Questions and answers about food webs

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Corvus orru eating *Gallus gallus*

Motivation

ZM: *(Idea set 1)* The goal would be to establish why food webs are scale free. We could find an abstract mathematical structure that generates scale-free topology in such a way that, despite its deviations from the real world, is a good explanation for the scale-free food webs observed in the real world. Another approach would be to take simulated food webs and subject them to various kinds of evolutionary stressors, see in which cases scale-free graphs emerged, and try to connect the stressors to biological reality.

   (Idea set 2) Or, we could try to elucidate how food webs come into existence and change over time. When a new species or group of species arrives, how is connectance established? We can try out different assumptions and see how well they match reality. Also, we could try to describe how entire food webs interact with each other (either through gradual exchange or catastrophic collision). Are food webs themselves units of evolution?

AK: *(Re: Idea set 1)* Food webs generally do not have a scale-free link distribution, despite a few studies that claimed the opposite based on limited data. Research continues into other possibly scale-invariant food web parameters such as connectance (Martinez, 1992) or transport efficiency (Garlaschelli et al., 2003). But food webs seem to share neither the assembly mechanisms nor the link structure of scale-free networks as described by Barabási and Albert (1999).

Little is known about the processes by which food webs assemble and evolve. Due to the time scales involved, there is an almost complete lack of empirical data. (I'll have to read more about this...)

Summary

(to be written last)
(maybe to subsume "Motivation," at least my section of it, because that's not so much motivation as refutation...)

What is a food web?

Q: What is a food web and how is it different from a food chain?

A food web is an assemblage of organisms that eat and are eaten by each other. Food webs are usually described within the boundaries of a particular *location* (e.g. a pond, an island, a meadow). A geographical boundary keeps the scope of the food web manageable; otherwise, the food web would have to include increasingly distant interactions until it encompassed every species on the planet[1].

A food web contains food chains, and can be described as a series of food chains. It is possible to calculate the average length, or the maximum length, of all the individual food chains contained within a given food web, and these are frequently used metrics of food web structure. (Isolated food chains are nearly unheard of in nature, but for the sake of simplicity they are sometimes still used in dynamic simulations.)

Food webs can include *looping* (A eats B, B eats C, and C eats A – like "rock paper scissors"), and *cannabalism*, both of which occur in real communities but cannot be represented in terms of a food chain.

Q: How does the idea of "trophic levels" relate to food web structure? In the context of a food web, *is* there any such thing as a clearly defined trophic level?

In food webs, trophic levels can still be described, but their interpretation becomes blurred (Polis, 1991). A decision must be made between one of three definitions:
1. The *minimum* number of links between a species and its non-living resources.
2. The *maximum* number of links (as above).
3. The *average* number of links (as above).

Considering the system in Figure 1, a human could thus be defined as having a trophic level of 2 (the minimum number of links), 4 (the maximum), or approximately 3 (the average). The average chain length, though in some ways the most meaningful, is also the most complex, because it requires a knowledge of the amount of biomass consumed at each trophic level (e.g. Fretwell, 1987; Loeuille and Loreau, 2005).

Figure 1. Different definitions of the trophic level of an omnivore.

Once a trophic level is determined for each species in the food web, an average trophic level can be calculated for the food web *overall*. Sugihara et al.
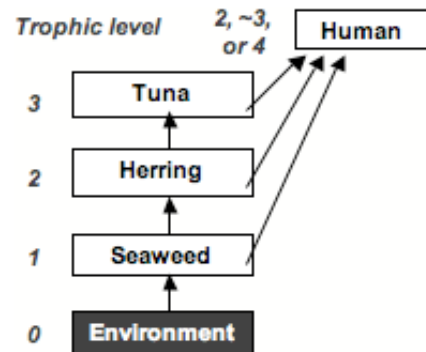
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[1] As the spatial extent of the food web changes, its quantitative parameters necessarily change. For example, in a small freshwater stream, species X may eat 8% of the other species present. But species X certainly does not eat 8% of the other species in the watershed, nor 8% of the other species on Earth. So the definition of the spatial boundaries of a food web is both important and arbitrary.

(1989) suggest that average minimum chain length is a better metric than average maximum chain length, because only the former tends to be robust in the face of different taxonomic resolution.

Note: Cannibalism and looping have to be ignored in calculations of trophic level, for obvious reasons; however, cannibalism and looping are both common and important in real communities (Polis, 1991). This calls into question the usefulness of the "trophic level" concept in food webs.

In one food web (REF), slightly more than half of the species could be assigned to an integer trophic level.

Another commonly used metric is the maximum single chain length (not the average maximum) that can be found within a given food web. It has been observed that food webs rarely have more than five trophic levels. This fact is most commonly attributed to inefficient energy transfer between each level (Sugihara et al., 1989), but may also be due to mathematical instability in long food chains (Pimm, 2002?).

Q: What types of interspecific interactions does a food web describe? Does it only describe predation, or does it also describe parasitism, mutualism, etc.?

As a rule, food webs only describe *trophic* interactions, i.e. predation. Competition, commensalism, and mutualism are not considered (see below).

Parasitism is a controversial issue in food webs. Sometimes, parasitism is considered a type of predation, and is included; but often it is not. Parasites are, essentially, the top predators in most food webs, but their characteristics are quite different to what we normally expect of "top predators" (Polis, 1991). Parasites are difficult to observe because of their life history traits and small biomass, so they are often omitted from food webs for the sake of convenience.

In Ythan Estuary, one of the largest published food webs, the inclusion or omission of several dozen metazoan parasites seemed to have little effect on the structure of the food web (Montoya and Solé, 2002; Dunne et al., 2004). (Someone disagrees with this – REF?) But many researchers are concerned that the exclusion of parasites may introduce unacceptable biases (Marcogliese and Cone, 1997).

Q: Does the neglect of certain kinds of interactions limit the usefulness of food webs as a model?

It is generally accepted in the food web literature that non-trophic interactions (such as competition) are significant, and their omission may reduce the relevance of food webs as models (Berlow et al., 2004). However, trophic interactions are generally seen as the *single* most important force shaping ecological communities (Worm and Duffy, 2003). Thus, food webs are still useful even if not ideal.

An evolutionary food web model (Loeuille and Loreau, 2005) found that realistic results could be achieved with competition but not without it. Competition intensity was more important than niche width in many cases. Competition favors diversity, which in turn favors stability.

N.B. I am not aware of any models that attempt to incorporate *all* possible classes of ecological interactions.   Perhaps this will be a goal for ecology in the next fifty years or so.

Read a good reference on this recently, that included competition. Competition makes it more realistic...

(not sure if this is the right place for this comment, but...)
Polis (1991) delivers a scathing critique of the inadequate resolution of most existing food webs. His paper calls into question essentially all generalizations that have been made about empirical food webs up to that point. It's both inspiring and somewhat sobering... makes the rest of the literature seem like a house of cards. Few researchers have invested anywhere near the amount of time Polis invested in the Coachella Valley food web (10 y and many thousands of hours). If they were to do so, how would their results change?

Constructing food web models

Q: Are food webs usually described statically or dynamically?

There is a clear division between static (a.k.a. structural or topological) food web models and dynamic food web models (Bascompte and Melián, 2005). Most food web models to date have been static; that is to say, they describe the interconnections between nodes, and can simulate extinctions, but ignore changes in population density. (I guess. This still confuses me.) Static models can describe a very large number of species, >100.

