, Jordano (1987) and Bascompte et al. (2006) used b_{ij} as a measure of dependence of species i on its partner j. Asymmetries of interaction strength can be defined as $AS_{ij} = (b_{ij} - b_{ji})/(b_{ij} + b_{ji})$, where b_{ji} is the reciprocal dependence of species j on species i (see Bascompte et al. 2006, Blüthgen et al. 2007, Vázquez et al. 2007).

Interaction diversity

The Shannon diversity of links is $H_i = -\Sigma_{j=1}^{J} [(a_{ij}/A_i) \ln(a_{ij}/A_i)]$ for species i, or for the whole web, $H_2 = -\Sigma_{i=1}^{I} \Sigma_{j=1}^{J} [(a_{ij}/m) \ln(a_{ij}/m)]$, with $A_i = \Sigma_{j=1}^{J} a_{ij}$ and $m = \Sigma_{i=1}^{I} \Sigma_{j=1}^{J} a_{ij}$. Their reciprocals e^{H_i} and e^{H_2} express the equivalent "effective" number of links (see Bersier et al. 2002).

Interaction evenness

Based on Shannon diversity, the interaction evenness is $E_i = H_i/\ln L_i$ for each species, or for the whole web, $E_2 = H_2/\ln L$, where L_i is the number of links of species i, and L is the number of all links. First suggested by Bersier et al. (2002), these measures or other standard diversity metrics have been applied to different interaction networks (e.g., Sahli and Conner 2006, Albrecht et al. 2007, Tylianakis et al. 2007).

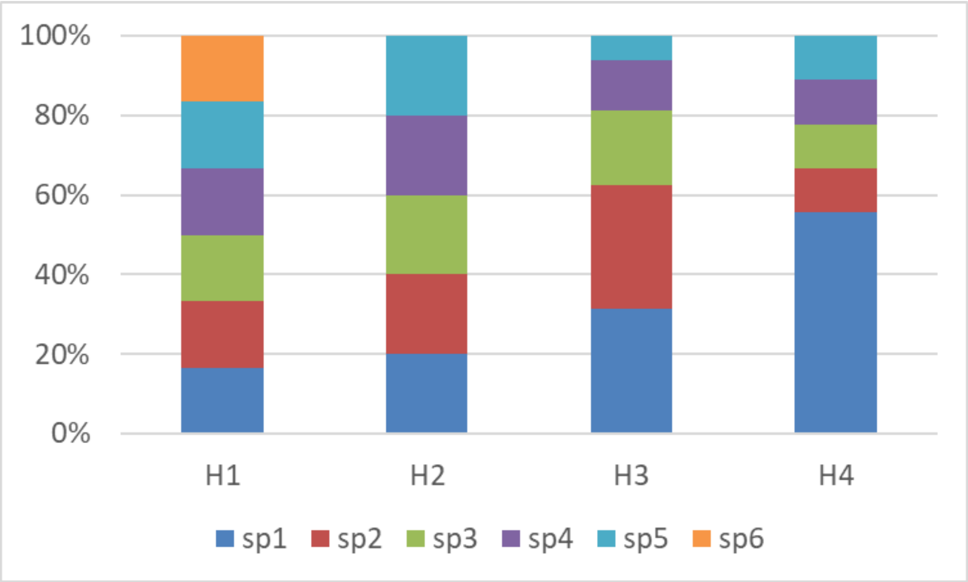
Weighted generality and vulnerability

The weighted analog of generality can be derived from Shannon diversity of links (H_i), representing the mean "effective" links per consumer $G_q = (1/I) \Sigma_{i=1}^{I} e^{H_i}$, or as the weighted mean $G_{qw} = \Sigma_{i=1}^{I} (A_i/m)e^{H_i}$ (Bersier et al. 2002, with equations based on $\log_2$ instead of ln). For weighted vulnerability, replace i by j and I by J.

Bluthgen et al. Ecology, 89(12), 2008, pp. 3387–3399

Shannon diversity

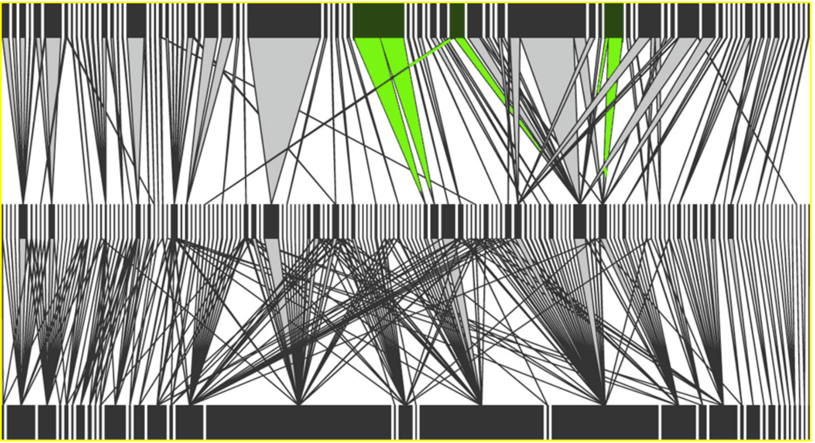
$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$



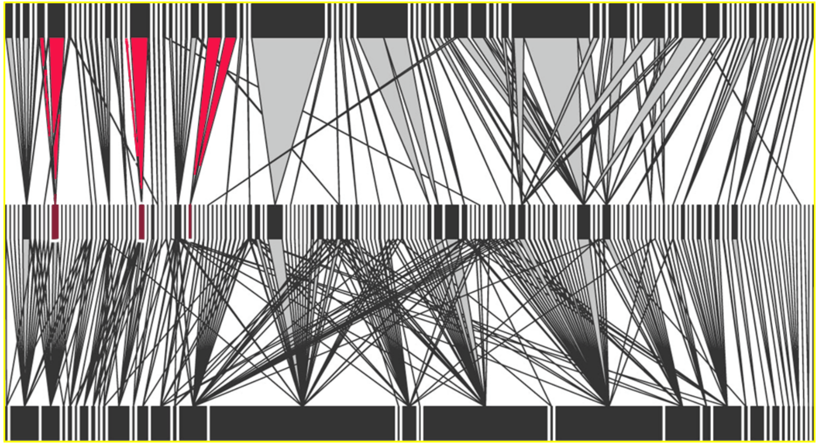
H1 > H2 > H3 > H4

Quantitative food web descriptors

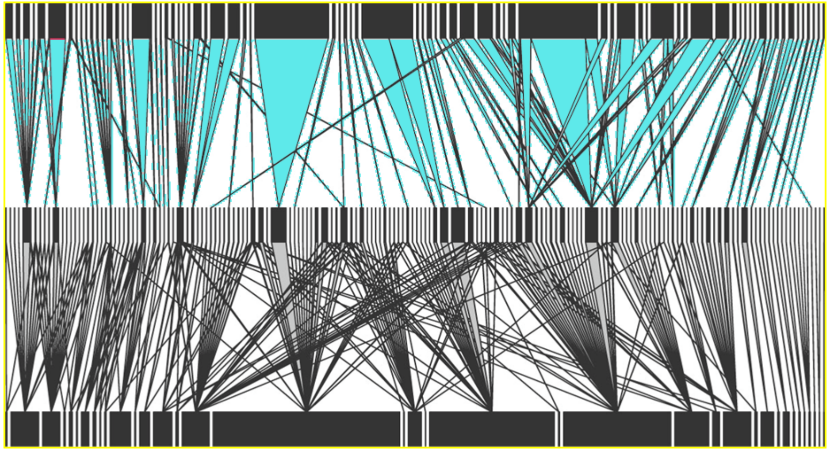
Generality G1>G2 < G3



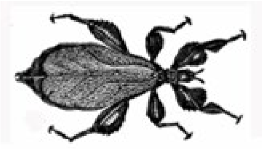
V1 = V2<V3 Vulnerability



Interaction diversity



Quantitative plant - herbivore matrices and their uses



	H1	H2	H3	H4	Sum
P1	0	0	0	8	8
P2	5	5	0	0	10
P3	2	2	1	0	5
Sum	7	7	1	8	23

plant-herbivore matrix

Diversity of host plants

$$H_{N,k} = -\sum_{i=1}^{s} \frac{b_{ik}}{b_{\cdot k}} \log_2 \frac{b_{ik}}{b_{\cdot k}}$$

Diversity of host plants for herbivore H1:

H: - [(5/7)*$\log_2$(5/7)+(2/7)*$\log_2$(2/7)] = 0.863

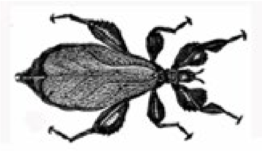
2^H = 1.82 = the number of interactions occurring in equal proportion that would produce the same value of *H*.

