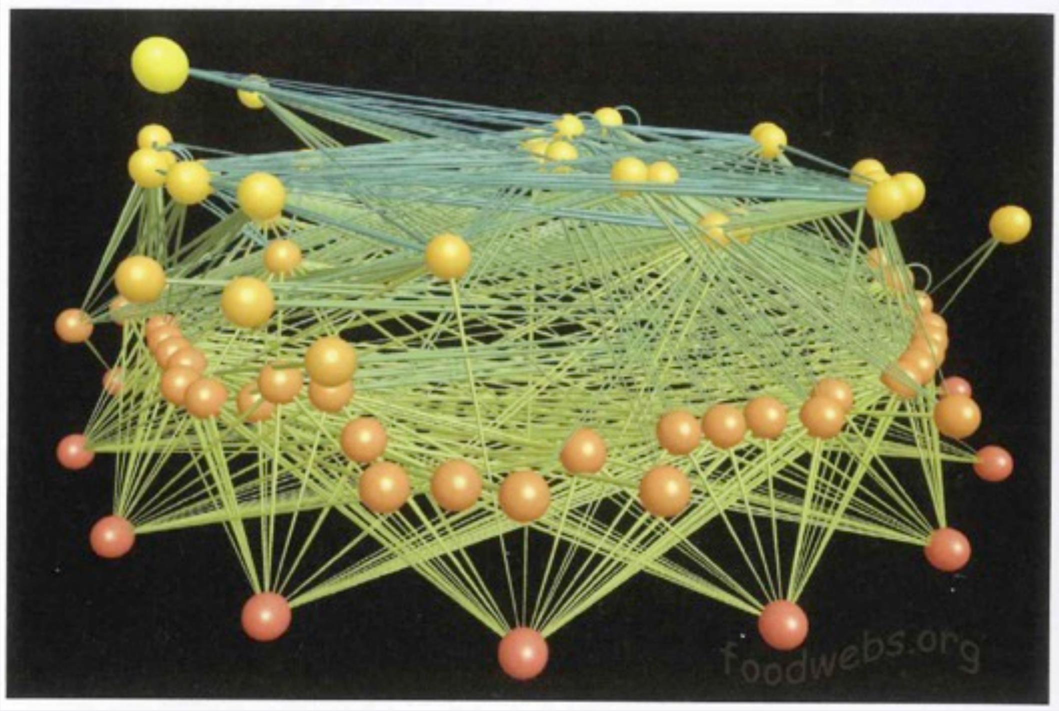
Week 8:

Food Webs and Ecological Networks



Recommended Reading for this Week:

Mittelbach 2012 Community Ecology – Ch. 10

Week 8:

Food Webs and Ecological Networks

- Interactions among the species in a community can be diagrammed as ecological networks.
- Food webs focus on "typical" predator-prey interactions, in which consumers are usually larger than their prey.
- Less commonly studied are:
  - mutualistic webs
  - host-parasitoid webs
  - roles of parasites and herbivores

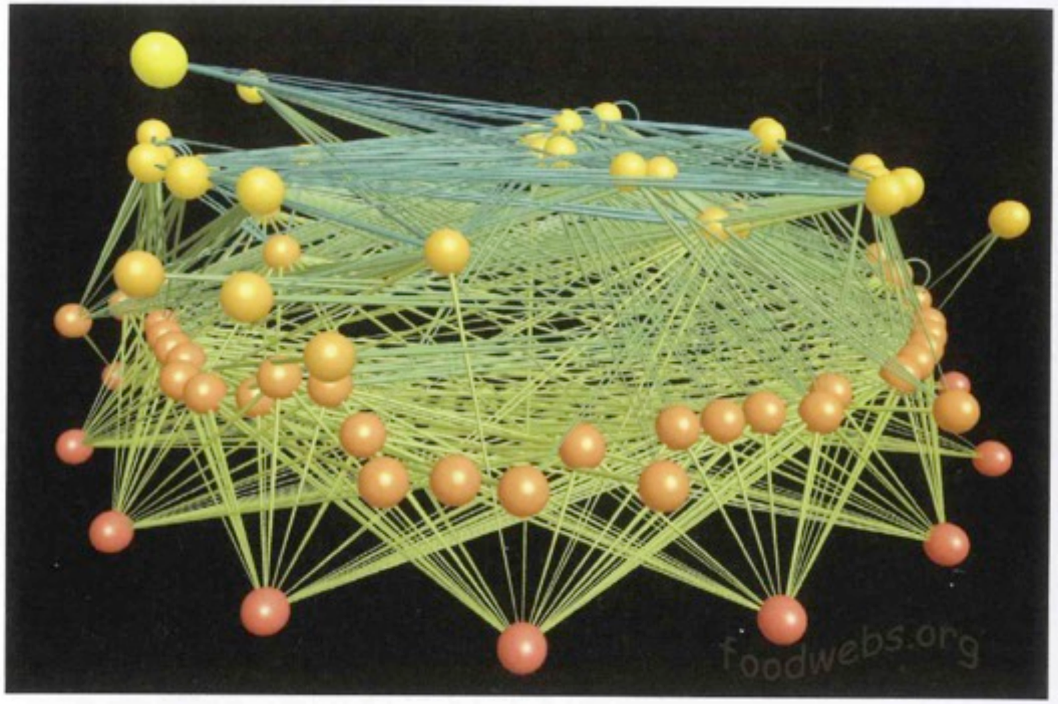
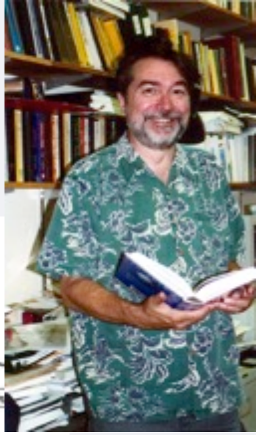


Figure 10.1 An ecological network, or food web, for species in the East River Valley, near Crested Butte, Colorado (based on the research of Neo Martinez and Brett Harvey). Node colors represent trophic levels: red nodes represent basal species, such as plants and detritus; orange nodes represent intermediate consumer species; yellow nodes represent top consumers (predators). Links characterize the interaction between nodes, with the link being thicker at the consumer end and thinner at the resource end. (Image produced with FoodWeb3D, written by R. J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab: www.foodwebs.org.; Yoon et al. 2004.)

Food Webs. I Connectedness Webs



Food webs tend to be better resolved at the top than at the bottom, in part because:

1. species richness is greater at lower trophic levels
2. species at lower trophic levels tend to be small and difficult to identify
3. have feeding relationships that are hard to quantify.

Food webs often separated into those in which basal trophic level is made up of primary producers ("green food webs") vs. those in which the basal trophic level is detritus ("brown food webs").