Dynamic food web models are necessarily very computationally complex, and the lack of mathematical tools has hindered their study (Williams and Martinez, 2004a). It has until recently been difficult to get a dynamic model with >3 species to reach a state of stability. Williams and Martinez (2004a) found that with a modification of assumptions about feeding behavior, a stable web could be achieved with up to 10 species. But, the state-of-the-art for dynamic models lags far behind that for static models. Berlow et al. (2004) assert that "analytical solutions for food webs are limited currently to those that make many unrealistic assumptions." Dunne et al. (2004) call for efforts to *integrate* structural and dynamic models.

(The dynamic model used by Williams and Martinez was called McCann's "bioenergetic consumer-resource model" and included matrices of terms for the effects of every species on every other species).

The dynamic model used by Montoya and Solé (2003) was based on Pimm's multitrophic assembly model (Lockwood et al., 1997). Includes different types of functional responses to determine the Lotka-Volterra terms:

      Holling type I – constant interaction strength (this is the most straightforward, say M&S, 2003)

      Holling type II – saturating interaction strength

      Holling type III – sigmoidal interaction strength

Their assembly model could not reproduce the degree distribution observed in actual food webs.

Food webs are not *spatially explicit*. By virtue of defining something as a food web, you assume that all the species are able to interact. However, this is not literally true. (Has anyone tried making spatially explicit food webs I wonder?
(see Holt, 2002)

Q: What are some widely used null models for food webs?

In the context of food webs, a null model is a simplified network structure that takes several key parameters of real food webs as input (usually S, the number of nodes, and C, the connectance) and then its output is tested for agreement with other parameters (e.g. fraction of top predators, presence of compartmentalization, etc.) This can help to elucidate the mechanisms underlying food web structure (Dunne et al., 2004). Some of the prevalent null models are:

- Random model. This model draws links randomly between S nodes until the desidred C is attained. It tends to perform poorly at replicating properties of real food webs.
- Cascade model (Solow and Beet, 1998). Assigns each species a "niche value" and gives each predator prey that have a lower niche value.
- Niche model (Williams and Martinez, 2000). Assigns each species a "niche value" and gives each predator prey from an adjacent range of niche values (can be higher or lower).
- Nested hierarchy model (Cattin et al., 2004). Attempts to create similar sets of prey for similar predators. Its descriptive accuracy is similar to that of the niche model (Stouffer et al., 2005).

Loeuille and Loreau (2005) criticize the whole idea of using S and C to parameterize the null model: why not try to *predict* these instead, from more basic principles? They created a dynamic model based upon the evolution of body size: start with an initial population of a single species with body size x, which at each time step has a 10^{-6} chance of giving rise to a new species with body size in the interval $[0.8x, 1.2x]$. By adjusting niche width (ASDF) and competition intensity (ASDF), the authors could reproduce realistic values for connectance, food chain length, omnivory, and % T, I, B, as well as or better than the niche model.

More abstract, computationally-based null models:

- Preferential attachment model (Barabasi and Albert, 1999) – not specific for food webs
- Local rewiring algorithm – take a FW, choose any two pairs of links, and swap them, etc., until you have entirely mixed it up. But you preserve the total number of links. Ref: Gotelli (2001). Note: this model uses *directed* links. Also, it's not exactly a null model.

Melian and Bascompte found that, among these null models:
Random was worst. Cascade next worst. Niche, preferential attachment, and local rewiring all about equally OK for predicting connectance. (wait... connectance is usually a given.)

$n_j \equiv$ Niche value of species j (used in the niche model). This is a randomly chosen value $\in [0, 1]$ and represents a species' place in an ecosystem (its predators and prey are drawn from amongst species with similar niche values).

Bascompte and Melián (2005) recommend using multiple null models because all tend to give somewhat different results.

Q: Do food web models use directed links or undirected links?

It varies. (REFs)
Dynamic models obviously use directed links, because a predator will not effect the population dynamics of its prey in the same way that the prey will effect its predator. Static models vary.
(maybe combine this with "does causality flow up... that is, do prey control their predators?"

Most theoretical food web graphs are undirected (Montoya and Solé, 2002).
Montoya and Solé (2003) used undirected links. Many other authors don't even bother to mention it. That seems odd, as it is a rather fundamental decision to make...

Q: In graphical representation of food webs, does an arrow from A to B mean "A eats B" or "B eats A"?

It varies, but is usually easy to figure out from context.

A → B "A eats B": Milo et al. (2002)

A → B "B eats A": Polis (1991), Neutel et al. (2002), Garlaschelli et al. (2003), Wilhelm (2005), Vandermeer (2006).

Q: Are the links in food webs of a binary nature, or can they have different interaction strengths? If the latter, how are differences in interaction strength described – by biomass consumed, number of individuals consumed, or some other way?

Interaction strengths are a cause of much contention in food web research! For a thoroughly referenced review, see Berlow et al. (2004).

Interaction strengths are difficult to measure empirically, and greatly increase the complexity of a food web model. Accordingly, many models – both empirical and theoretical – do *not* account for interaction strength. Instead, a link is drawn between species A and B if A eats *any* amount of B (perhaps cut off at some predetermined threshold). The choice of this threshold can affect almost any food web parameter, including connectance, food chain length, and predator/prey ratio (Loeuille and Loreau, 2005).

The niche model (Williams and Martinez, 2000), a popular null model, uses this simplified binary approach, and has nonetheless succeeded in reproducing certain food web properties. So the structure of a food web can, to some extent, be approximated without the use of weighted links.

On the other hand, evidence is mounting that different interaction strengths play an important role in food web structure (Bersier et al., 1999; Berlow et al., 2004).

There are multiple different approaches for quantifying interaction strengths. Standardization is needed:

The percentage of species X's diet accounted for by consumption of species Y. (Winemiller, 1990; described in Bersier et al., 1999).

Interaction strengths can be measured in exclosure experiments, by measuring "the effect of excluding a species on the populations of other species" (Martinez and Dunne, 1998). But pairwise interaction strengths may be misleading, because the presence of other species can affect the interaction (Berlow et al., 2004). For example, a coyote might eat primarily grasshoppers if those are the only prey it can find, but if mice are also present it may consume the mice instead and have very little effect on grasshoppers. Indirect effects are also likely (e.g., if hawks outcompete coyotes for mice, then the presence of hawks will increase the effect of coyotes on grasshoppers...) Ideally, interaction strength would account for indirect effects, but the challenges of measurement are nearly insurmountable.

Weak interactions seem to prevail in most known food webs (Berlow et al., 2004, and references therein).
It's argued that weak links are key to stabilizing food webs (Neutel et al., 2004) – and others (REF) - so this makes the question especially interesting and important..

Interaction strengths are defined by May (2001) are the values of the elements of the community matrix, and they represent the magnitude of the effect of species on each others' dynamics near equilibrium. (seek out better definition?) (quoted in Neutel et al., 2004). (how can you measure that empirically?)

Increasing species richness (S) could be correlated with a decrease in average interaction strength. (Martinez and Dunne, 1998)

There is a big gap between theoretical (mostly static / binary) food web research and empirical food web research (Berlow et al., 2004).

The existence of "keystone predators" indicates that unweighted links are not always a sufficient descriptor of food web structure. (Berlow et al., 2004.)

There are many different definitions of interaction strength. Berlow et al. (2004) list 11 definitions that occur in the literature. A large energy flow is not the same thing as a large propagation of a perturbation.

"A topological keystone may not be the same species as the biomass flow keystone or the population dynamics keystone. So we should be careful about what species we call 'weak.'" (Berlow et al., 2004)

There is at present no widely agreed-upon H_0 for interaction strengths (Berlow et al., 2004).