QUANTITATIVE DESCRIPTORS OF FOOD-WEB MATRICES

Louis-Félix Bersier,[1,2,3] Carolin Banašek-Richter,[1] and Marie-France Cattin[1]

Ecology, 83(9), 2002, pp. 2394–2407

Quantitative plant - herbivore matrices and their uses



	H1	H2	H3	H4	Sum
P1	0	0	0	8	8
P2	5	5	0	0	10
P3	2	2	1	0	5
Sum	7	7	1	8	23

plant-herbivore matrix

dominance of herbivores on each plant

	H1	H2	H3	H4	Sum
P1	0.00	0.00	0.00	1.00	**1.00**
P2	0.50	0.50	0.00	0.00	**1.00**
P3	0.40	0.40	0.20	0.00	**1.00**
Sum	0.90	0.90	0.20	1.00	

dominance of plants in herbivore's diet

	H1	H2	H3	H4	Sum
P1	0.00	0.00	0.00	1.00	1.00
P2	0.71	0.71	0.00	0.00	1.43
P3	0.29	0.29	1.00	0.00	1.57
Sum	**1.00**	**1.00**	**1.00**	**1.00**	

two matrices multiplied:

	H1	H2	H3	H4	Sum
P1	0.00	0.00	0.00	1.00	**1.00**
P2	0.50	0.50	0.00	0.00	**1.00**
P3	0.40	0.40	0.20	0.00	**1.00**
Sum	0.90	0.90	0.20	1.00	

x

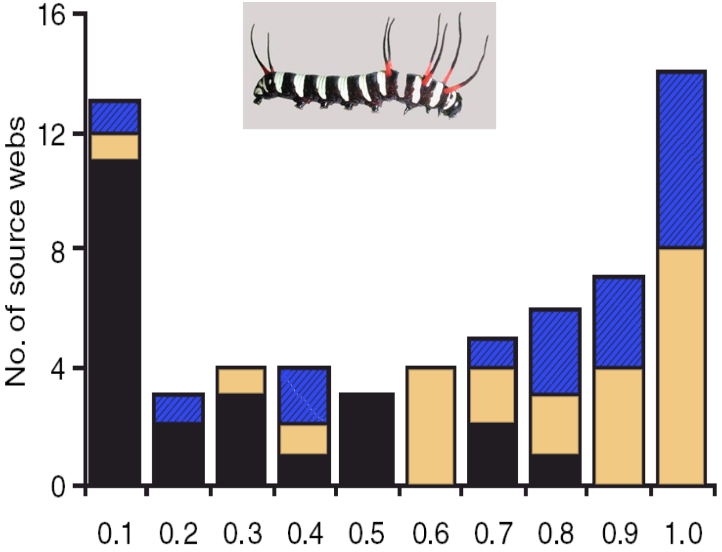
	H1	H2	H3	H4	Sum
P1	0.00	0.00	0.00	1.00	1.00
P2	0.71	0.71	0.00	0.00	1.43
P3	0.29	0.29	1.00	0.00	1.57
Sum	**1.00**	**1.00**	**1.00**	**1.00**	

=

	H1	H2	H3	H4	Sum
P1	0.00	0.00	0.00	1.00	**1.00**
P2	0.36	0.36	0.00	0.00	**0.71**
P3	0.11	0.11	0.20	0.00	**0.43**
Sum	**0.47**	**0.47**	**0.20**	**1.00**	

Host plant isolation: Probability that a randomly selected conspecific herbivore feeds on the same plant species

Leaf chewing rainforest herbivores New Guinea



Isolation of herbivore community

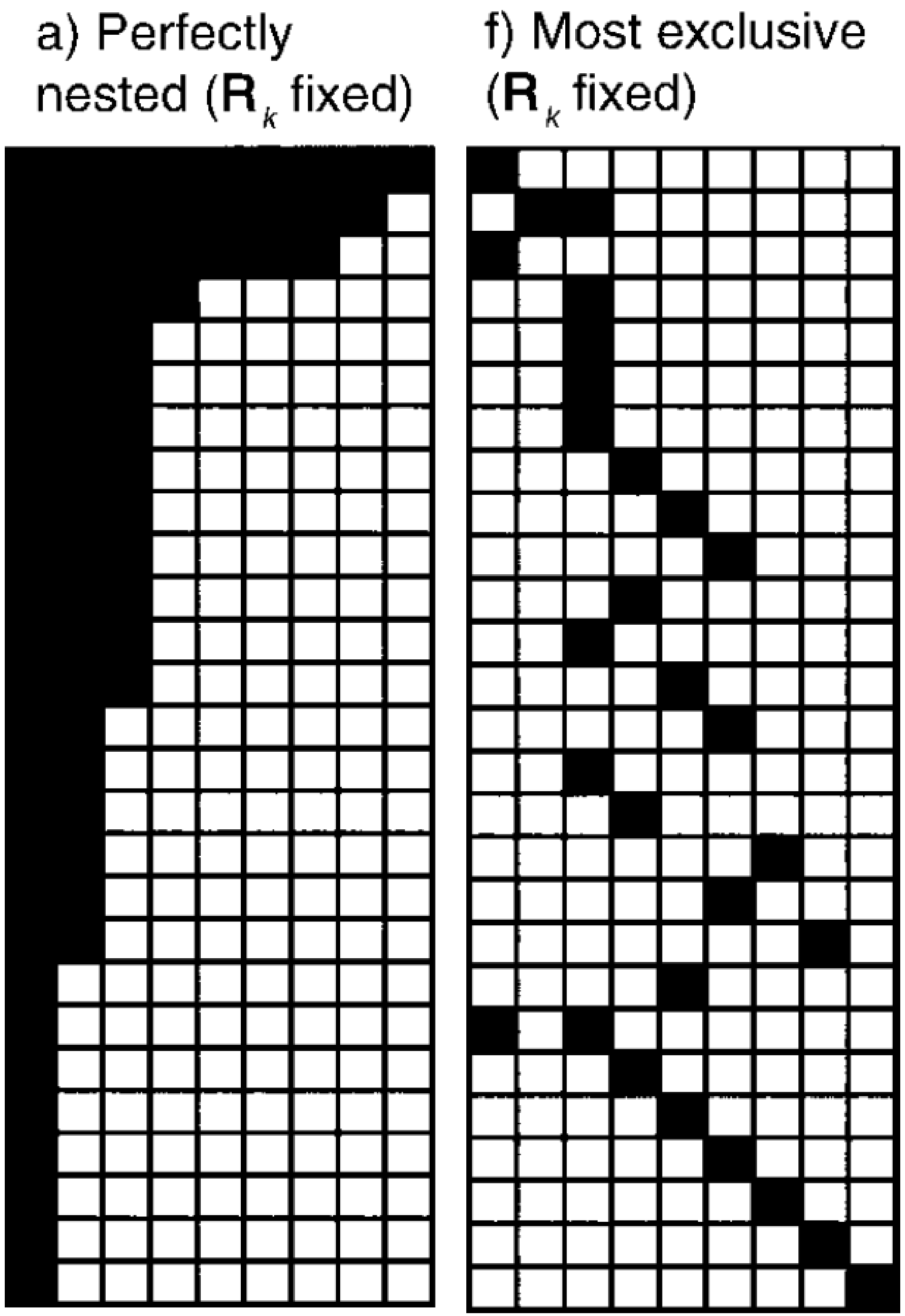
plants:

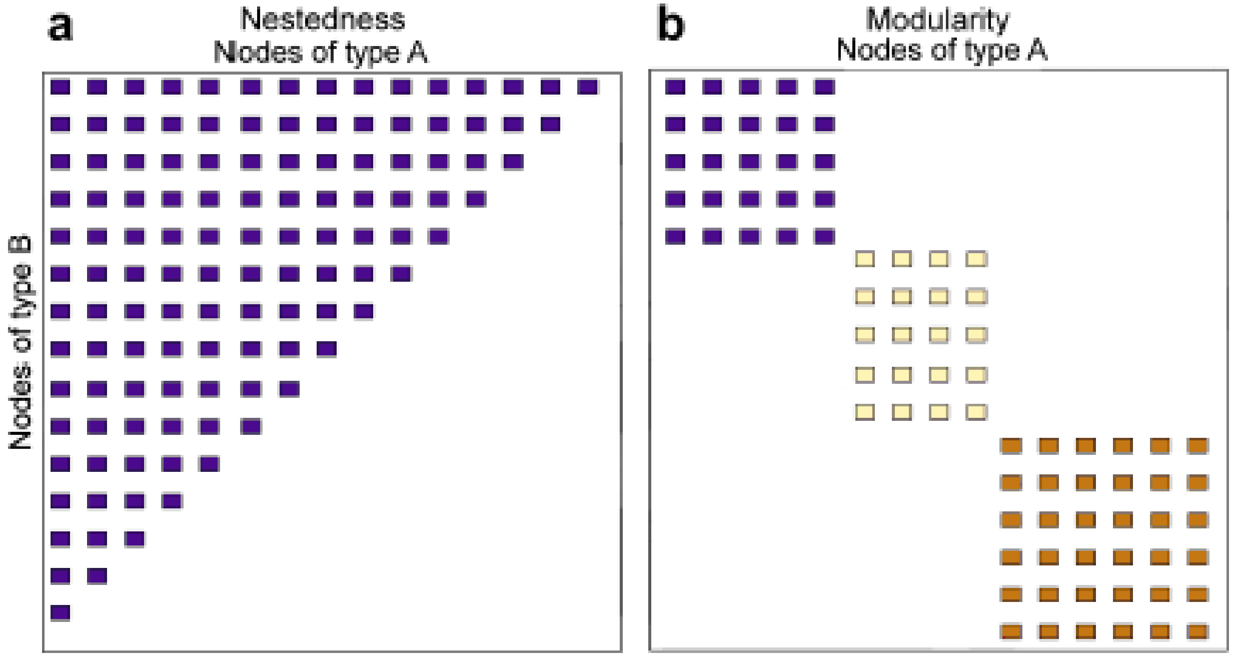
from locally monotypic families

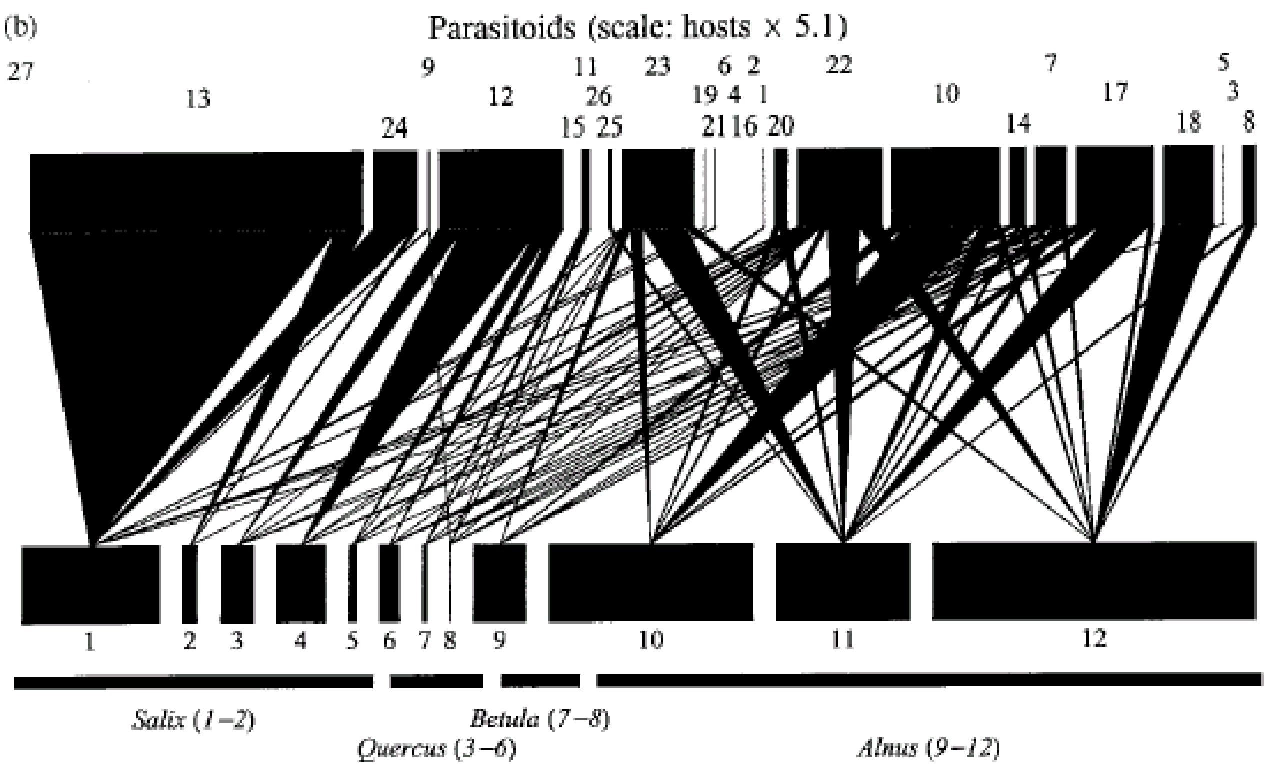
coexisting with confamilial species

coexisting with congeneric species

Nestedness:
the extend to which are species-poor communities subsets of species-rich ones





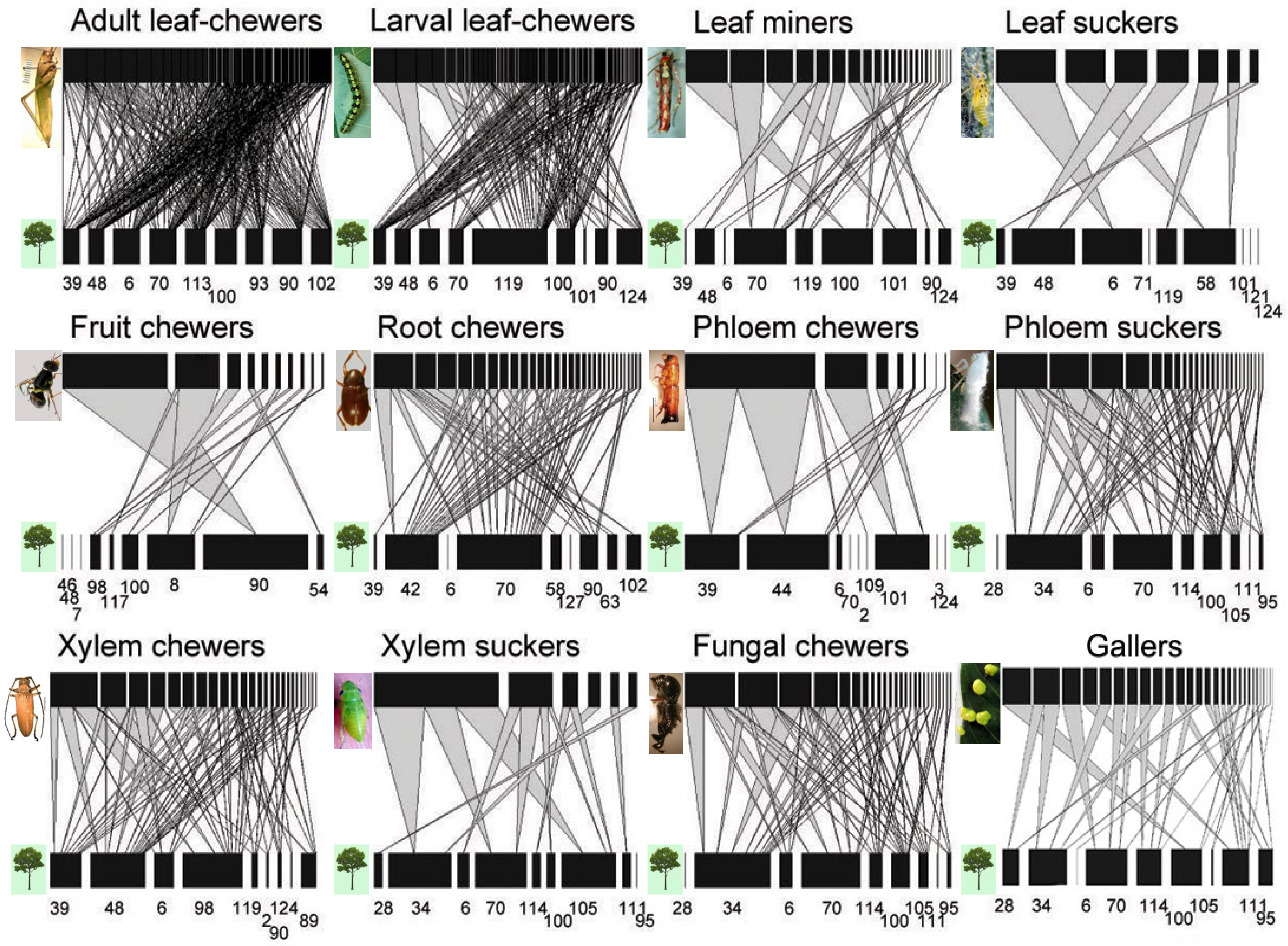


Parasitoids of a leaf-mining genus *Phyllonorycter* in England

Pollinators in England

Memmott J. 1999. Ecol. Letters 2: 279.