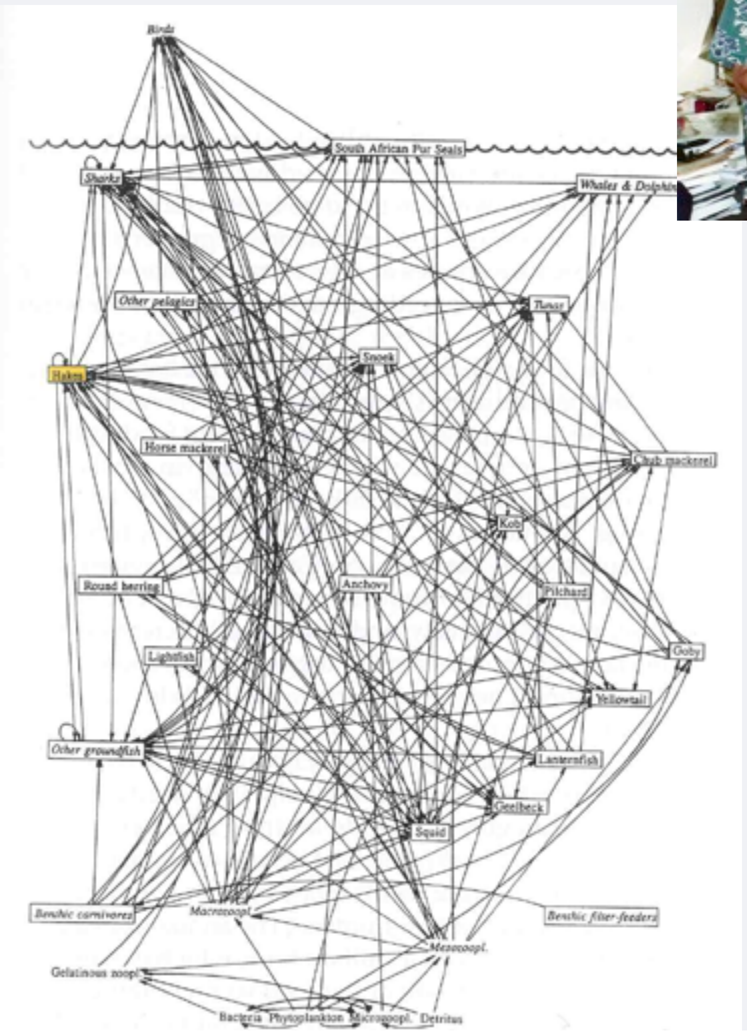
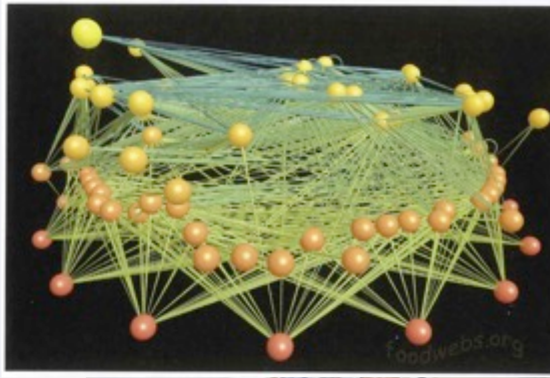


Figure 10.2 A food web for the Benguela marine ecosystem off the coast of South Africa. Arrows point from a resource to a consumer. Hake, the commercial fish of interest in this food web, are located near the upper left. (From Yodzis 2001.)

Food Webs. I Connectedness Webs

Connectedness (or structural) webs show presence of an interaction between species but do not specify the strength of that interaction.



Are there generalities in the way food webs are constructed?

Initial work (Pimm, Cohen) suggested general topological patterns*:

- proportions of species at different trophic levels constant across webs of different richnesses
- ratio of total # of links to total # of species roughly constant at 2 (each species interacts with ~ 4 species on average, independent of total richness)

Recent work with more detailed food webs suggests this is not the case

Some properties (connectance, nestedness, modularity) seem robust

Jennifer Dunne, Neo Martinez

*Structural properties of networks are known as network topology.

Food Webs. I Connectedness Webs

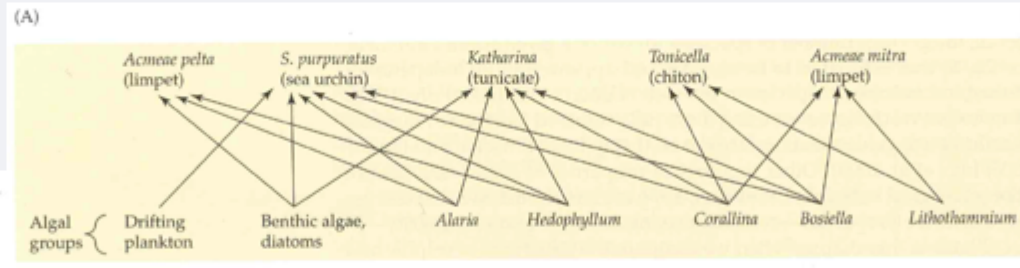


Figure 10.3 Three distinct approaches to constructing food webs, illustrated for the same set of species/functional groups found in the marine intertidal zone of Tatoosh Island, off the coast of Washington State. Arrows point from algal groups to consumers of algae (grazers). (A) A connectedness web, based on observations of who eats whom. (B) An

Paine 1980

Food Webs 2. Energy Flow Webs

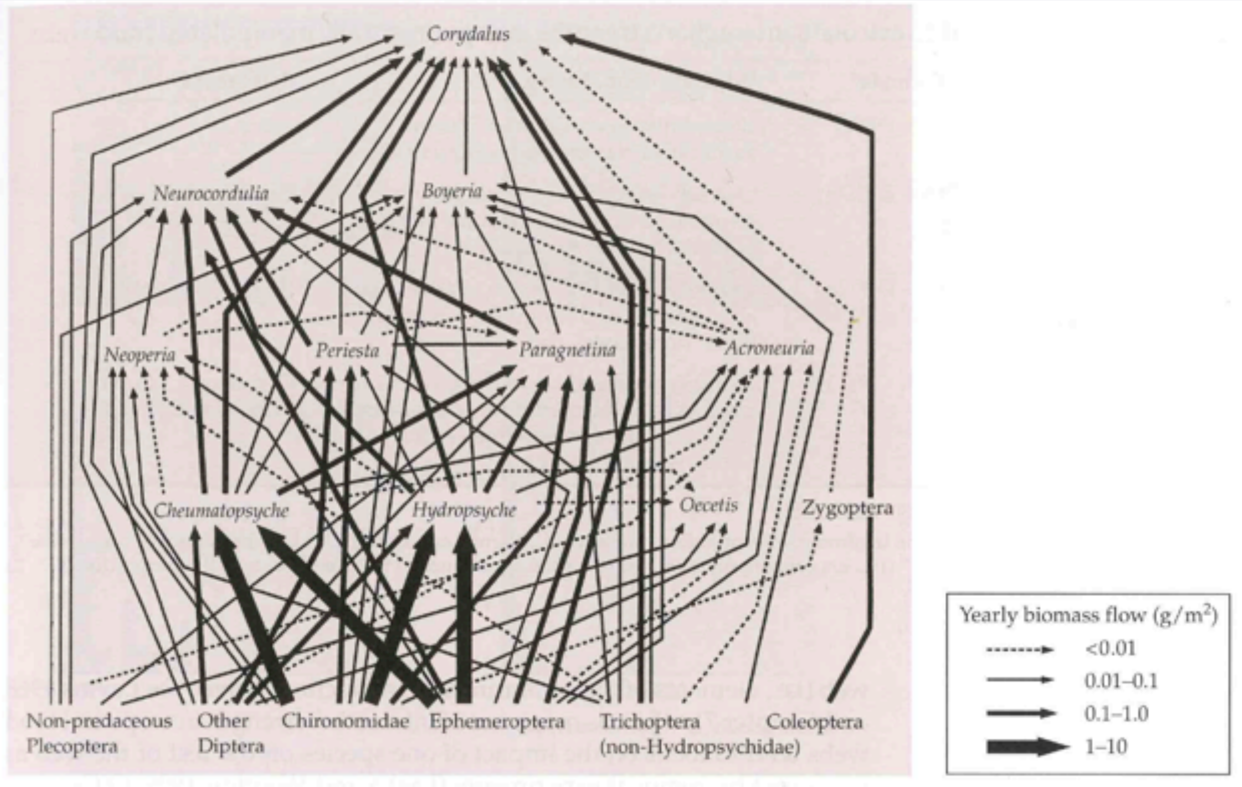
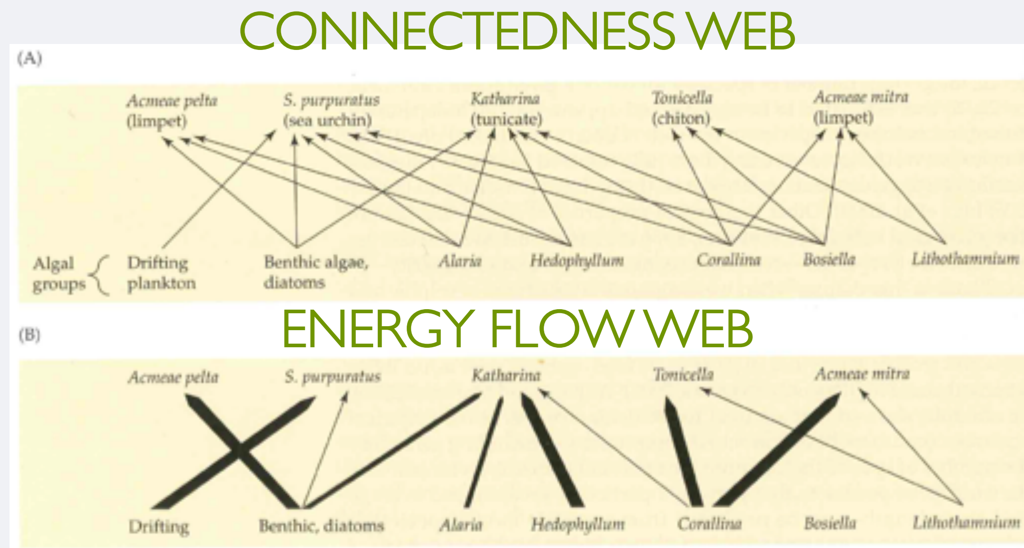


Figure 10.4 An energy flow web for the major predaceous invertebrates living on woody debris in the Ogeechee River, Georgia. Arrows point from prey to predators; arrow thicknesses indicate the amount of energy (biomass) flow. Primary consumers (non-predators) are in the bottom row. Predators are arranged in a hierarchy according to their distance, in food chain links, from the primary consumers. *Cheumatopsyche* and *Hydropsyche* are omnivores, and their ingestion of basal food resources is not shown. (From Benke et al. 2001.)