Q: What methodologies are used for collecting empirical food web data?

The gold standard for food web data collection is to actually do gut contents analysis (e.g. Bersier et al., 1999) or other forms of direct observation, such as behavioral observation in the field. However, it is not uncommon to draw trophic links based on indirect evidence (expert opinion; comparison of related species; comparisons of body size; etc.) Indirect evidence is more expedient, but it is likely to be less accurate, and it cannot provide any information on interaction strengths.

Q: Is it necessary to describe every *single* species when making a food web model? Or is it sometimes useful to group together similar species into "functional groups"?

This is another major issue of contention!

Nearly all food webs include some degree of aggregation, because it can be impossible to distinguish organisms at the species level. A widely accepted standard for aggregation is the *trophic species* concept. Any species that share exactly the same predators *and* exactly the same prey can be lumped together into the same trophic species[2,3]. The aggregation of a food web into trophic species usually affects less than 10% of the nodes (e.g., Dunne et al., 2002).

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[2] Interestingly, sometimes a single taxonomic species can be split into *several* trophic species (for example, larval versus adult stages of an aquatic insect, or roots versus leaves of a plant.) Polis (1991) emphasizes that age structure is an important and oft-neglected aspect of trophic interactions.

[3] The term "trophic species" is sometimes used less rigorously than this: e.g. Montoya and Solé (2003) define trophic species as those "sharing a *fraction* of prey and predators." However, it seems

However, aggregation usually goes much further than this. Species may be grouped into genera, families, or sometimes even broad functional groups like "phytoplankton." Due to ease of sampling, there is a tendency to describe top species (e.g. herons) and intermediate species (e.g. fish) at much higher taxonomic resolution than basal species (e.g. algae). Some food webs completely neglect to resolve basal species and microorganisms.

It has been shown that aggregation, especially if it is taxonomically uneven, can substantially modify key properties of a food web. For example, inappropriate aggregation can result in artificially high connectance (Dunne et al., 2004), spurious "scale-invariant" behavior of L/S and other quantities (Martinez and Dunne, 1998; Bersier et al., 1999), disappearance of compartments (Krause et al., 2003), and overestimation of omnivory (Dunne et al., 2002). See Polis (1991) for a critique of the distortions caused by aggregation in food webs.

Other authors have run analyses using both aggregated and non-aggregated versions of the same food webs (e.g. Sugihara et al., 1989; Montoya and Solé, 2003) and have concluded that key structural aspects of food webs are usually preserved even after moderate aggregation. However, such studies usually involve "equitable" aggregation, not biased aggregation such as failing to resolve basal species whilst carefully resolving top predators.

Despite these differences of opinion on the acceptable uses of aggregation, researchers generally agree that it is preferable to have data at the species level wherever possible, and that there is a great need for more empirical food-web data at high taxonomic resolution. REF() take this further and say "guilty until proven innocent."
I would tend to think that aggregation is only appropriate to the extent that *other species* also fail to distinguish between the aggregated species.

Note: Sometimes data from different food webs are lumped together. There is disagreement as to whether this is appropriate, because it may be incorrect to assume that published food webs represent a random sample from the universe of all food webs. (Bersier et al., 1999). And... (REF, I know I have another one)
Polis (1991) thinks that it is absurd to directly compare food webs from systems that are as different as "Arctic seas and toad carrion."
But, nevertheless, lumping is often done (e.g. Allesina and Bodin, 2005).

A novel approach was proposed by Wilhelm (2005), who suggested using "equal node webs" in which each node represents the same amount of biomass. He proposed this due to difficulty in identifying species. The approach hasn't so far caught on, though, but give it time...

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that departures from the strict definition may invite undue subjectivity: what "fraction" is large enough?

Q: Does causality in food webs ever flow up trophic levels – that is, do prey control their predators?

Yes, prey species do affect pred sp. Interaction coefficient in both directions. Usually the predator's effect on its prey is on the order of 100 times stronger than the prey's effect on its predator (Neutel et al., 2004). But there are many important exceptions to this rule.

(I think some FWs have directed links and others have undirected links – need to confirm)
See Q above on directionality of links.
It's remarkable how little description is devoted to this issue. It's as though the authors assume that everyone knows already.
The local rewiring algorithm of Gotelli (2001) uses directed links.
To calculate path length, undirected links are used (Dunne et al., 2002).

Q: What assumptions do food webs make about population dynamics? Are population densities, birth rates and death rates explicitly described?

First of all, most food web models are not dynamic, only topological.

Pimm (2002) says that many different assumptions can be made, and that the different assumptions often profoundly affect the model predictions. For example, in Lotka-Volterra systems, in which predators affect prey populations, the removal of a predator species will have a profound effect on the rest of the web. In (one-way) models, the removal of a predator species will have no effect.

Many (all?) of them do explicitly include population, birth and death rates, and other parameters such as the metabolic efficiency of species i consuming species j. (REF)

Q: How are detritivores / scavengers accounted for in food webs? Although detritivores don't directly prey upon other species, they are nonetheless directly dependent upon other species for their nutrition and survival.

(An extreme way of looking at this would be "What if species X individuals always followed around species Y individuals until the moment the Y individuals died, and then immediately ate them?" But I guess even in this case, species X isn't directly causing the death of species Y. Nevertheless, in food web models where predators don't affect the populations of their prey (see above), a scavenger would be indistinguishable from a predator.)

Sometimes "detritus" is counted as a "species." So are plants. So are phytoplankton. Argh!

Q: Do food web models assume that species evolve? If so, how is the direction of evolution predicted?

Evolution of species is not considered in food web models. (It's difficult enough just dealing with the present!) However, some food web models do consider *adaptation* of species' feeding behavior (e.g. Kondoh 2003a, 2006).

Of course, in the real world, species do evolve. Strauss et al. (2006) have reviewed the literature on evolution of native species in response to introduced species, and vice versa, concluding that it can happen to a significant extent even on an observable time scale. This suggests that it is fallacious to consider the characteristics of species in food web models as fixed. But, what's a poor ecologist to do?

Loeuille and Loreau (2005) created an evolutionary food web model that allowed species to evolve from other species, and found it to be a successful approach. This, they say, allows for elucidation of the mechanisms underlying the emergent parameters, rather than taking the parameters for granted.

Characteristics of real food webs

Note: For questions specific to food webs' network architecture, stability, or evolution, see the headings following this one.

Q: What structural parameters have been measured in real food webs, and what are some typical values of these parameters?

Note: The food web literature is somewhat inconsistent in the uses of variable names; I have tried to choose the variable names that are the most widespread.

$S \equiv$ Number of "species" in the food web. This can refer to taxonomic species, trophic species, functional groups, or any other level of aggregation; it simply means the number of nodes. Most published food webs have $10 < S < 200$, with a typical value being about 45.

$L \equiv$ Number of links in the food web. (This does not account for different weightings of the links). Links are usually undirected in food web models, despite the fact that trophic interactions have directionality in the real world.

$L/S = z \equiv$ Average number of links per species. Several different patterns have been proposed for this quantity: (**a**) it is roughly constant at $L/S \approx 2$ (the "link-species scaling law"; Cohen et al. 1990); (**b**) it ranges from 10-100 but is hugely underestimated due to lack of sampling effort (Polis, 1991)[4]; (**c**) it increases linearly with S and can be approximated as $L/S = 0.11 \times S$ (Martinez, 1992); (**d**) it increases non-linearly with S; specifically $L/S \approx S^{0.4}$

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[4] For example, a five-year study of the desert sand scorpion *Paruroctonus mesaensis* documented >100 different prey species, and failed to reach an asymptote after 2,000 person-hours of observation (Cohen 1978, cited in Polis 1991).