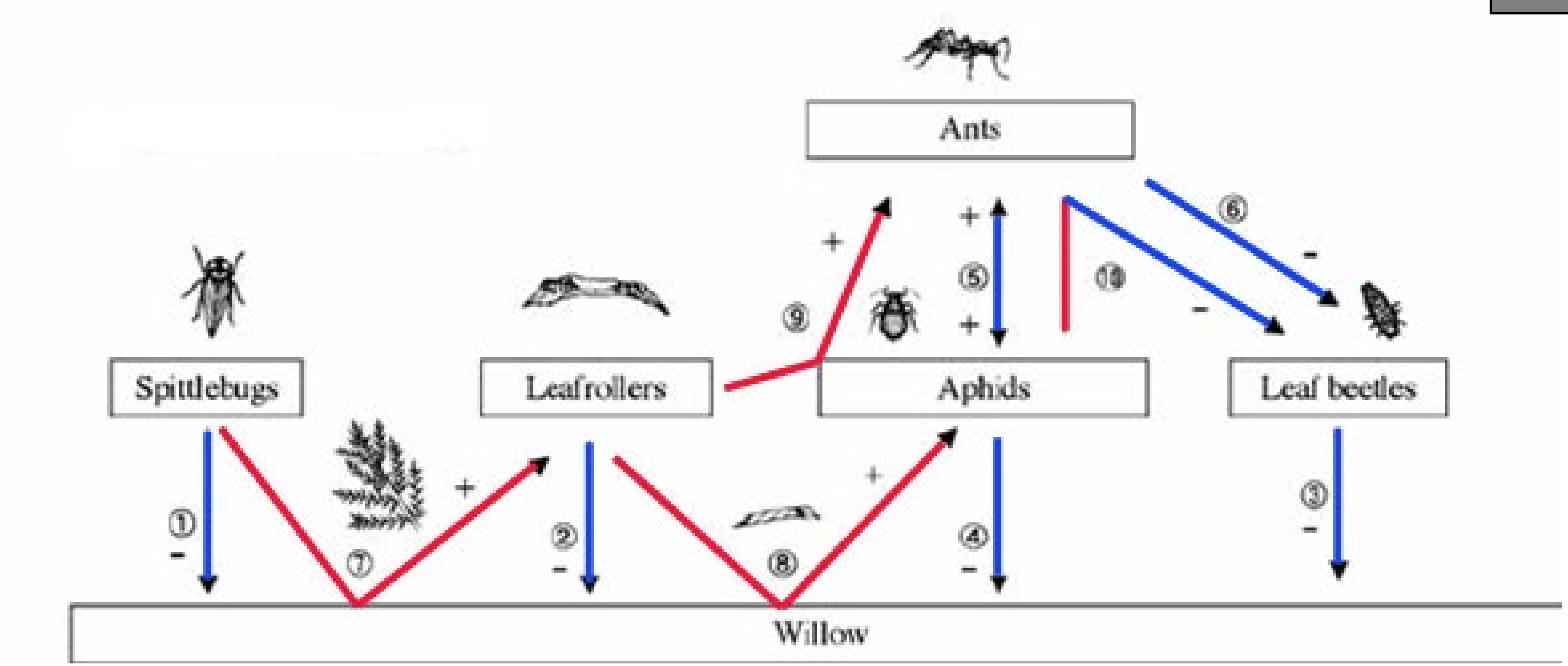
Rott & Godfray 2000, J. Anim. Ecol. 69:274



Herbivore guilds in tropical rainforest New Guinea

Novotny et al. 2010
J Anim Ecol

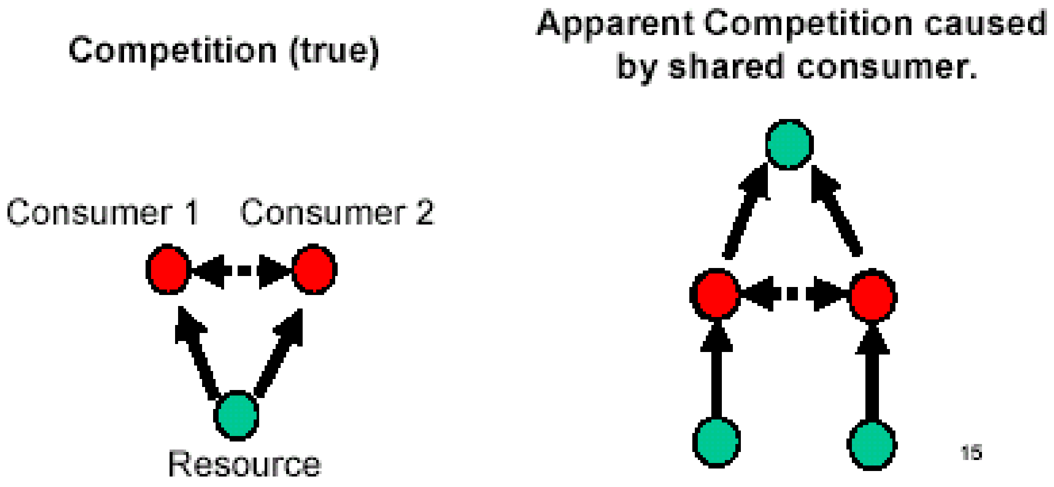
Direct and indirect interactions in a simple food web



Direct [blue] and indirect [red] interactions between willows and insects in Japan.
Plus and minus signs indicate effect on the target species.

Ohgushi, Annu. Rev. Ecol. Evol. Syst. 2005. 36:81–105

Apparent competition



Indirect interaction: an effect of one species on another, mediated through the action of shared natural enemies.

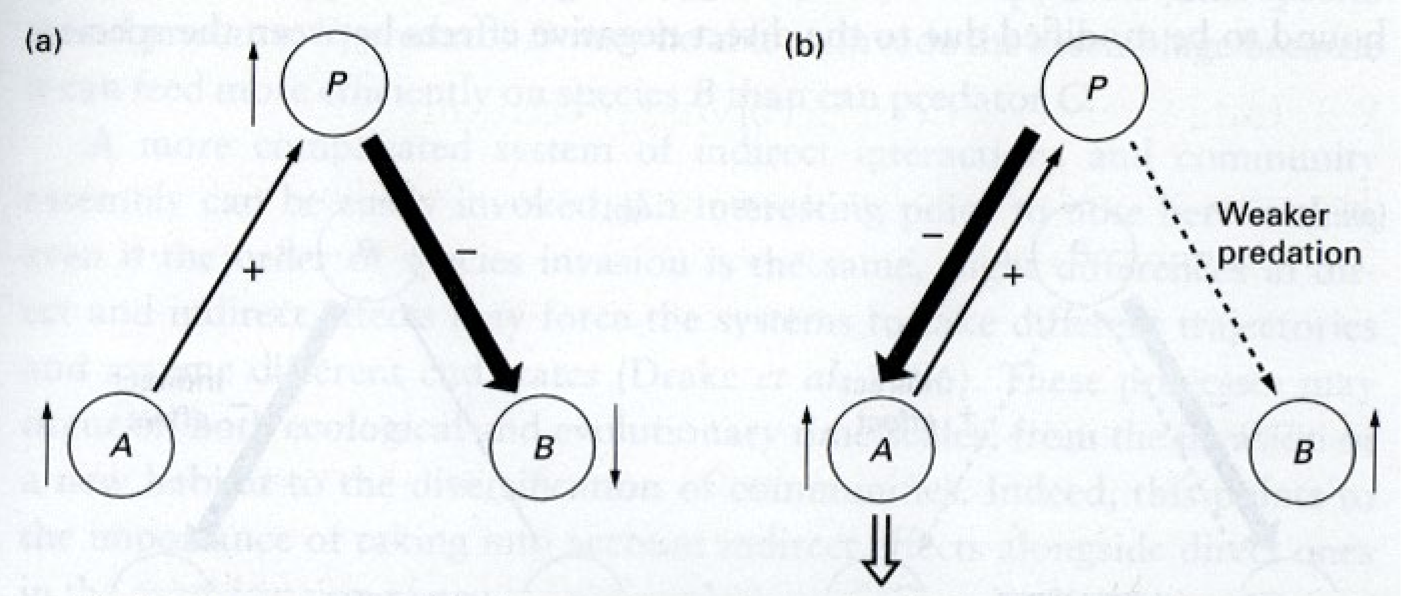


Fig. 9.6 Apparent competition between two species *A* and *B* through their shared predator *P*. In (a), an increase in *A* leads to an increase in *P*, which, in turn, feeds more heavily on *B*. In (b), an increase in *A* prompts *P* to feed more heavily on *A*, resulting in the latter's overall decline, whilst *B* suffers less predation.

Plant-leaf miner-parasitoid food web in a forest understorey in Belize

Removal of a single host plant species eliminated its specialist leaf-miners (hatched) but also caused an increase in abundance and lower parasitism of other spp. (red, blue) connected via shared parasitoids.