Energy flow webs measure amount of energy (biomass) moving between species in a food web. Implicit in this approach is the idea that there is a relationship between the amount of energy flowing though a pathway and the importance of that pathway to community dynamics.

Food Webs 2. Energy Flow Webs

Figure 10.3 Three distinct approaches to constructing food webs, illustrated for the same set of species/functional groups found in the marine intertidal zone of Tatoosh Island, off the coast of Washington State. Arrows point from algal groups to consumers of algae (grazers). (A) A connectedness web, based on observations of who eats whom. (B) An energy flow web, based on estimates of biomass consumption (plus values from the literature). Arrow thicknesses correspond to different amounts of energy flow. (C) A functional web, based on species removal experiments. Arrows connect strongly interacting species. (From Paine 1980.)

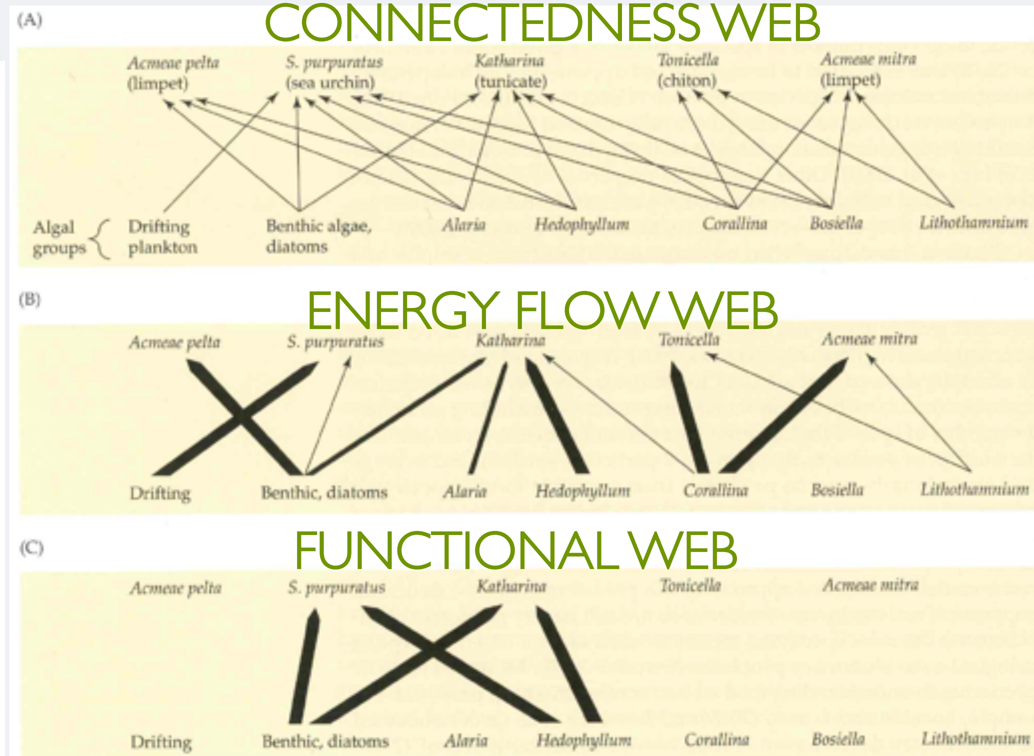


Energy flow webs measure amount of energy (biomass) moving between species in a food web. Implicit in this approach is the idea that there is a relationship between the amount of energy flowing though a pathway and the importance of that pathway to community dynamics.

However, energy flow has been shown to be a surprisingly poor predictor of the strength of interactions between species or of the impact of removing a particular species from a community.

Food Webs 3. Functional Webs

Figure 10.3 Three distinct approaches to constructing food webs, illustrated for the same set of species/functional groups found in the marine intertidal zone of Tatoosh Island, off the coast of Washington State. Arrows point from algal groups to consumers of algae (grazers). (A) A connectedness web, based on observations of who eats whom. (B) An energy flow web, based on estimates of biomass consumption (plus values from the literature). Arrow thicknesses correspond to different amounts of energy flow. (C) A functional web, based on species removal experiments. Arrows connect strongly interacting species. (From Paine 1980.)



"few strong interactions embedded in a majority of negligible effects"-Paine 1992

I.S. = (N-D) / Y

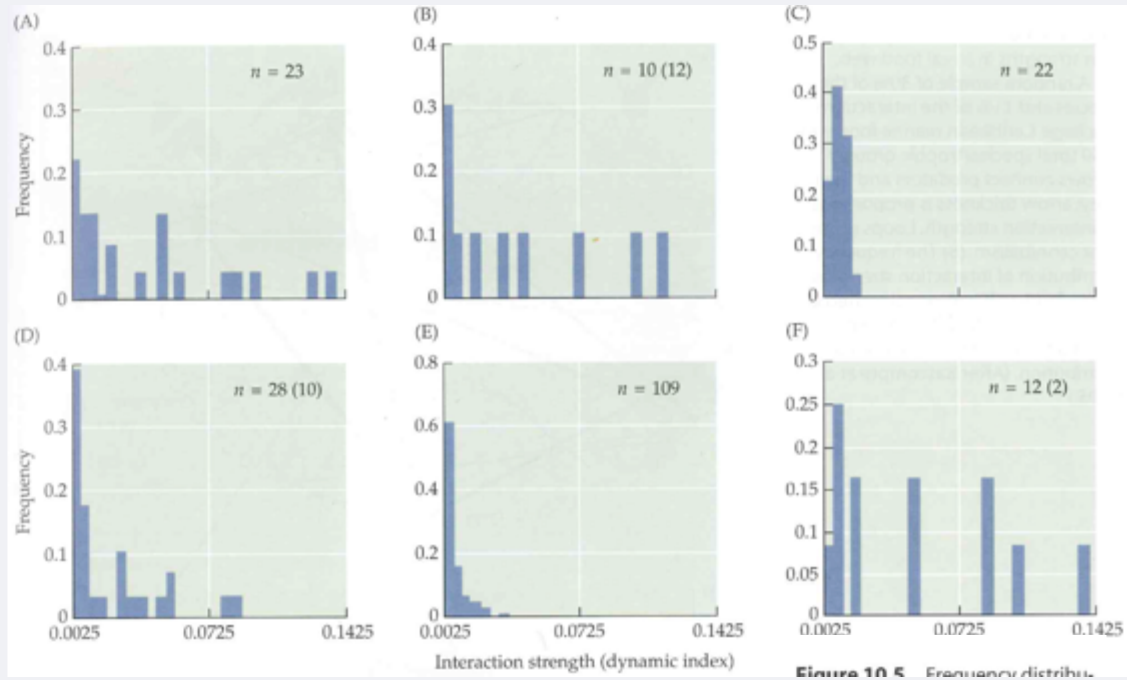
where N = # of prey with predator, normal condition;
D = # of prey when predators are 'deleted',
Y = abundance of predator

Functional webs: measure the strength of the interactions between species within a community, implicitly recognizing that not all species and interactions are equally important.