(Havens, 1992, who criticized the methods of Martinez); or (**e**) it should not be calculated, because the link density distributions of food webs are highly skewed (Aldana and Cruzel, 2003) and so a simple average is meaningless.

$L/S^2 = C \equiv$ Connectance (or "directed connectance"). This can be interpreted as "the fraction of the total *possible* links that actually exist," since the total number of possible links is S^2. C may be unrelated to S (the "constant connectance" hypothesis; e.g. Bersier et al., 1999) or may be negatively related, as $S \sim C^{-0.5}$ (Montoya and Solé, 2003). Empirical values of C range from about 0.01 to 0.3 (Martinez and Dunne, 1998). C may be systematically underestimated in empirical food webs for the same reason that L/S is underestimated: it is difficult to observe the full range of a species' feeding behavior under different conditions (Kondoh, 2003b).

d or $D \equiv$ Average number of links separating any two species in a food web. Also called "characteristic path length" and "average trophic distance." Williams et al. (2002) assert that typically $d \approx 2$; however, Polis (1991) disputes this as an artifact of poor taxonomic resolution (his Coachella Valley food web had $d = 7.3$.) $d \approx 2$ is close to the expectation for a random network, and much lower than expected for a "lattice" network. (ref?) *Also, does d increase as S increases?* In a scale-free network, d increases as $\log(n)$ where n is the number of nodes (Amaral et al., 2000). Dunne et al. (2002) state that path length is almost certainly shorter than random in FWs. So go with this unless you find a ref for the above...

Cl or $c \equiv$ Clustering coefficient. $\in [0, 1]$ Represents the fraction of nodes linked to a given node that are also linked directly to each other. In a random graph, Cl decreases as $1/S$. Comparing a food web to its random equivalent, the ratio Cl_{FW} / Cl_{rand} can be as high as ~5.0 (Montoya and Solé, 2002), but this is unimpressive compared to other types of networks, for example coauthorship networks, in which the ratio can exceed 14,000 (Dunne et al., 2002). Many authors believe that clustering in food webs is not significantly greater than random (Dunne et al. 2002; Stouffer et al., 2005).

$T \equiv$ % of species that are top predators (i.e., they have no predators themselves). This has been estimated as 0.06 (Havens, 1992, based on 50 pelagic webs), and as 0.01 (Martinez, 1991). Certainly it is very low, especially when allowing for parasitism and cannibalism.

$I \equiv$ % of species that are intermediate (i.e., they have both predators and prey). This has been estimated for marine food webs as 0.44 and 0.86 by Havens (1992) and Martinez (1991), respectively, and as 0.90 for the Coachella Valley desert food web (Polis, 1991). I may be systematically higher in large food webs and in marine food webs (Dunne et al., 2004).

$B \equiv$ % of species that are basal (i.e., they have no prey, so they must be autotrophs). Basal species tend to be highly aggregated in food webs, so B is often an underestimate. Havens (1992) estimated B as 0.50 in pelagic food webs, and Polis (1991) calculated $B = 0.10$ in Coachella Valley. Species-rich webs may have smaller B and larger I, on average (Martinez and Dunne,

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1998). It was formerly believed that *(T+I)/B*, the ratio of predator to prey species, was constant (e.g. Briand and Cohen, 1984), but Wilson (1996) refuted this supposed constancy.

$\gamma \equiv$ Scaling parameter that describes the decay of the link density distribution: the probability *P(k)* that a node will have *k* links is described as $P(k) \sim k^{-\gamma}$. This functional form does not usually apply to food webs, so the parameter γ is rarely calculated. (One exception is Montoya and Solé (2002), who calculated γ as 0.94, 1.04, and 1.13 for three different food webs). For other types of networks, $\gamma \approx 2.1$ to 4.0 (Barabási and Albert, 1999). Stability of scale-free networks tends to be enhanced when $\gamma > 2.0$ (Aldana and Cluzel, 2003).

Q: Do parasitism and parasite avoidance play a role in shaping food web structure?

Probably... haven't read too much about this. See earlier question about "what kinds of trophic interactions are included."
Cite Marcogliese and Cone (1997).

"Incorporation of parasites in food webs can substantially alter basic web properties, including connectance, chain length, and proportions of top and basal species." (Marcogliese and Cone, 1997).

little effort has been made to address the role of parasitism in FWs (M & C, 1997).

Most sp. are infected with parasites, and <50% the animals sp. may be parasitic at some point in their life cycle (!!!) (Price, 1980)

Parasites can be thought of as a type of top predator, but they obviously differ in many ways from what we usually think of as top predators. For example, they do not follow the expected body-size feeding hierarchy, in which large species prey upon smaller species (M&C 1997).

For example: in Norwegian coastal waters, the populations of kelp-eating sea urchins are kept in check by the parasitic nematode *Echinomermella matsi*, thus allowing kelp forests to persist. Nematode infestation is density-dependent and thus the ecosystem experiences a (stable limit cycle) of urchin population fluctuations. (Hagen, 1992) Could the system be meaningfully described without this parasite? What do you think?

** In fact, examples like this suggest that food webs' whole focus on *energy transfer* is fundamentally limited, because pathogens and parasites can regulate community structure without consuming a significant amount of energy. (Marcogliese and Cone, 1997)

Q: In real food webs, is there a consistently small ratio of generalists to specialists (i.e. are generalists uncommon)? If so, how is this pattern explained by theory?

ZM: The scale-freeness of food-webs suggests that ecologies can support only a few generalists, but lots of lean mean machines. So why can't there be lots of generalists?

Extreme generalists (lots of links) are even more uncommon that predicted by scale-free theory.
Well, it's all relative. If you define a "generalist" as a species with far more links than average, then of course generalists will be rare.

Note that marine food webs are somewhat different, seemingly. High *L/S*. (see Q on marine food webs for refs)

The proportion of specialists tends to increase over time as community assembly proceeds (Belyea and Lancaster, 1999).

Q: Are omnivores (species that feed at more than one trophic level) rare in food webs? If so, what is the explanation for this? Note that generalists ≠ omnivores.)

There can be! Some food webs have over half omnivores! In general, the % of omnivores increases with the total # of species (REF?).

Wait, remember that generalists are not omnivores.

Omnivory is a common phenomenon and one that is important in nature (Vandermeer, 2006). Omnivory is not rare, although people used to think it was (Polis, 1991). In fact, it seems to be the "norm" in Coachella Valley.

(By definition, is anything with a *fractional* trophic level an omnivore?)
Hmmm.
Vandermeer (2006) considers only closed-loop omnivores, that is, those that eat something that one of their prey also eats.

there are different ways in which omnivores can evolve (Vandermeer, 2006). Hard to generalize about the phenomenon.

Milo et al. (2002), in their study of network motifs, showed that the "three-node feed-forward loop" motif (Figure 2) was relatively uncommon in food webs (as compared to the null expectation or to other types of networks). They interpreted this to mean that there must be some kind of selection against omnivory (in which X is the omnivorous predator).   But I don't know if I agree with that interpretation.
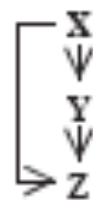
Figure 2. Feed-forward loop (from Milo et al., 2002).