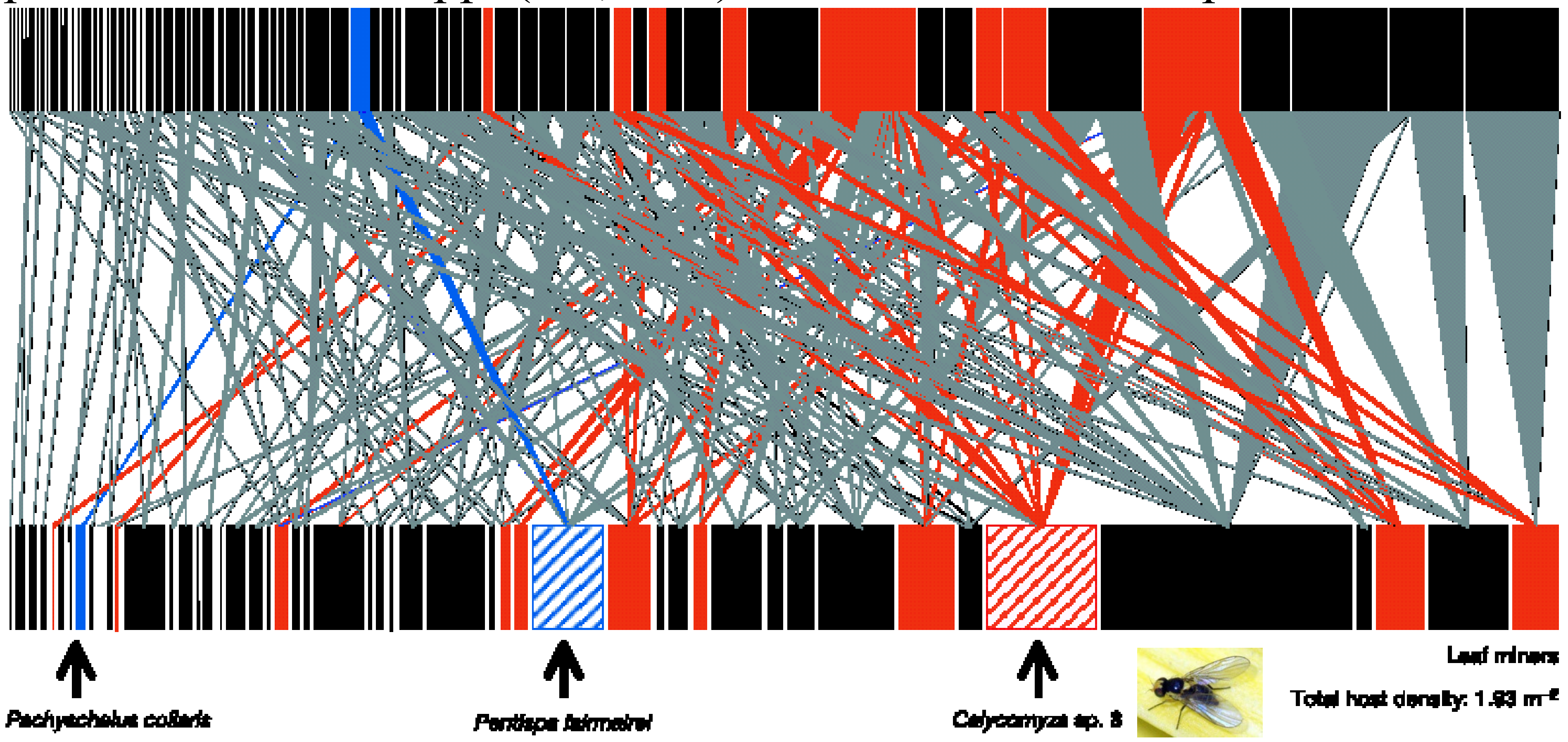
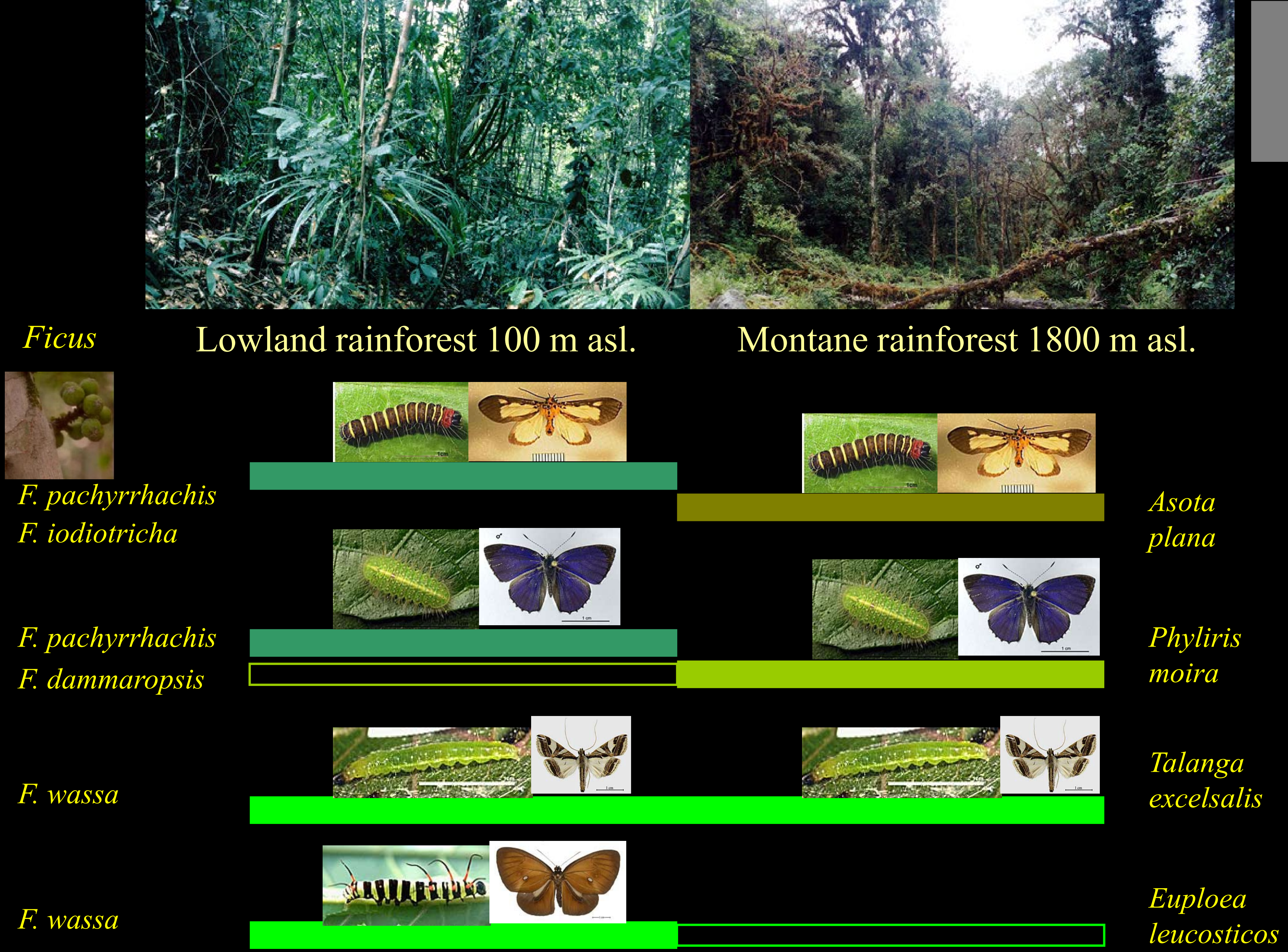
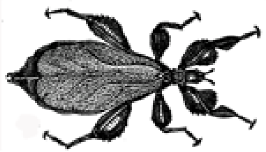


Figure 1 Quantitative food web[17] showing leaf-miner species (bottom bars), parasitoid species (top bars), trophic links among them, and the species predicted to be affected by the manipulation. *Calycomyza* sp. 8 and *P. fairmairei* were directly affected by host plant removal. Dipteran leaf-miner species present during the sampling period and predicted to be affected indirectly via parasitoids shared with *Calycomyza* sp. 8 are shown in red. The beetle *P. collaris* (blue) was also predicted to be affected indirectly by the manipulation through parasitoids that it shares with *P. fairmairei*. Only hosts from which parasitoids were reared are shown in the web.