Measures of interaction strength in model food webs tend to focus on the individual interactions between species pairs, *whereas measures of interaction strength in empirical food webs tend to focus on the impact of one species on the rest of the web, as measured by removal experiments.*

Food Webs 3. Functional Webs

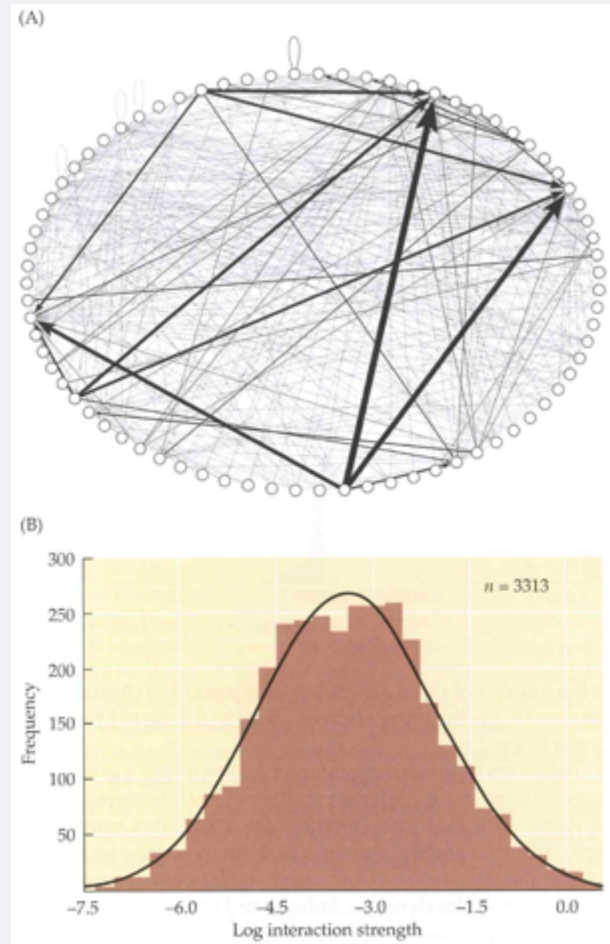
Figure 10.5 Frequency distributions of the absolute values of per capita effects of consumers on their prey. Interaction strengths between consumers and prey were calculated as ln(*C*/*E* × *P*), where *C* and *P* are the abundances of prey and consumers, respectively, in control treatments and *E* is the prey abundance in consumer removal treatments (Osenberg et al. 1997; Wootton 1997). The distributions were calculated using raw data obtained from the studies detailed in (A) Paine 1992, (B) Raffaelli and Hall 1996, (C) Sala and Graham 2002, (D) Wootton 1997, (E) Fagan and Hurd 1994, and (F) Levitan 1987. All distributions are skewed toward many weak interactions and few strong interactions, a pattern that is consistent across all systems studied. Numbers on each graph represent sample size (number of interactions); numbers in parentheses indicate the number of interaction strengths found above the scale of the graphs. (After Wootton and Emmerson 2005.)



[Most food webs contain a few strong and many weak links.](#)

Food Webs 3. Functional Webs

Figure 10.6 Variation of interaction strengths in a real food web. (A) A random sample of 30% of the species and 11% of the interactions in a large Caribbean marine food web (249 total species/trophic groups). Arrows connect predators and their prey; arrow thickness is proportional to interaction strength. Loops represent cannibalism. (B) The frequency distribution of interaction strengths in the food web in A, as calculated by Equation 10.1. The solid line represents the best fit to a lognormal distribution. (After Bascompte et al. 2005.)



Most food webs contain a few strong and many weak links.

Recall: Food web structure and stability

Interaction Strength (IS): the dynamic influence of one species on another; often measured by energy or biomass flux .e.g IS of predator on prey is equivalent to the amount of biomass consumed by the predator

-Peter Yodzis (1981) showed FWs with real IS more stable than randomly constructed ones, but reason unknown

-Increasing diversity can increase stability under one condition: distribution of consumer-resource ISs must be skewed towards weak ISs =

-Weakly interacting species stabilize community dynamics by dampening strong, potentially destabilizing consumer-resource interactions.

Weak trophic interactions and the balance of nature

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Ecological models show that complexity usually destabilizes food webs[1,2], predicting that food webs should not amass the large numbers of interacting species that are in fact found in nature[3–5]. Here, using nonlinear models, we study the influence of interaction strength (likelihood of consumption of one species by another) on food-web dynamics away from equilibrium. Consistent with previous suggestions[1,6], our results show that weak to intermediate strength links are important in promoting community persistence and stability. Weak links act to dampen oscillations between consumers and resources. This tends to maintain population densities further away from zero, decreasing the statistical chance that a population will become extinct (lower population densities are more prone to such chances). Data on interaction strengths in natural food webs[7–11] indicate that food-web interaction strengths are indeed characterized by many weak interactions and a few strong interactions.

Keystone Species

One whose effect on the community is <u>disproportionately large relative to its abundance.</u>

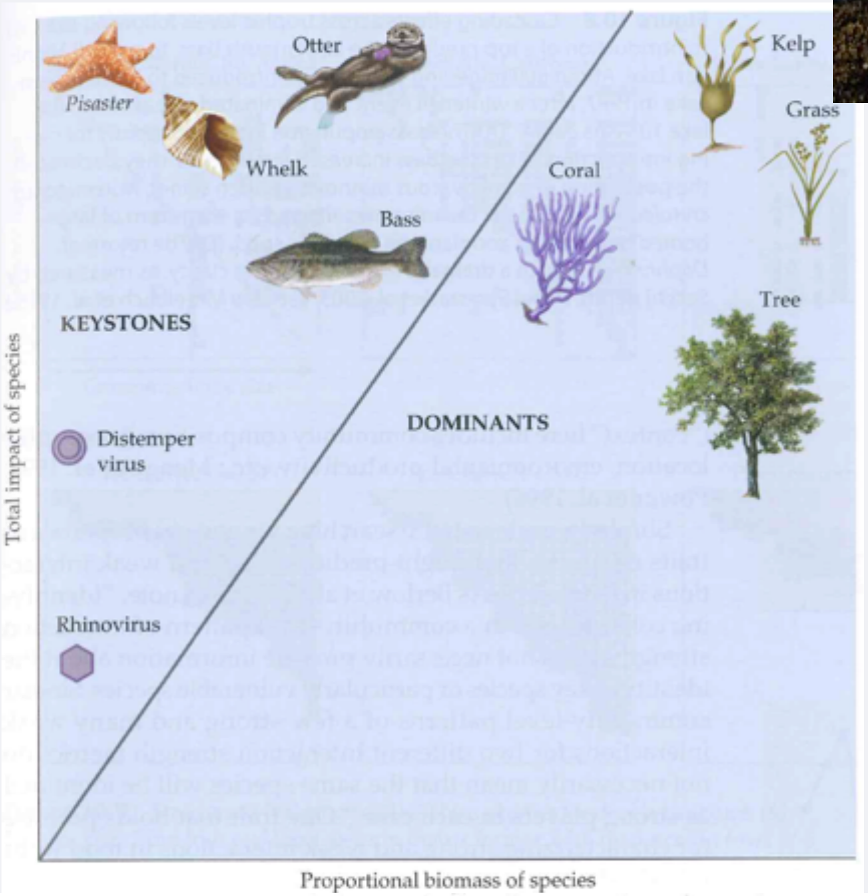


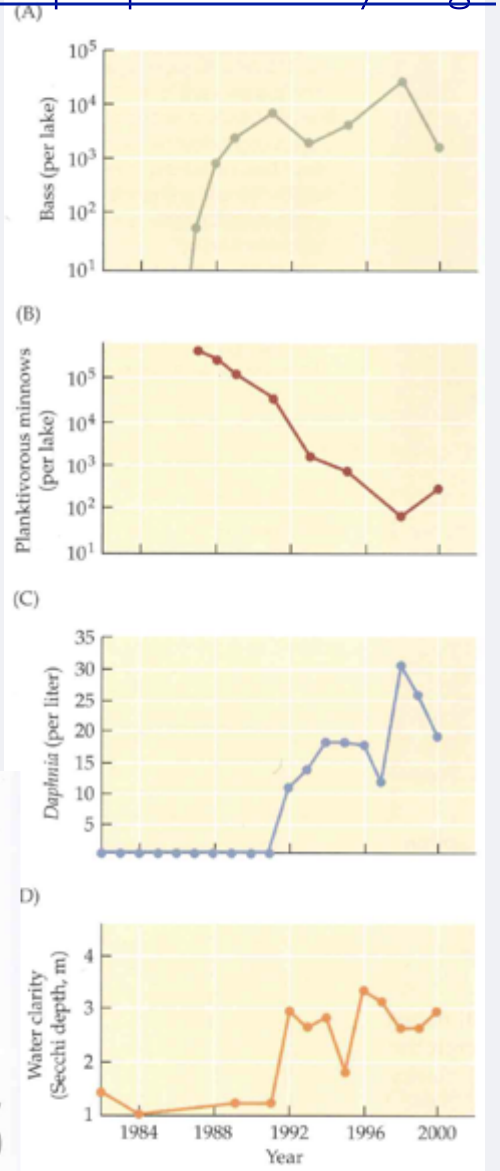
Figure 10.7 Keystone species (upper left) are defined as species whose impacts on the community are large relative to their biomass. Dominant species (upper right) are those that constitute a large fraction of a community's biomass and whose impacts are large but not disproportionate to their abundance. (After Power et al. 1996.)