Actually, Bascompte and Melián (2005) extended the analysis of Milo et al. (2002) to a greater number of food webs, and larger food webs. They found that in some webs the omnivory module was overrepresented, in some cases underrepresented, and in other cases it

conformed to the null expectation. This helps to resolve the debate between Polis (1991) who emphasized the prevalence of omnivory, and Williams and Martinez (2004b) who downplayed it.

Note that the prevalence of omnivory *modules* is not exactly the same as the prevalence of *omnivores*. One omnivorous species can be involved in many modules.

The prevalence of omnivores may be overestimated if taxonomic aggregation is excessive (Dunne et al., 2002).

Q: Do aquatic food webs show consistent structural differences from terrestrial food webs?

Yes, perhaps. Link (2002) claimed that L/S (link density) and L/S^2 (connectance) are much higher in marine food webs than in terrestrial and freshwater food webs. That is to say, "In marine food webs, everything eats everything else." Link claimed that this represents a fundamental structural difference between marine food webs and other types of food webs. These differences might be due to the high proportion of filter-feeders in marine communities (Havens, 1997).

Dunne et al. (2004) to some extent corroborated this opinion, but with the caveat that parameters of marine food webs do tend to fall within the *range* of values reported for other food webs.   They examined three highly resolved marine food webs and noticed high values of L/S, L/S^2, *I* (% intermediate taxa), *Omn* (% omnivorous taxa), and *Can* (% cannibalistic taxa). However, they point out that the niche model (Williams and Martinez, 2000) can successfully predict many properties of both marine and non-marine food webs, indicating a fundamental similarity of structure.

Basal species tend to be very poorly resolved in marine food webs, and easy-to-measure species such as large fish seem to be overrepresented. So the apparently unique characteristics of marine food webs may be, at least in part, an artifact of the imperfect data (Dunne et al., 2004). I myself also wonder if the non-distinct boundaries of marine food webs are partly responsible for any differences they show from other food webs.

Q*: Are there generalizable differences within aquatic habitats (e.g. a pond vs. the open ocean) or within terrestrial habitats (e.g. a tropical rainforest vs. an alpine fellfield)?

Currently, the number of thoroughly described empirical food webs is insufficient to answer this question. There are several hundred food webs described in the literature (e.g. Cohen et al., 1990; Martinez and Dunne, 1998), but only about twenty of them have sufficiently high taxonomic resolution to be useful for rigorous quantitative analysis (e.g. Dunne et al. 2004; Stouffer et al., 2005). These food webs are from a variety of habitats such as marine, estuary, freshwater pond, freshwater stream, island, grassland, and so forth. There are too few examples of any particular habitat to draw conclusions about that habitat.

Network architecture of food webs

Q*:* How do food webs tend to differ from other types of networks that have been studied?

smaller, also energy flow rather than info processing

It is difficult to figure out the genesis of a network simply by looking at its end state. Therefore, new topological measures are needed that might provide additional insight into network genesis (Guimarães et al., 2005), especially for networks such as food webs whose genesis cannot be directly observed.

Food webs have very few "motifs" in common with other networks (Milo et al., 2005). (Give examples?) None in common with WWW, only one in common with neuronal networks. That's because...

Most networks that have been studied are large, with thousands or even millions of nodes (Barabási and Albert, 1999), whereas most food webs are described with 200 nodes at most. This in itself makes it difficult to compare food webs with other networks.

Despite recent efforts to come up with general rules, networks in the real world show much variety in their topological properties (Aldana et al., 2000, and other REFs).

Figure X (Figure 1 from Garlaschelli et al., 2003). Transformation of a food web (a) into a minimal spanning tree (b). Species are arranged in trophic levels; the black node represents the abiotic environment. See the authors' paper for details.

Garlaschelli et al. (2003) suggested that food webs be thought of as *transportation* networks, such as watersheds or vascular systems. (Food webs are transporting energy across trophic levels). There exists well-developed theory to determine the maximal transport efficiency in these systems; however, the theory does not allow loops, so Garlaschelli et al. reduced the food web to a "minimal spanning tree" based on shortest path lengths (Figure X). In so doing, they found that food webs can be described as self-similar trees with an efficiency exponent of $\eta = 1.13$. (1 is maximally efficient, and 2 is maximally inefficient.) They found that this exponent η was remarkably consistent across different webs, not related to web size or connectance. Presumably this is due to an optimization process in ecological communities (the only reason trophic levels exist at all is b/c of competition; they're necessarily inefficient).

But, van Veen and Murrell (2005) refuted this seemingly interesting result, showing that, given a realistic number of trophic levels, Garlaschelli et al's method of constructing a minimum spanning tree would inevitably lead to $\eta \approx 1.13$.

Allesina and Bodini (2005) also published a refutation, saying that minimal spanning trees are an unacceptable simplification, as they reduce everything to its lowest trophic level.
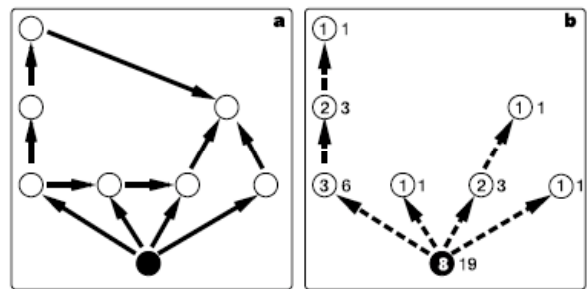
They considered food webs as directed acyclic graphs (DAGs), the only modification from a real food web is the removal of loops. Their calculated values of η indicated systems that were far from optimal transport efficiency. That is to be expected, due to the presence of various biological interactions such as competition.

Q: Can food webs be thought of as information-processing systems, like neural networks?