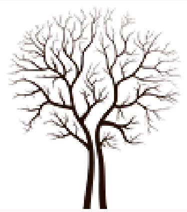
Morris et al. 2004. Nature 428:30



Novotny et al. 2005, J. Biogeogr. 32:1303



Food web 1



	H1	H2	H3	H4
P1	x	x	x	
P2	x	x	x	
P3				

Food web 2

	H1	H2	H3	H4
P1				
P2			x	x
P3		x	x	x

P1 - P3: plant species
H1 - H4: herbivore species
x - plant-herbivore interaction

	H1	H2	H3	H4
P1	x	x	x	
P2	x	x	x	x
P3		x	x	x

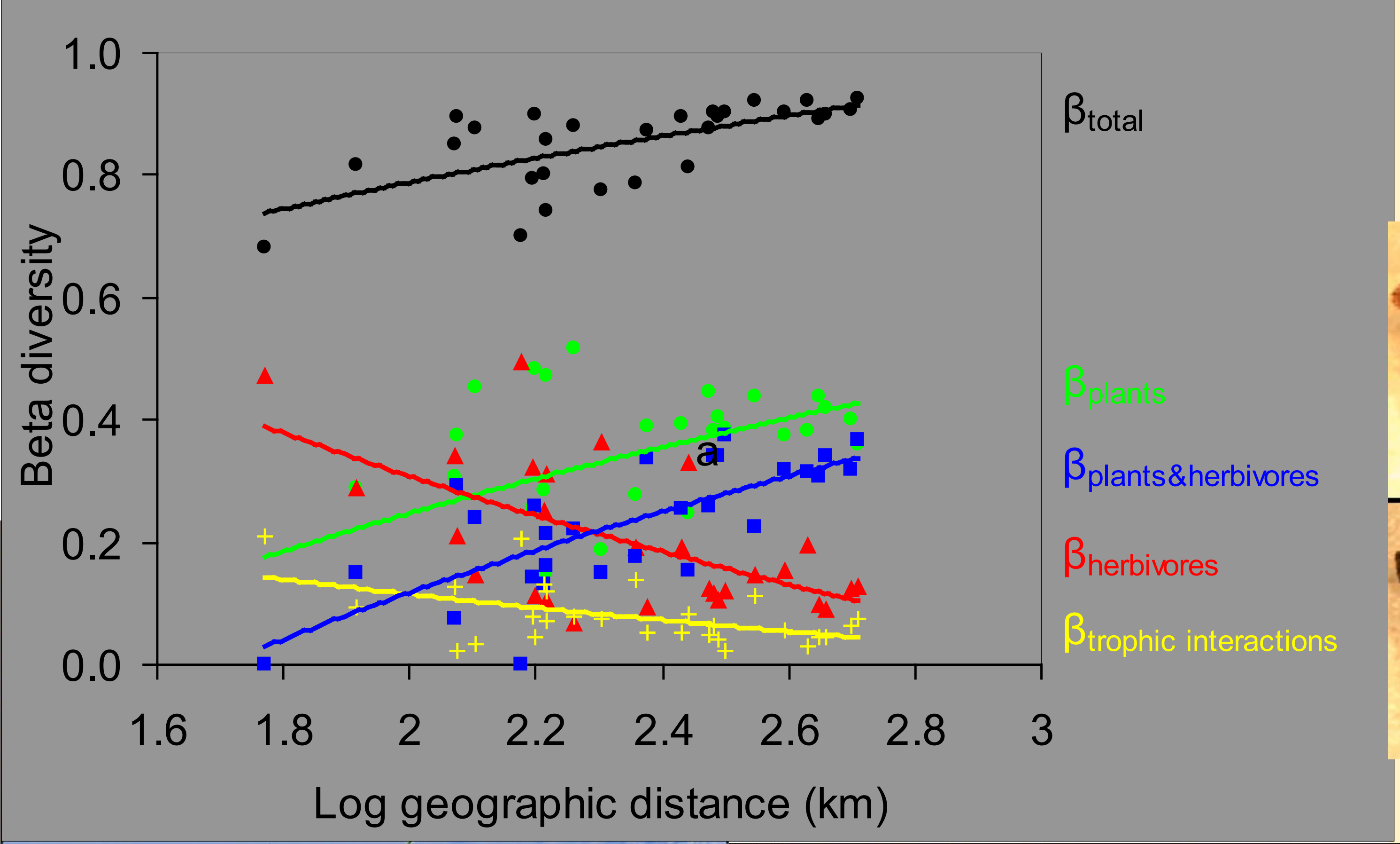
- x – Food web 1 only
- x – Food web 2 only
- x – Both food webs

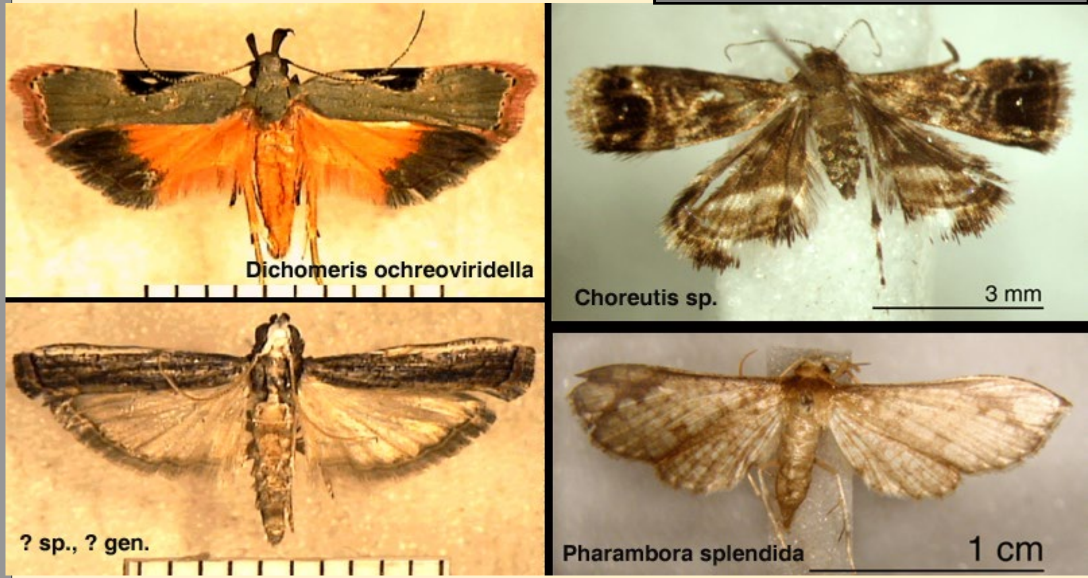
	H1	H2	H3	H4
P1	ph	p	p	
P2	h	0	x	h
P3		p	p	ph

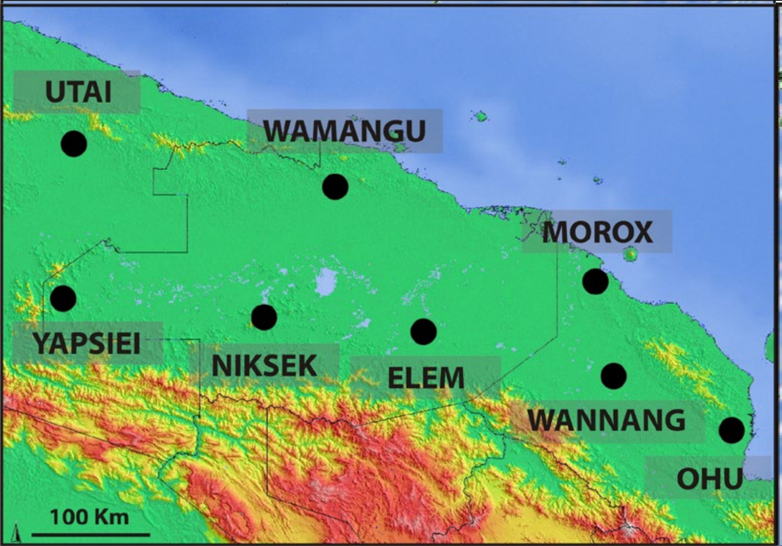
- p – Plant species in 1 web only
- h – Herbivore species in 1 web only
- ph – Plant & herbivore spp. in 1 web only
- 0 – Plant & herbivore spp. in 2 webs