Examples

- *Pisaster* starfish increases species diversity by preventing monopolization of space by mussels
- Sea otters limit the abundance of grazing urchins, allowing kelp forests and associated species to flourish

Keystone Species

One whose effect on the community is <u>disproportionately large relative to its abundance.</u>



Examples

- Piscivorous bass control the abundance of small fishes in lake, resulting in a trophic cascade down to grazer and algal trophic levels, ultimately affecting water clarity

Figure 10.8 Cascading effects across trophic levels following the reintroduction of a top predator, the largemouth bass, to a small Michigan lake. About 600 fingerling bass were reintroduced to Wintergreen Lake in 1987, after a winterkill event had eliminated all bass from the lake 10 years earlier. (A) The bass population increased rapidly following introduction. (B) As the bass increased in numbers, they decimated the population of planktivorous minnows (golden shiner, *Notemigonus crysoleucas*). (C) Loss of the minnows allowed for the return of large-bodied herbivorous zooplankton (*Daphnia* spp.). (D) The return of *Daphnia* resulted in a dramatic increase in water clarity, as measured by Secchi depth. (After Symstad et al. 2003; see also Mittelbach et al. 1995.)

How do you identify keystone species a priori?

How to predict strong vs. weak interactions in food webs?

Body Size Relationships

play a major role in determining the pattern and strength of trophic interactions within food webs

"A little consideration will show that __size__ is the main reason underlying the existence of these food chains, and that body size explains many of the phenomena connected with the food-cycle [food web]." – Elton 1927

Many species attributes scale with body size.

Q: Do the relative body sizes of predators and prey help determine who eats whom within food webs?

- Incorporated size-specific handling times for predators along with size-based energy content of prey to predict trophic links
- Correctly predicted up to 65% of trophic links in four real world food webs

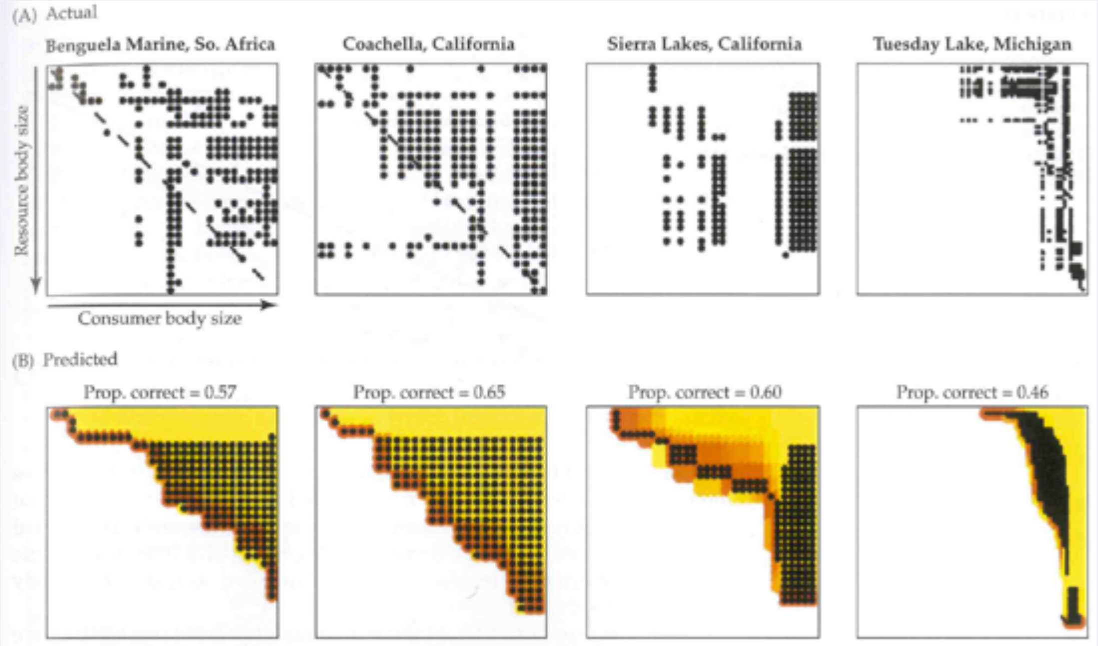


Figure 10.9 Size-based foraging relationships predict food web structure. (A) Trophic links from four real food webs in matrix format, with resources in rows and consumers in columns. Body size increases from left to right and top to bottom. A black dot indicates that the consumer in that column feeds on the resource in that row. (B) Trophic links predicted by a model of optimal foraging with parameters tuned to the data in A. Yellow to red indicates low to high resource profitability. Consumer diets always include the darker red (most profitable) resources and extend by different amounts into the yellow (less profitable) resources. (From Petchey et al. 2008.)

Body Size Relationships

Q: Is there a connection between the relative sizes of predators and prey and the strength of their interactions?

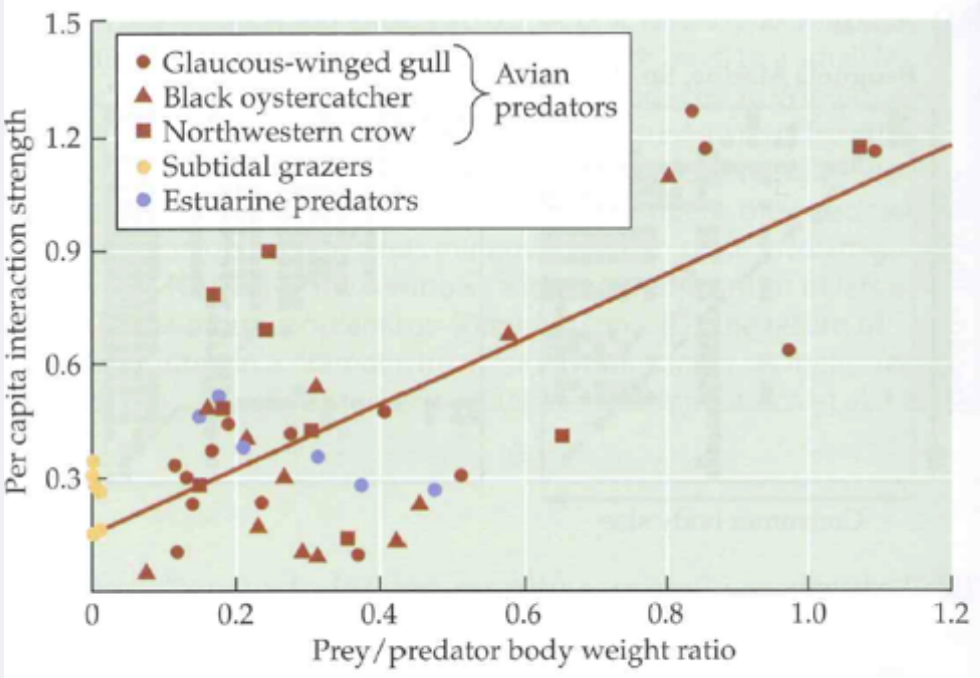


Figure 10.10 Per capita interaction strength increases with the ratio of prey to predator body weight (fourth-root transformed data). This conclusion is based on data from avian rocky intertidal predators, subtidal grazers, and estuarine predators. The regression line shown is for avian intertidal predators only. (After Wootton and Emmerson 2005.)