ZM: It would be neat if a gestalt shift could be made, and the food web could be seen as computing some function, in the same way that a gas released in an evacuated cylinder tries to fill the cylinder, even though the molecules don't care.
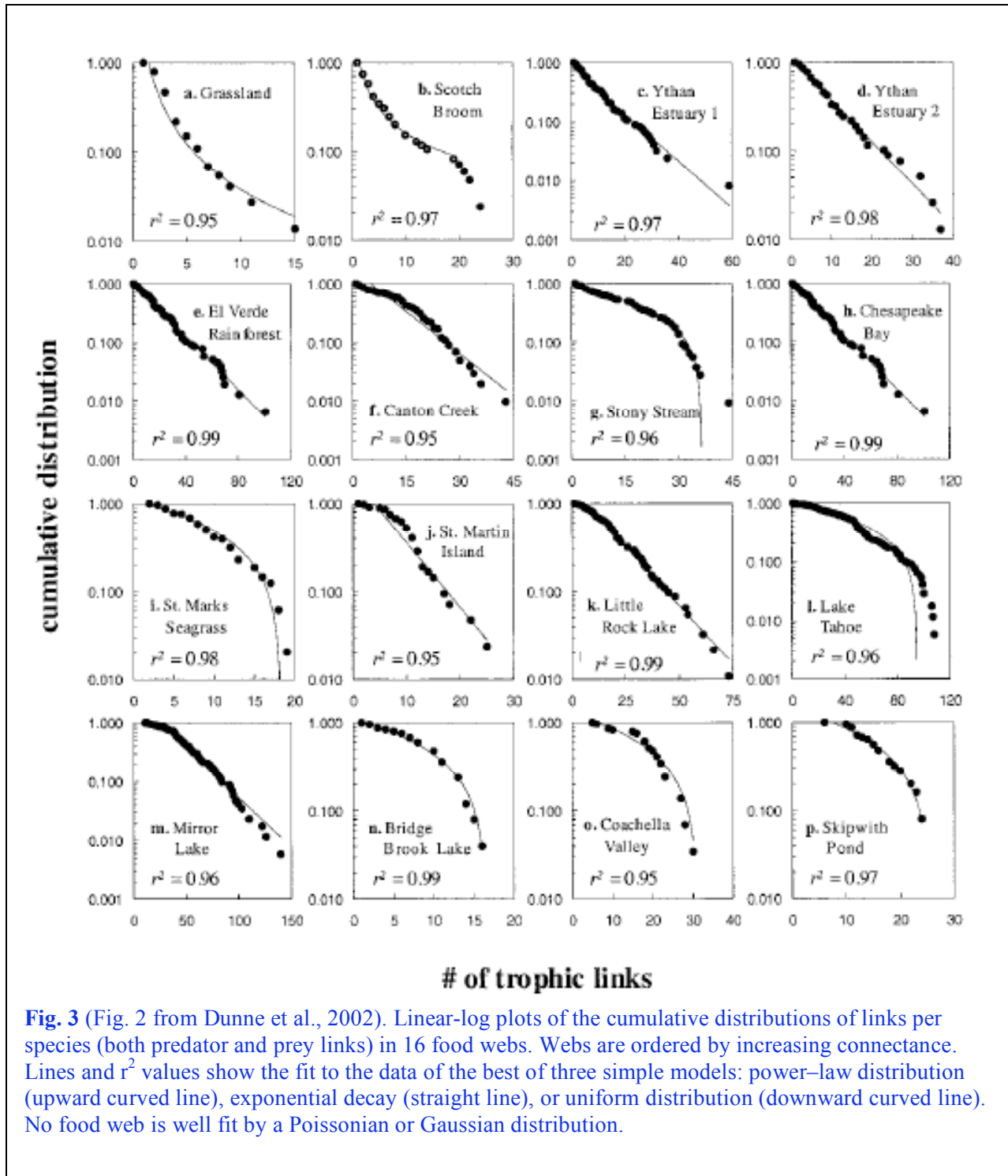
So far I haven't come across any research that compares trophic networks to computational networks. To the contrary, Milo et al. (2005) postulate that because food webs represent *energy flows*, not information processing, it is reasonable to expect their network structure to be fundamentally different from neural networks or the World Wide Web.

(REF) studied various kinds of networks ranging from electric power grids to friendship circles. They found that....

Q*: Do food webs show scale-free architecture, that is, does the link density decay as a power law?

Not exactly.

It seems that food webs are not, as a rule, scale-free (Dunne et al. 2002; Garlaschelli et al.,

Fig. 3 (Fig. 2 from Dunne et al., 2002). Linear-log plots of the cumulative distributions of links per species (both predator and prey links) in 16 food webs. Webs are ordered by increasing connectance. Lines and r^2 values show the fit to the data of the best of three simple models: power–law distribution (upward curved line), exponential decay (straight line), or uniform distribution (downward curved line). No food web is well fit by a Poissonian or Gaussian distribution.

2003; Williams et al., 2004; Guimarães et al. 2005; Stouffer et al., 2005). Most food webs are more homogenous in their link structure than the scale-free model would predict (i.e., food webs don't have as many highly-linked nodes as predicted). Instead, food webs tend to fall into the category of "broad-scale" networks (usually, the number of connections per node *initially* decays as a power law, but the tail is truncated by an exponential decay; Guimarães et al., 2005). This may be due to the small size of food webs relative to the scale-free networks that have been studied; it may be due to their mechanisms of network formation (namely, a lack of preferential attachment, and restrictions on forming new links); or it may be due to the presence of an initial "core" of links that follows different rules.

Note that this usage of the term "scale-free" is not synonymous with "scale-invariant." The latter, as applied to food webs, means "does not vary across food webs as a function of S (the number of species in the food web)." For some examples of which food web parameters are scale-invariant, see the list beginning on page 12.

Early assertions of scale-freeness are largely a result of limited data (Dunne et al., 2002). Of the 16 high-resolution food webs examined by Dunne et al. (2002), only one showed a scale-free degree distribution, whereas eight showed an exponential distribution and six showed a uniform distribution. Stouffer et al. (2005) agreed that the exponential distribution seems to be the most common type of distribution for food webs.

(Montoya and Solé, 2002) studied three food webs (Ythan Estuary, Silwood grassland, and Little Rock Lake) and reported that the the first two followed a power-law decay of link density distribution, with $\gamma = 0.94$ and $\gamma = 1.13$. They explained the lack of fit for the third food web, and other food webs in general, as an artifact of poor taxonomic resolution.

Dunne et al. (2002) criticize Montoya and Solé (2002) for looking at only three food webs, using absolute rather than cumulative degree distributions, and dismissing a contradictory result as an artifact.

No reason to think that food webs would have the same assembly processes, and therefore the same architecture, as other types of networks (Dunne et al., 2002).

The tail of the link distribution may contain information about how the network formed (Guimarães et al., 2005).

There are three types of network: single-scale (link density distribution decay is Gaussian), broad-scale (decay is exponential), and scale-free (decay is power-law). (Amaral et al., 2000). (and other REFs).
Scale-free networks can be created by preferential attachment. But this doesn't apply when nodes "age" or have a "cost" of adding links. (Amaral et al., 2000); that can discuss .

Some FWs are scale free, but most are not if they exceed relatively low levels of connectance. (Dunne et al., 2002).

It is agreed, however, that the degree distributions of food webs certainly are *not random* (Dunne et al., 2002). Smaller food webs seem to be closer to random (Montoya and Solé, 2003), but even those do not have homogenous degree distribution.

Important to use cumulative, rather than absolute, degree distributions for small networks, because otherwise the "bins" will be too small and the data will be too noisy (Dunne et al., 2002).

From an e-mail to ZM, 7/23/06:
"So as a small food web accumulates more species, and thus grows bigger, and thus (as described above) each individual species accumulates a larger number of links on average... that doesn't necessarily disrupt the scale-freeness, it just changes the exponent thereof. Right?" *Umm... actually, that doesn't sound right to me.*

Q*:* Do food webs show small-world architecture, that is, do neighbors of a given node also tend to be connected to each other?

Some say yes, some say no.
Again, early assertions of small-worldness are largely a result of limited data (Dunne et al., 2002).
Food webs are not scale-free (Garlaschelli et al., 2003).

Small-world networks (as defined by Strogatz, 2001) show an exponential decay of degree distribution (Barabási and Albert, 1999).

Scale-free networks are necessarily small-world networks, but not vice-versa (Amaral et al., 2000).

Small-world structure can contribute to network homeostasis (Montoya and Solé, 2002).

Q: Is there evidence of compartmentalization of food webs?

Disagreement abounds on this issue. Melián and Bascompte (2004) studied 12 empirical food webs and found subwebs in all of them: that is, the "densest subweb" their algorithm could find was always significantly *denser* in the *real* food web than in its random equivalent. Similarly, Krause et al. (2003) presented a detailed study of a Chesapeake Bay food web and found that it contained two clearly defined subwebs: benthic organisms and pelagic organisms. Other authors disagree that compartmentalization is a characteristic of food webs (REF).

If there is significant compartmentalization, that would imply that C (connectance) is not an adequate measure of food web structure. Melián and Bascompte found that C of the densest subweb does not depend on the size of the subweb, whereas C of the whole web does depend on the size of the web (note that this conflicts with Martinez, 1992). This can't be adequately explained by any null model except for the local rewiring algorithm, which isn't exactly a null model.