Novotny 2009, Insect Conservation & Diversity **2**:5-9

Caterpillars on *Macaranga* trees

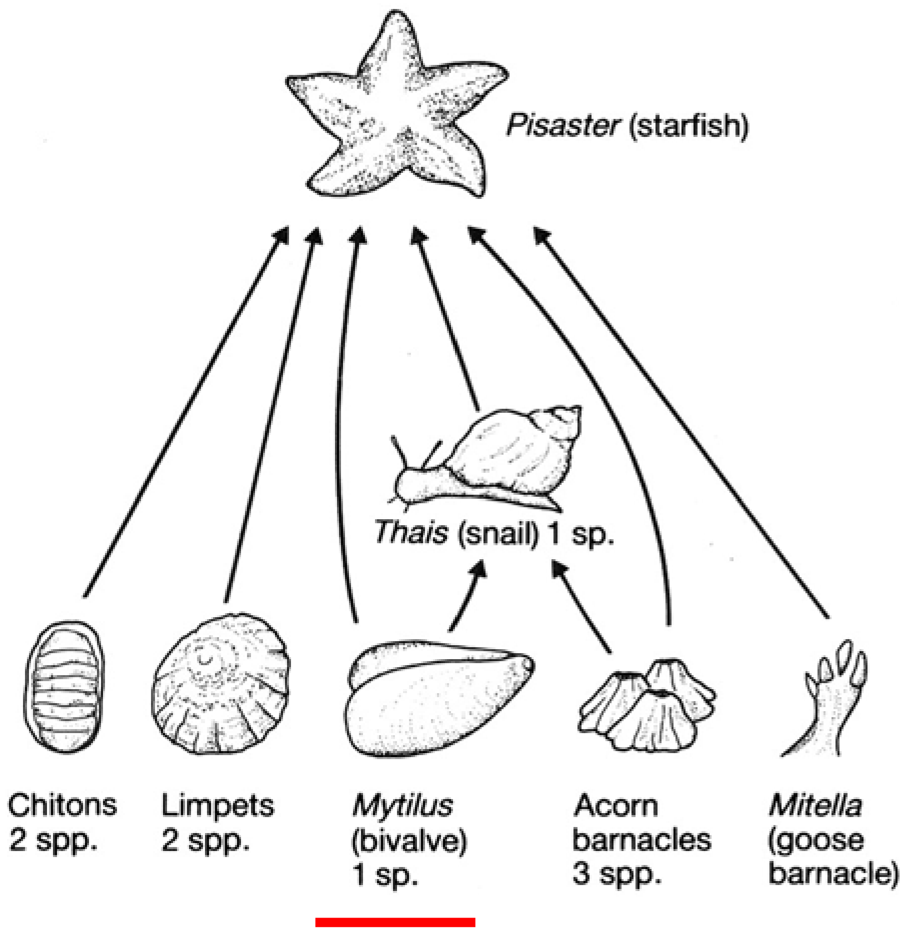






Novotny et al. 2007, Nature 448:692

Predators can reduce inter-specific competition among their prey species



Paine's intertidal zone experiment: Removal of starfish predator *Pisaster* resulted in one *Mytilus* species competitively dominating the system and driving other species to extinction

Robert Paine
1933-2016

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Analysis | Published: 13 November 2017

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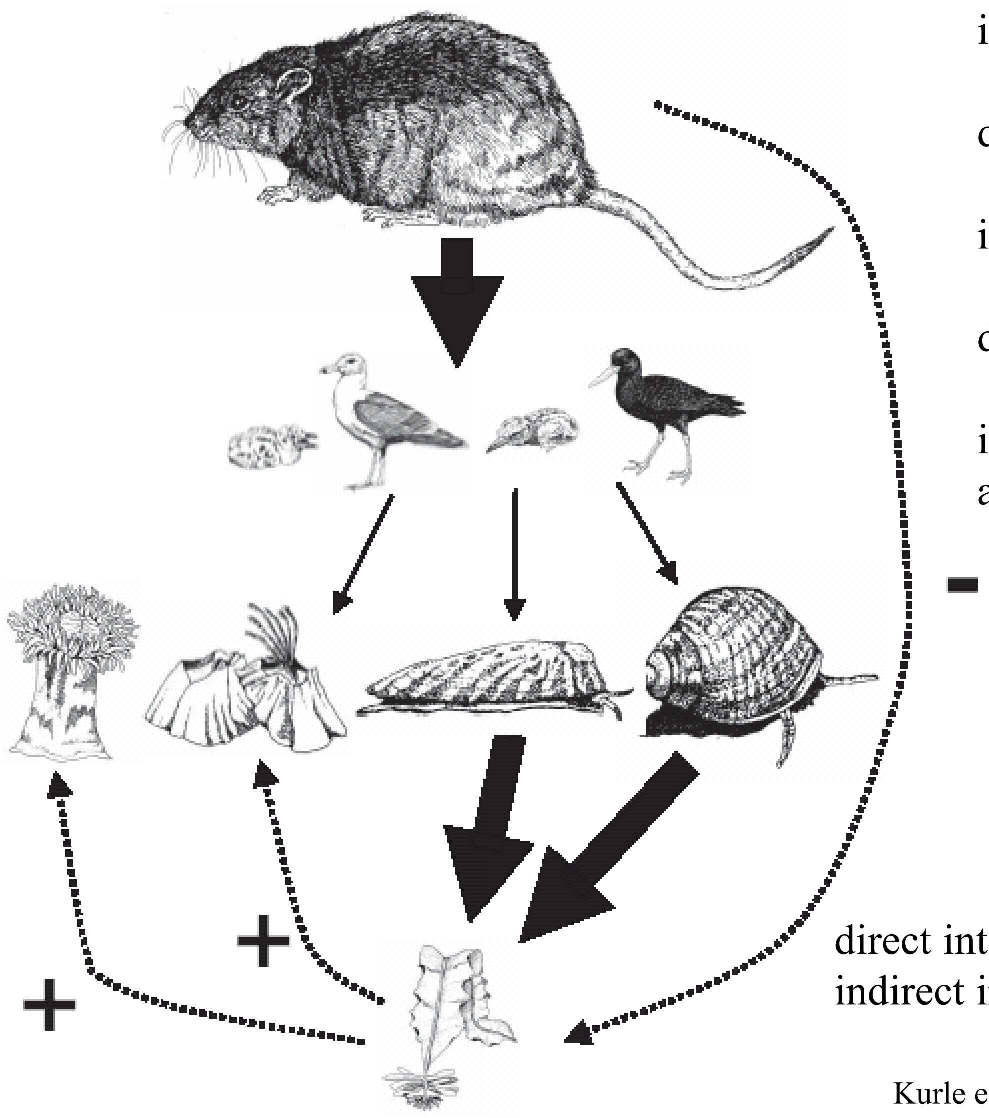
Franck Courchamp & Corey J. A. Bradshaw

Darwin, C.R.; Wallace, A.R. 1858. **On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection.** *Journal of the proceedings of the Linnean Society of London Zoology* 3:45-62
Hardin, G.J. 1968. **The tragedy of the commons.** *Science* 162:1243-1248
Paine, R.T. 1966. **Food Web Complexity and Species Diversity.** *The American Naturalist* 100:65-75
Hutchinson, G.E. 1961. **The Paradox of the Plankton.** *The American Naturalist* 95:137-145
Hutchinson, G.E. 1959. **Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?** *The American Naturalist* 93:145
MacArthur, R.H.; Wilson, E.O. 1963. **An Equilibrium Theory of Insular Zoogeography.** *Evolution* 17:373-387
Hutchinson, G.E. 1957. **Concluding Remarks.** *Cold Spring Harbor Symposia on Quantitative Biology* 22:415-427
Hairston, N.G. ; Smith, F.; Slobodkin, L. 1960. **Community structure, population control, and competition.** *The American Naturalist* 94:421-425
Connell, J.H. 1978. **Diversity in tropical rain forests and coral reefs.** *Science* 199:1302-1310
Janzen, D.H. 1970. **Herbivores and the Number of Tree Species in Tropical Forests.** *The American Naturalist* 104:501

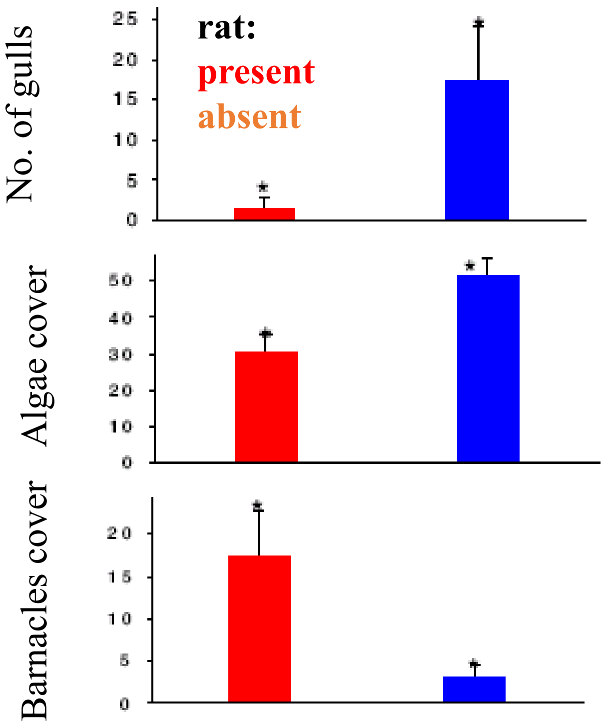
Authors all UK/USA, nine papers published between 1957 and 1978. Hutchinson authored 3 papers! Average 1.4 authors per paper.