- Collection of four food web studies
- Results: interaction strength was positively related to the ratio of prey weight to predator weight
- Relationship may be unimodal rather than linear

Body Size Relationships

Q: Is there a connection between the relative sizes of predators and prey and the strength of their interactions?

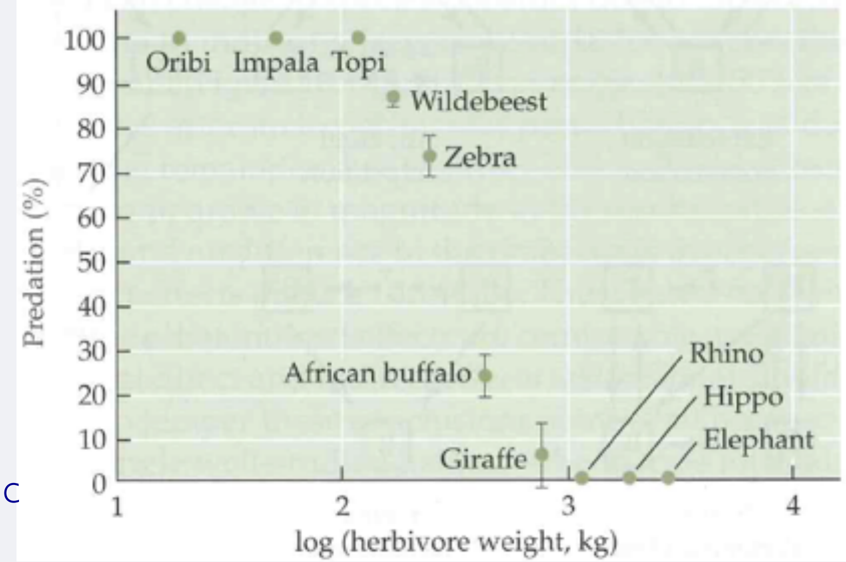


Figure 10.12 Predator-related adult mortality in non-migratory African ungulates drops off sharply at a body size of about 150 kg. Error bars are 95% confidence limits. (After Sinclair et al. 2003; photo © Images of Africa/ Alamy.

SUMMARY: **Elton's intuition was correct:** body size does play a major role in determining the pattern and strength of trophic interactions within food webs.

Developing general foraging models in which parameters (handling time) scale with predator and prey body sizes, allows linkages between individual behaviours and structure of ecological networks

Indirect Effects

Evidence suggests that the net effects of indirect interactions—when the actions of one species influences a second species via a third species—are important in food webs. Four most common:

- Exploitative competition (resource competition) when a species consumes a shared resource that limits its and other species' population growth
- Apparent competition – species that share a predator may have negative indirect effects on each other
- Cascading effects
- Keystone predation

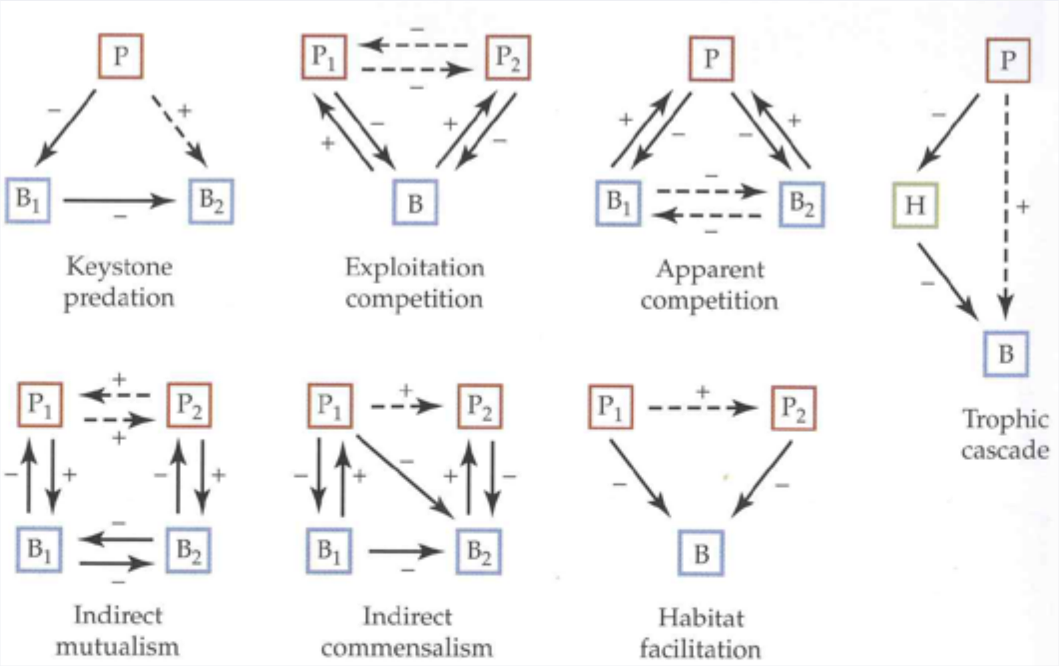


Figure 10.13 Models of seven types of indirect effect sequences. Solid arrows represent direct effects; indirect effects are shown by dashed arrows. Plus and minus signs indicate positive and negative effects, respectively. B, basal species; P, predator; H, herbivore. (After Menge 1995.)

Indirect Effects

Pathway for an indirect effect is necessarily longer than that for a direct effect, thus we might expect:

(1) Indirect effects will take longer to develop than direct effects
(2) Indirect effects will be weaker than direct effects

Menge 1995:

- Examined results of perturbation experiments in 23 marine rocky intertidal habitats
- Conclusion: indirect effects are comparable in magnitude to direct effects and direct/indirect effects take place at similar rates
- *however this is based on only one habitat

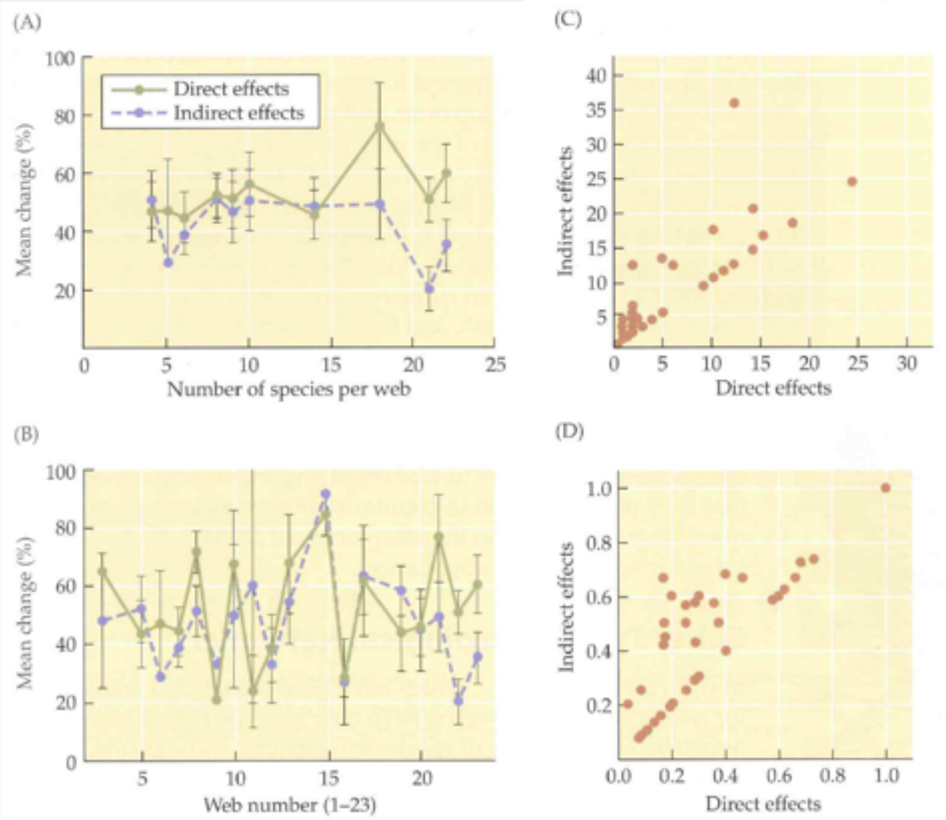


Figure 10.14 Importance of direct and indirect effects in marine intertidal food webs. (A) Mean percentage change in the abundance of organisms (absolute value) caused by experimentally manipulated direct and indirect effects plotted against the number of species in each food web. Webs with equal numbers of species are lumped. (B) The same data plotted for each food web individually (webs are not lumped). Error bars are ±1 SE. (C) The number of months required to demonstrate significant direct and indirect effects. (D) The same data expressed as the proportion of the duration of each experiment, in order to adjust for variation in experiment duration. (After Abrams et al. 1996; data from Menge 1995.)