How does this relate to the definition of food webs as "small-world" networks? Are they small-world networks? (REF)

Various methods exist for determining and quantifying compartmentalization (contrast the *k*-subweb approach of Melián and Bascompte with the KliqueFinder algorithm of Krause et al. with the "uplinked mutual dyad" motif of Milo et al. (2002).) (well uh... maybe not that last one)

In small-world networks the average path length increases as $\log(n)$, where n is the number of nodes (in food webs, S). Clustering coefficients are much higher than expected in small-world networks. (Amaral et al., 2000).

Scale-free networks are necessarily small-world, but small-world networks are not necessarily scale-free (Amaral et al., 2000).

One unanswered compartmentalization problem is: do the "loner" species (those not very closely connected; on the periphery) tend to fall into any particular category?

Stability of food webs

Q: How is stability defined with respect to food webs? Does it mean resistance to change, resilience from change, or both?

General note: Both dynamic stability and topologic stability are important considerations for food webs (Melián and Bascompte (2004) . I don't understand what "topologic stability" means, though.

"Population persistence in large and complex natural food webs remains a long-standing dilemma in ecology." (Brose et al., 2003)

This is a matter of some confusion. There is no single agreed-upon measure of stability.

Brose et al. (2003) define "community robustness" as the fraction of species within a network that persist (presumably as t goes to infinity).

The concept of stability may or may not include the idea of an outside perturbation.

Montoya and Solé (2003) define stability as the speed with which the system recovers after a disturbance.

In the general ecology literature, "stability" usually has connotations of both resistance and resilience. The mathematical definition we learned of "stability" in ER 202 was something

along the lines of "the system will, eventually, return to its initial state after a perturbation of arbitrary size." (Virtually all systems are stable within *certain* limits, that is, if the perturbation does not exceed ε.)

This mathematical definition only includes the concept of resilience (returning to an initial state), and ignores resistance. It sets no limit on how wildly the state of the system can fluctuate *before* it returns to the initial state, nor how long the system can take to regain its initial state (the answer is usually ∞, of course.) I'm not sure if stability for food webs is, or should be, defined similarly...

ZM: Other notions come to mind. For instance, meta-stable states. Maybe the system is stable in terms of always being in some region of phase space - perturb it and it moves, and possibly doesn't ever come back to its original position, but stays in its phase space region.

Dunne et al. (2004) define "robustness" as the fraction of species that must be removed to cause the loss of 50% of the total species. Maximum robustness, therefore, is 0.5 (there are no "secondary extinctions").

(There's much more to say on this... it's not at all complete.)

"Stability" of ecosystem processes (for example, nutrient cycling) is not necessarily the same as stability of any particular species or even group of species (Tilman, 1996 – don't have REF). Therefore, a food web could be "unstable" in that its species are fluctuating or disappearing, but the ecosystem could still work just fine overall.

The most strictly mathematical definition, but not a very useful one, is the "Lyapunov point-set stability." A more general definition is "tendency to persist over time," or "tendency to recover from disturbance." (Vandermeer, 2006)

Aldana and Cluzel (2003) define "robustness" as the "ability... to perform a sequence of biological tasks in the presence of perturbations." They were referring to intracellular processing networks, not food webs, but the principle is perhaps the same.

Neubert et al. (2004) define a system as stable if "small perturbations to the equilibrium eventually decay," and define resilience as the asymptotic rate of decay. He also introduced a term called "reactivity," which means "how much worse things get before they get better" – i.e., after the initial disturbance, the system tends to continue to move *away* from equilibrium for awhile. Mathematically, they show that most dynamic food web models with *density-independent* mortality rates tend to be reactive. Density-dependence, on the other hand, reduces reactivity. This is an example of a potentially important non-trophic effect that is usually omitted from food web models.

Q: What types of food webs tend to be most stable in real life? Does this align with what is predicted and/or observed for other types of networks?

The ongoing complexity / stability debate is still unresolved. (For a mediocre review, see Worm and Duffy, 2003).

There haven't been many empirical studies of food web stability; it's been mostly model simulations. The main question everyone seems to want to answer is "How can (all) food webs be so stable when we have so much trouble making our models turn out stable?"

The niche model and the cascade model generally predict that, all other things being equal, increasing connectance should decrease robustness. (Brose et al., 2003). Here, robustntess is defined as "the fraction of species that persist" after a long time period.

One can see why that would be so: disturbances could more easily propagate through the web. But, on the other hand, being more connected may give you more "options" if one of your prey species goes extinct.

(I really don't understand "topological stability," that is, the stability of static food web models, at all... how can you model extinctions without dynamics?)

Compartmentalization in food webs should, theoretically, make them more resistant to disturbance, as the effects of disturbance should be mainly limited to one compartment (Krause et al., 2003). (Compare this to theory on small-world networks).

Neutel et al. (2002) propose that weak interactions in long "trophic loops" are crucial for the stability of food webs. They attribute these weak interactions to both the pyramidal structure of biomass at different trophic levels, and to the presence of omnivores. I found their paper tricky to understand... perhaps I should read it again.

Neutel et al. (2002) introduced a new idea called "loop weight," the geometric mean of the absolute values of the interaction strengths within a closed chain of trophic links. (They used directed links, considering a Jacobian matrix of interaction strengths for each species pair. Hence any two or more species would form a loop: A ⇆ B.)

They demonstrated mathematically that stability was enhanced by long trophic loops that were made up mostly of weak links and a few strong links. In accordance with this, they found that maximum loop weight was much lower in *real* community matrices than in randomized ones. They attributed this to (1) omnivores, who feed at many different levels and thus "spread their weights around," and (2) pyramidal biomass structures, which encourage feeding at lower trophic levels simply because that's "easier" (hence weakening the links to higher trophic levels).

Community tends to be stable when the intra-specific interactions tend to be strong compared to the inter-specific interactions (Neutel et al., 2002).

As far as *empirical* studies go – that is, resistance of real ecosystems to disturbance – attention has focused mostly on the basal species of ecosystems (Worm and Duffy, 2002) and not given enough consideration to predator-prey interactions.

Need to say something about deleting heavily connected nodes versus random nodes. (REF)

Omnivory can be either stabilizing or destabilizing depending on the conditions (Vandermeer, 2006). In this simulation, a stable system was sometimes destabilized by an omnivore, and vice versa. Intermediate values of omnivory seemed to be the most stable. He didn't use parameters that had much to do with biological reality, though.

Dunne et al. (2004) found that, in marine food webs, higher connectance (L/S^2) seemed to confer robustness to species loss, even though theory might have predicted the opposite.

Food webs with skewed degree distributions (ie power-law or exponential decay) tend to be robust to the removal of most species, but fragile when the highly-connected species are removed. By contrast, food webs with Poissonian degree distributions are fragile to the removal of *any* species. (Montoya and Solé, 2003).

Q: In empirical and/or theoretical food webs, what generalizations can be made about (1) nestedness / fractal behavior; (2) density of connections; (3) interaction strength? (Of course this may end up being several separate questions if I get enough material.)

These answers may end up overlapping with the answer to "What makes a food web stable"?

ZM: I don't know what a theoretical food web is. Well, any graph I want to call a food web, I suppose, but hard to say anything sensible about those.

Q: Is there any *a priori* reason to expect scale-freeness, or complexity, to enhance stability?