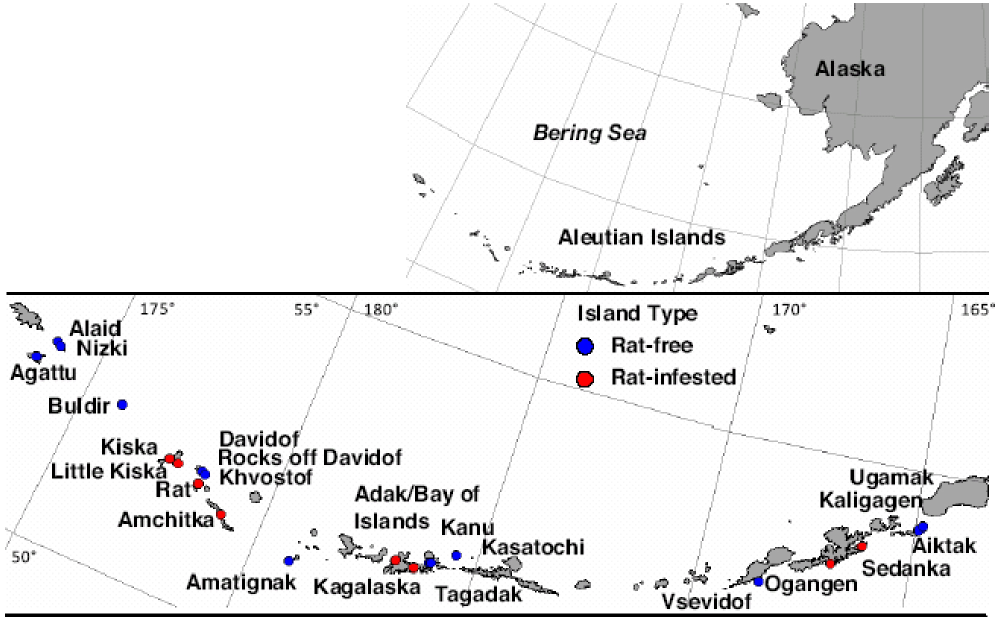
Top-down regulation: introduction of rats on polar islands caused decrease in marine birds, increase in molluscs, decrease in algae and thus increase in anemones and barnacles



introduction of rats
↓
decrease of birds
↓
increase of molluscs
↓
decrease of algae
↓
increase of anemones and barnacles

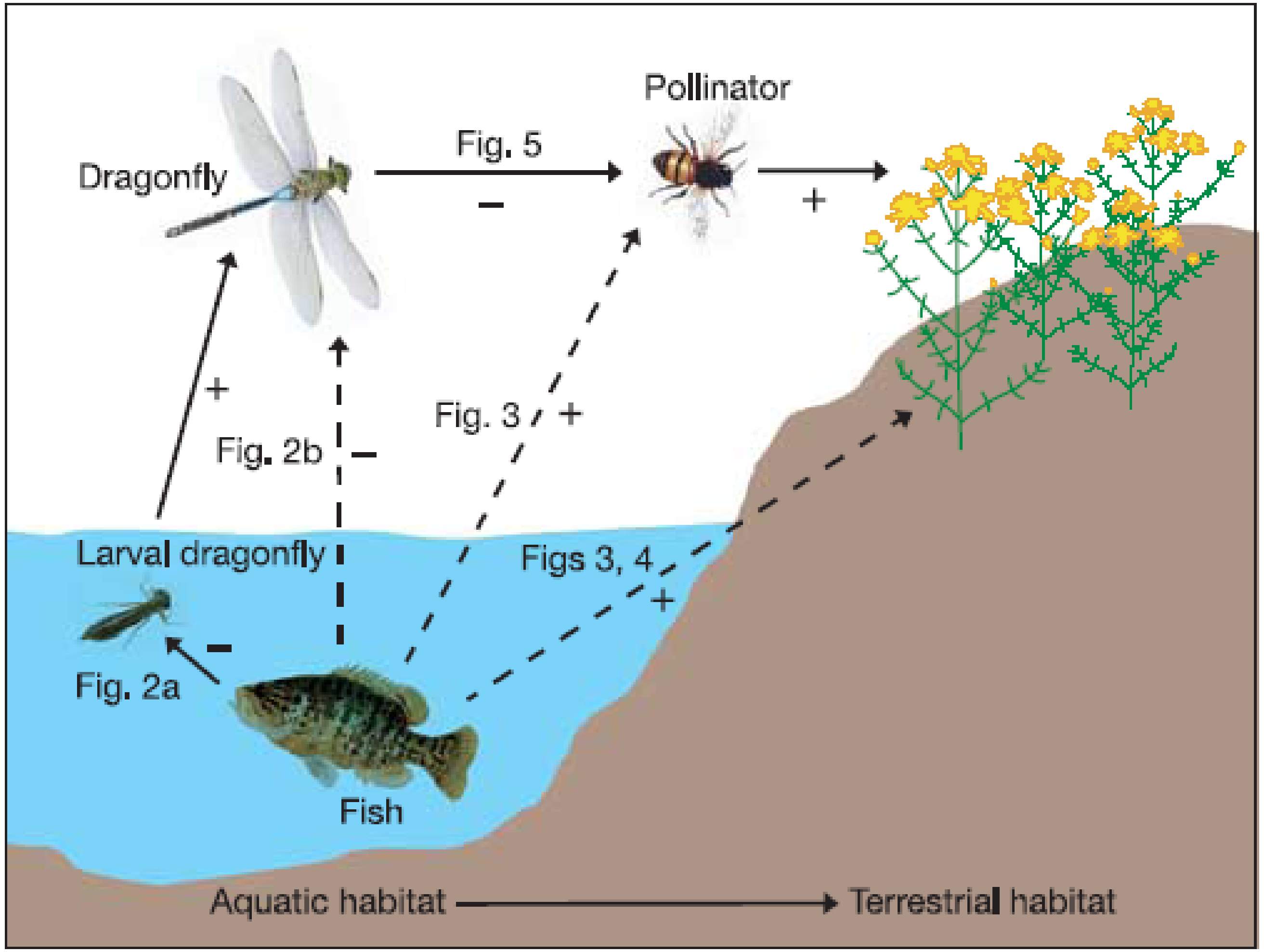
direct interactions →
indirect interactions ⇢





Kurle et al. 2008, PNAS 105:3800

Trophic cascades across ecosystems



More pollinators visited *Hypericum* plants near ponds with fish, which reduced larval density of dragonflies, predatory in their adult stage on the pollinators

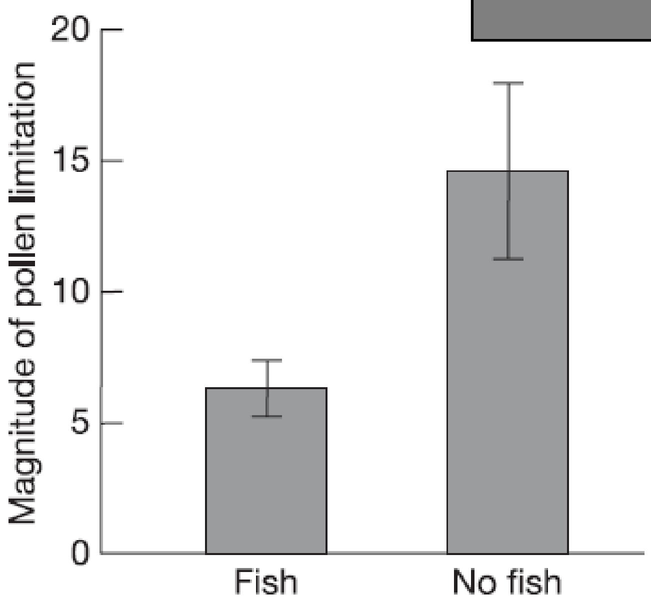


Figure 3 | Pollinator visitation rates to *Hypericum fasciculatum*. The total number of pollinator visits to *Hypericum fasciculatum* was higher near ponds with fish (ANOVA: $F_{1,6} = 11.45$, $P < 0.02$). There was a marginally significant difference between the compositions of pollinators at fish-containing and fish-free ponds (MANOVA, Pillai trace = 0.79, $F_{3,4} = 4.9$, $P = 0.07$). The number of visits by all three groups of pollinators (black bars, Diptera; grey bars, Lepidoptera; white bars, Hymenoptera) was less near ponds with fish (univariate *F*-tests: Diptera (primarily Syrphidae, Bombyliidae) $F_{1,6} = 4.62$, $P < 0.07$; Hymenoptera (primarily *Agapostemon* spp. (Halictidae)) $F_{1,6} = 15.50$, $P < 0.05$; Lepidoptera (primarily Noctuidae) $F_{1,6} = 5.72$, $P = 0.05$). Results are shown as means ± s.e.m.

Food webs: the end