Other types of Ecological Networks:

Mutualistic Networks

Mutualistic Interactions depicted as webs of links between species with <u>two well-defined types of nodes</u> (e.g. plants and their pollinators), in which interactions occur between, but not within, node types.

- Known as bipartite interaction webs

Figure 10.15 A plant–pollinator interaction network. Boxes represent pollinating bee species; circles represent plant species. The thickness of the line connecting bee and plant indicates the number of visits by a bee species to a plant species (thicker lines indicate more visits). There are an equal number of bee and plant species in this example simply due to chance. (From Bezerra et al. 2009.)

Mutualistic Networks

Mutualistic Interactions depicted as webs of links between species with <u>two well-defined types of nodes</u> (e.g. plants and their pollinators), in which interactions occur between, but not within, node types.

Properties:

1. high level of connectance
2. high degree of nestedness
3. relatively low modularity.

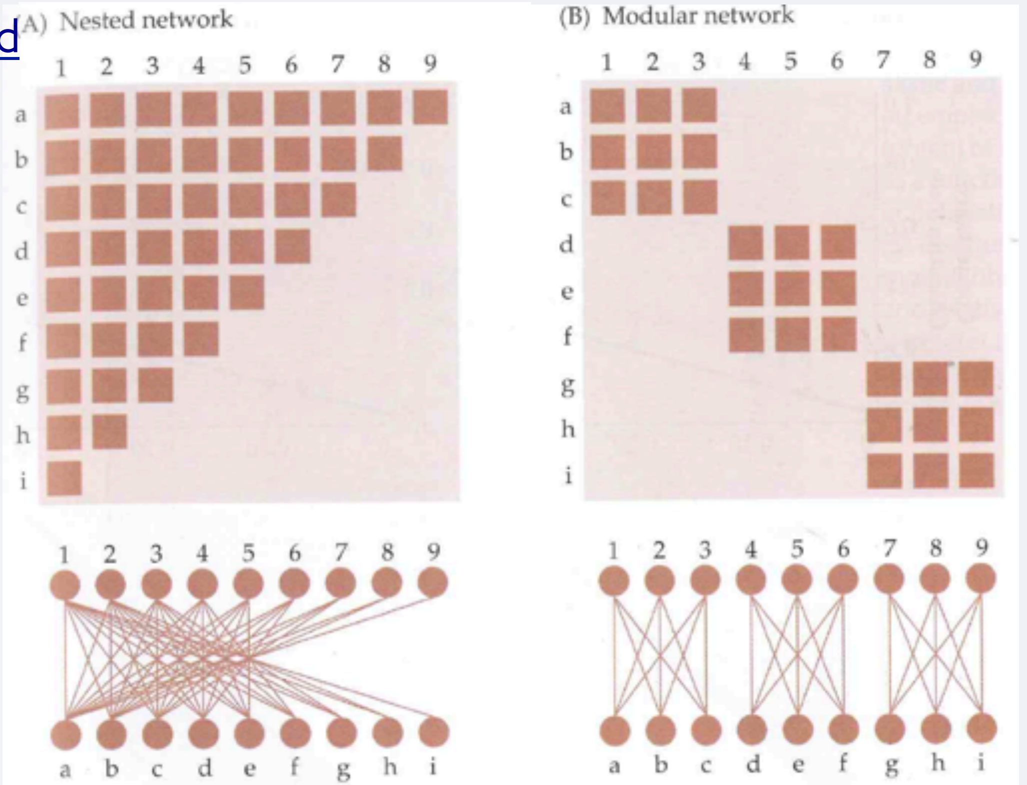


Figure 10.16 Schematic representation of nested (A) and modular (B) bipartite networks. In matrix representations (top), each row and column corresponds to a species; squares represent species interactions. In web representations (bottom), each node represents a species, and interacting species are connected by lines. (From Fontaine et al. 2011.)

1. **Connectance**: observed number of links in the network
2. **Nestedness**: specific type of interaction structure in which species with many interactions (generalists) form a core of interacting species and species with few interactions (specialists) interact mostly with generalists
3. **Modularity**: groups of species interact more among themselves than with species from other groups

Other types of Ecological Networks:

Mutualistic Networks

Properties:

1. high level of connectance
2. high degree of nestedness
3. relatively low modularity.

Fig. 10.17 – *How do differences in network topology affect the persistence and resilience of mutualistic and trophic networks?*

- increased nestedness and connectance promoted stability in model mutualistic networks
- increased modularity promoted stability in model trophic networks

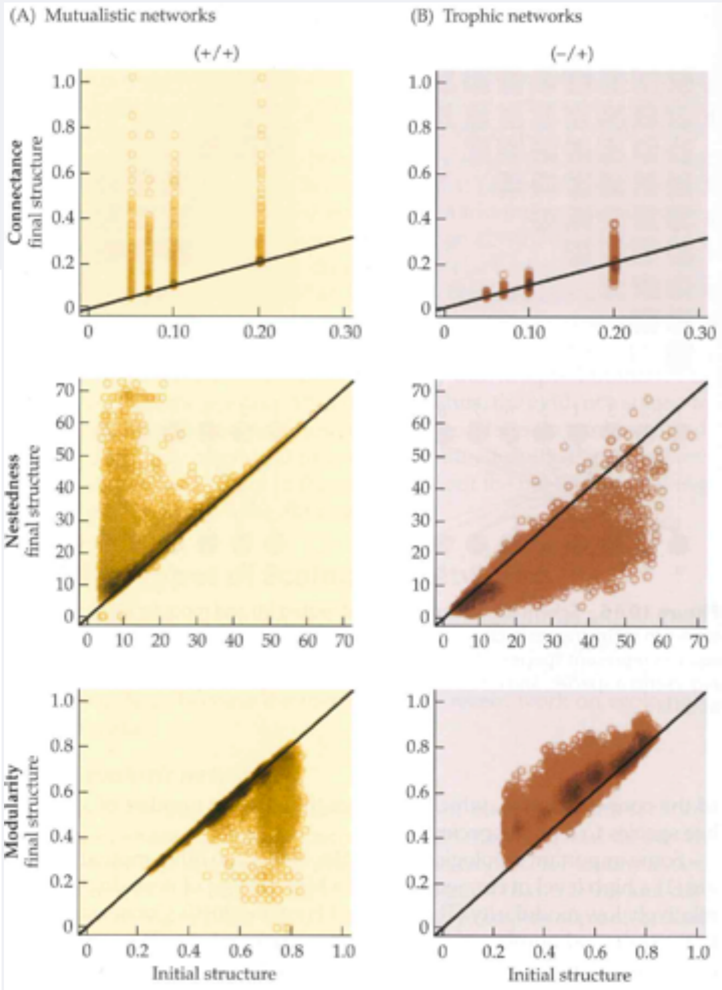


Figure 10.17 The relative importance of connectance, nestedness, and modularity in the stability and architecture of mutualistic (plant–pollinator in this study) and trophic (plant–herbivore) model networks. Final network structure is plotted against initial network structure for a series of model simulations in which mutualistic (A) and trophic (B) networks were allowed to develop over time. During the simulations, some species became extinct before equilibrium was reached, thus altering network structure. These extinctions caused mutualistic networks to become more connected and more nested over time, whereas trophic networks became more modular over time. (After Thébault and Fontaine 2010.)