Uhhh...
Scale-freeness, yes. See Aldana and Cluzel (2003). Food webs may be scale-free *enough* to see *some* of those benefits, but it seems unlikely, since (as far as I know) there are few published examples of food webs that show scale-free behavior at all, and (as far as I know) none that calculate a γ greater than 2.

Complexity... well, the jury's still out (Worm and Duffy, 2003). The debate is between "portfolio theory," which (as applied to ecology) suggests that diverse food sources make a species resistant to environmental fluctuations, versus May (1974) who created food web models in which increasing trophic complexity increased the probability of destabilizing positive feedbacks (Martinez and Dunne, 1998).

Kondoh (2003a, 2006) published the controversial idea that a complexity/stability relationship emerges if one assumes *adaptive foraging*. That is, if a predator focuses its foraging efforts on "easy prey" in order to maximize energy gain and minimize effort, it will tend to shift *away* from prey species when their population densities get low, thus making extinctions much less likely.   Yay! I explained that better than they did! :-)

25

Dunne et al. (2004) did not find that robustness increased with *S*.
High connectance means (usually) high robustness to species loss, because everything has alternate prey sources.

Short path length would tend to *decrease* stability, because everything effects everything else. But small-world networks get around that problem by compartmentalization. (REF?)

Evolution of food webs

Q: How do current food web models account for change of food webs over time?

They don't, usually.

Most of the community assembly literature bypasses the issue of trophic structure (Montoya and Solé, 2003) and focuses instead on competition.

Loeuille and Loreau (2005) were able to create a simple evolutionary food web model, based on body size, that recreated many of the results found in the community assembly literature. E.g. after enough time has passed, basic structure remains even though species composition may change; and invasability decreases over time.

(Montoya and Solé, 2003) created a simple dynamic assembly model but failed to reproduce key properties of food webs. (Need to look at their Methods.) based on Pimm, 1987.

Q: What sorts of processes can lead to a change in food web structure?

- adjacent food webs interacting? (ZM) (yes, they do interact – examples?)
- Evolution of new species from within
- Immigration of species from outside
- Extinction of species, either through biotic or abiotic factors
(I would say "immigration" just to be parallel, but that's the same as local extinction)

Q: What empirical evidence do we have (direct or indirect) of changes in food webs over time?

There is very little empirical data on this question. Three different possible approaches come to mind:
- Paleontological evidence (e.g. Crame, 1990)
- Recent introductions of species to existing food webs
- Comparison of similar food webs that have diverged allopatrically[5]
(assuming we can't just directly observe changes)

---

[5] Thanks to Rex Kerr for this suggestion.

It would help to understand and explain the network structure of food webs if we could actually "see" how the networks evolved, that is, how new nodes (species) attached themselves. This point is made by Montoya and Solé (2002) although they don't say anything about *how* to do it.

Presence of scale-freeness or other topological properties may tell us how networks evolve (Barabási and Albert, 1999).

The best we've been able to do for paleo food webs is to estimate different prevalences of functional groups (e.g. predators, suspension feeders, and detritus feeders), roughly estimate stock and flux between each of these compartments, and fill in for the organisms we know must not have fossilized. (Crame, 1990). The biased incompleteness of the fossil record is a big problem here, though we can try to compensate. Estimating energy *flow*, as opposed to just biomass, is particularly difficult. It's difficult to guess what the prey of extinct predators must have been.

Q: When a new species enters a food web, what attachment rules does it follow?

I think the only direct evidence we have for that is for recently human-introduced species, and it's not necessarily safe to assume that those are representative of species in general.

But, the following studies have been done...

And indirect assessments have also been made, for example...
(take an abstract model, give it some rules, try to replicate real FW structure, and then conclude, "Well, I guess real FWs must follow these attachment rules as well.)

Did a reasonably thorough literature search on this and found essentially nothing, altohough maybe my search strategies were not ideal.

Q: What tends to happen when exotic species are introduced into a food web? (And is this at all analogous to a new species evolving?)

I know there is quite a bit of empirical work on this [*oh yeah?*], but I don't know about the theory...

Note: Do not confuse *introduced* species (that is, any species that comes in from the outside) with *invasive* species (that is, introduced species with certain characteristics that allow them to proliferate aggressively).

Note also: Some authors *do* use the above two terms interchangeably.

See Strauss et al. (2006).

Follow-up Q: **Do invasive species tend to have different characteristics in a food web than do native, non-invasive species? I.e. do invasives tend to have more links or fewer links? Stronger links or weaker links?**

Perhaps this is straying too far from the general into the particular.

ZM: Oh, I don't think so at all. In so far as the immediate goal is to find a good theory explaining the scale-free topology of food-webs. If invasive species have unusual connective properties, that would be of great interest. (see Strauss et al. 2006)

Researchers seem to agree that this is an important question (REFs) but the only specific things I've read about it is that it's hard to answer. Takes place on a time scale too slow to measure.

Cite Strauss (2006). Wish I had a better ref for that.

Q: Is a food web itself a unit of evolution?

I am really not sure. No one else seems to be, either. Aldana and Cluzel (2003) mention natural selection as a possibility for networks in general, but they do not mention food webs.

Q: How do food webs come into existence – that is, how are they able to assemble themselves from nothing? Does the order of introduction of species matter?

Yes, it most certainly does! This is the place to review the community assembly literature.

ZM: Take a given food web. Have all the species involved been present and co-evolving since time out of mind? Have some been plopped down recently, while others have been hanging around and co-evolving for a long time? Is there any regularity in this? Is there a relationship between how recently a species entered a food web and its connectivity? (This seems a promising approach to scale freeness.)

(I haven't read anything about this yet.)

Q: Is a newly emerging island, or some other type of primary succession, a good empirical example of food web assembly? Or, in those cases, would we simply expect neighboring food webs to reassemble themselves in the newly available habitat?

AK: Should look into work on paleo food webs. This is one of Jennifer Dunne's current areas of research.

Guimaraes et al. (2005) describe how the initial core of a network may differ from its more recently added nodes. But they seemed to imply that it was not possible to examine these dynamics for food webs, because of the time scales involved. Need more refs on this.

Q: What happens when two food webs collide?

We could consider either a dynamic situation (i.e. one ecosystem literally crashing into another) or a static situation (e.g. the intermediate type of food web that might be found at the boundary between a forest and a grassland). Certain aspects of food web collision might be generalizable, whether it's an old dead tree falling down on the forest floor, or the subcontinent of India ramming into Asia. In any case, this question is meant to elucidate the previous question, about the genesis of food webs.

Didn't read any papers on this...

Q: Is there any sense in which food webs (or communities, or ecosystems) can be thought of as individuals undergoing natural selection? I.e., there are multiple types of species assemblages that *could* persist in a given abiotic environment, and it's a sort of competition that determines which one actually *will* persist?

And is the analogy of identical islands joined by intermittent land bridges a useful one?

Aldana and Cluzel (2003) suggest that it *does* make sense to consider "natural selection" as a force shaping network structure; specifically, they postulate that the prevalence of scale-free networks in nature can be explained by the fact that those networks tend to be robust to perturbations. This is the only reference in which I have encountered such a postulation. But follow-up is called for.

AK: This is starting to sound rather like the Gaia hypothesis.

ZM: [dismisses the Gaia hypothesis], but I'm in favor of finding higher level descriptions, if they can be correctly grounded out in the physics of their substrate.

Unresolved questions in food web research

Q: What are the general rules for community assembly and community disassembly?

The latter is called for by Worm and Duffy (2003).

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