Other types of Ecological Networks:

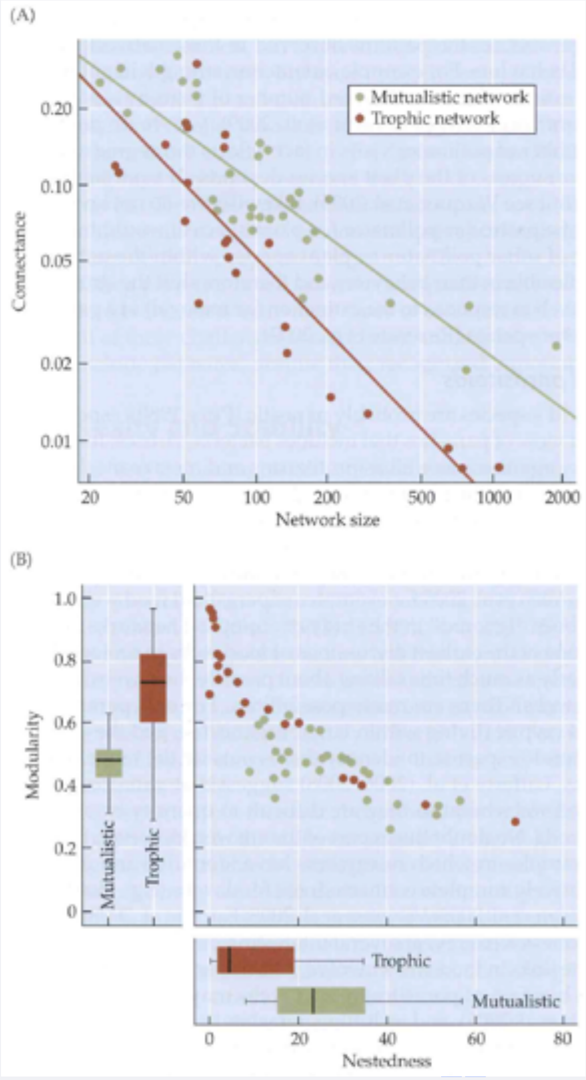
Mutualistic Networks

Properties:

1. high level of connectance
2. high degree of nestedness
3. relatively low modularity.

Fig. 10.18 – *Same properties differed in real-word mutualistic and trophic networks:*

Figure 10.18 The degrees of connectance, nestedness, and modularity differ among real mutualistic and trophic networks. Each dot represents an empirical network involving either pollination (green) or herbivory (red). (A) Connectance plotted as a function of network size. Connectance is greater in pollination networks than in herbivory networks. (B) Relationship between network nestedness and modularity. Box plots of relative nestedness (below) and relative modularity (left) show that nestedness is greater in pollination (mutualisitic) networks and modularity is greater in herbivory (trophic) networks. (After Thébault and Fontaine 2010.)



- *Suggests that food webs and mututalistic webs differ systematically in their topologies and these differences differentially affect network stability such that each type of network develops a structure that tends to stabilize that network.*

Other types of Ecological Networks:

Parasites & Parasitoids

Parasites are left out of most food webs because their interactions and impacts on other species are difficult to quantify by standard ecological methods.

1. Small, cryptic species and require a level of taxonomic expertise
2. Complex life cycles and multiple hosts
3. Feed on, but rarely kill their hosts = measuring energy transfer difficult
4. Affect the behaviors of their hosts e.g. often making them more susceptible to predators

- ~75% of links in complete connectedness webs involve parasites
- Total biomass of parasites in food webs may exceed that of top predators (Kuris et al. 2008)
- Including parasites in food webs increases food chain length and food web connectance (Lafferty et al. 2006)
- Ecologists need to find ways to better incorporate parasites and other infective agents into ecological networks.

CONCLUSION: The challenges of incorporating parasites into food webs are qualitatively no different from the challenges incurred with other types of consumers, however the sum total of these challenges is significant and explains why so few food webs include parasites

Are more diverse communities more stable?

- Robert May 1973
  - Suggested more diverse communities tend to be less stable
  - Randomly assigned interaction strengths to different species

- However, natural communities show a skew in the distribution of species interaction strengths.
  - Recent theoretical studies show this skewed distribution strongly supports stability.

- Therefore, diversity may promote stability in food webs if the number of weak trophic interactions increases with diversity.

- Empirical food webs
  - Webs are more modular or compartmentalized
  - Modularity shown to increase food web persistence

CONCLUSION: Food webs that are more diverse tend to have more weak interactions and greater modularity than simpler communities, and thus tend to be more stable.

What's Next:

Week 8 (March 2 - 6th) - Food webs and ecological networks

M: Skills Tutorial 7 - Diversity indices in R. **1st R assignment due**

T: L - Food webs and network models

W: D - Ecological networks - Led by Dr. Baum & Emily

Required Reading:

- *Classic: Paine (1966) Food web complexity and species diversity. The American Naturalist. 100(910): 65-75.*
- *Recent: Williams & Martinez (2000) Simple rules yield complex food webs. Nature*
- *Companion piece to the recent article: Wayt (2003) Virtual ecosystems. Conservation Magazine*

F: P - - Led by Marina and Jessica

Required Reading:

- *Thompson et al. 2011. Food webs: reconciling the structure and function of biodiversity. Trends in Ecology and Evolution.*

paine1966.pdf
Download File

williamsmartinez2000_foodwebs.pdf
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wayt2003_virtualecosystms.pdf
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thompsonetal_2012tree.pdf
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Body Size Relationships

Studies of theoretical and empirical food webs have shown that most food webs contain a few strong links and many weak links.

Key-stone species is one whose effect on the community is disproportionately large relative to its abundance.

Body size relationships play a major role in determining the pattern and strength of trophic interactions within food webs.

(2) Is there a connection between the relative sizes of predators and prey and the strength of their interactions?

- Laboratory study using beetles and spiders that feed on collembolans, crickets or fruit flies
- Unimodal relationship between predation rate and predator/prey body mass ratio was found

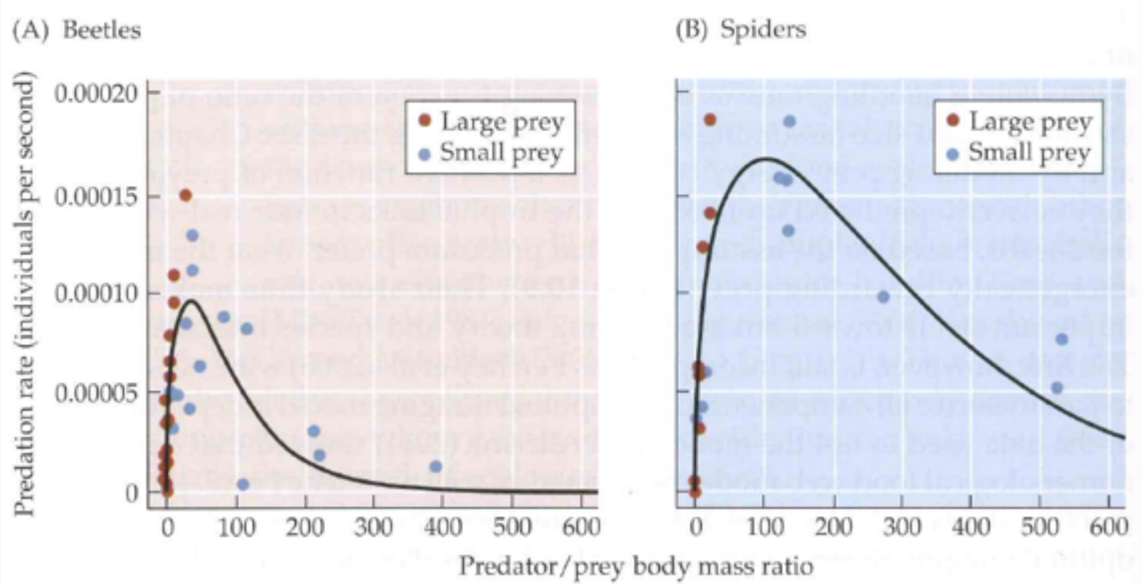

Figure 10.11 Predatory beetles (A) and spiders (B) feeding on large and small prey items in the laboratory show feeding rates that are a hump-shaped function of the ratio of predator mass to prey mass. Observations suggest that predation was limited by the relatively long time needed to subdue and handle prey at low predator–prey body mass ratios. At high predator–prey body mass ratios, predation was limited by the high escape efficiencies of prey species due to fast reaction times and their use of small refuges. (After Brose et al. 2008.)