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SMALL NETWORKS BUT NOT SMALL WORLDS: UNIQUE ASPECTS OF FOOD WEB STRUCTURE

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ABSTRACT:

Contrary to prior reports, we find that a set of 16 food webs, with 25 to 172 nodes, from a variety of aquatic and terrestrial ecosystems, generally display neither “small-world” nor “scale-free” topological properties. The food webs do display relatively short characteristic path lengths consistent with small-world topology. However, most food webs display less clustering than that expected in small-world networks, which appears related to the small size of food webs. The ratio of observed to random clustering coefficients across biological and non-biological networks increases linearly with network size over 7 orders of magnitude ($r^2 = 0.90$). A 1:1 clustering ratio occurs in networks with ~ 40 nodes. Most food webs display single-scale exponential or uniform degree distributions rather than the scale-free, power-law distributions previously reported for food webs and many other networks. Uniform degree distributions have not been reported previously for real-world networks. The failure to observe scale-free topology in most food webs appears related to the relatively small size, high connectance, and differences in the assembly of food webs compared to other real-world networks.

I. INTRODUCTION

Food webs, which depict networks of trophic relationships in ecosystems, provide complex yet tractable depictions of biodiversity, species interactions, and ecosystem structure and function. Although food web studies have long been central to ecological research (May 1986, Pimm et al. 1991, Levin 1992), there has been controversy over whether there are regularities in food web structure worth explaining (e.g., Paine 1988). Early analyses of topological properties of empirical food webs emerged from research on ecological diversity-stability relationships (e.g., MacArthur 1955, May 1973) and typically employed low resolution, species-poor ($S < 20$) depictions of food webs (e.g., Rejmanek and Stary 1979, Cohen and Briand 1984). Dramatic improvements in data (e.g., Warren 1989, Winemiller 1990, Martinez 1991) led to the successful description and modeling of general food-web properties among ecosystems (Williams and Martinez 2000), including how food-web properties vary with species richness, resolution, and sampling effort (e.g., Martinez 1993, 1994, Martinez et al. 1999).

Research on food web structure is one example of a wide range of scientific investigations of “real-world” network topology (Strogatz 2001). In particular, complex systems research across many disciplines has resulted in renewed interest in the study of “small-world” network topology (Watts and Strogatz 1998) inspired by the “six degrees of separation” sociology experiment by Milgram (1967). Most real-world networks have the two required small-world characteristics: (i) high clustering compared to a random graph, with neighbors of a node much more likely to be connected to each other than in a random graph, and (ii) small path length compared to a regular lattice, with the average shortest path length (“characteristic path length”) among all pairs of nodes increasing logarithmically with the number of nodes, similar to what is seen in random graphs (Watts and Strogatz 1998). Types of networks examined for these topological properties include social, technological, economic,

and biological networks (see Strogatz 2001, Albert and Barabási 2002 for reviews).

Researchers have explicitly examined a few food webs for small-world properties. A set of four food webs display greater clustering than in random webs and short path lengths (Montoya and Solé 2001) and an overlapping set of seven food webs display short path lengths which are slightly, but significantly, longer than path lengths of random food webs (Williams et al. 2001). Earlier research using low-quality (i.e., poorly resolved, highly aggregated, low diversity) food-web data concluded that path lengths are short but speculated they would increase with greater species richness (Schoener 1989), contrary to recent findings that path lengths decrease with increasing species richness (Williams et al. 2001).

A great deal of attention has been placed on the power-law, or “scale-free” distribution of node degrees of many small-world networks (Barabási and Albert 1999). Real-world networks display degree distributions that deviate from a Poisson distribution found for simple random graph models (Erdos and Renyi 1960, Bollobas 1985). Many networks including the WWW, Internet domains and routers, scientific co-authors and citations, metabolic and protein networks, and phone-call networks display a scale-free degree distribution, with power-law exponents ranging from ~ 1 to 2.5 (Albert and Barabási 2002). Also, Montoya and Solé (2001) report scale-free degree distributions with an exponent ~ 1 for three of four food webs they examined. However, real-world networks can display other types of degree distributions, including “broad-scale” distributions that show a power-law regime with a sharp cut-off in the tail (e.g., movie-actor collaborations) and “single-scale” distributions with fast-decaying tails including exponential (e.g., *Caenorhabditis elegans* neural network) and Gaussian (e.g., acquaintances among a Mormon social group) distributions (Amaral et al. 2000).

Using a set of 16 high-quality food webs from a variety of ecosystems, we develop the most comprehensive picture to date of whether food webs display small-world and scale-free structure (Montoya and Solé 2001), similar to topology of many other real-world

networks (Albert and Barabási 2002). We briefly discuss some potential ecological implications of observed food web network structure.

II. METHODS

The 16 food webs studied, two of which are variants of the same web, represent a wide range of species number, linkage densities, taxa, and habitat types (Table 1). There are five lakes or ponds, two streams, three estuaries, and five terrestrial ecosystems (temperate, desert, sub-tropical) represented. The food webs are described in more detail in Dunne et al. (2002) and in their individual references (Table 1). Food webs consist of L directed trophic links between S nodes or “trophic species.” Trophic species, functional groups of taxa that share the same set of predators and prey within a food web, are a widely accepted convention in structural food-web studies that reduce methodological biases related to uneven resolution of taxa within and among food webs (Williams and Martinez 2000). Trophic species webs are constructed by aggregating taxa from the original “taxonomic food webs” into trophic species. Taxonomic to trophic species aggregation occurs for <10% of nodes in nine of the food webs studied (Table 2).

We measured three properties central to recent network topology research for the 16 food webs: 1) characteristic path length (D), the average shortest path length between all pairs of species (Williams et al. 2001), 2) clustering coefficient (Cl), the average fraction of pairs of species one link away from a species that are also linked to each other (Watts and Strogatz 1998), and 3) cumulative degree distribution, the fraction of trophic species $P(k)$ that have k or more trophic links (both predator and prey links). We treated trophic links as undirected when calculating path length and clustering because effects can propagate through the web in either direction, through changes to both predator and prey species (Williams et al. 2001). For 100 random webs with the same C

and S as each empirical web, we also calculated mean D and Cl . We rejected random webs that had nodes or groups of nodes disconnected from the main web, since our empirical data lacks disconnected sub-webs or species.

III. RESULTS

The 16 food webs range in size from 25 to 172 trophic species, connectance (links/species²) from 0.026 to 0.315, and links per species from 1.59 to 25.13 (Table 2). The average connectance over all 16 webs is 0.11 (SD = 0.09), similar to mean connectance values reported for other reliable sets of community food webs (Martinez 1992: 5 webs, mean C = 0.11, SD = 0.03; Havens 1992: 50 webs, mean C = 0.10, SD = 0.04). Characteristic path lengths range from 1.33 to 3.74, generally decreasing with increasing connectance (Williams et al. 2001). Empirical food webs display similar, slightly longer (for 13 of 15 webs analyzed) path length values compared to random webs (Table 2).

A comparison of the clustering coefficients of empirical food webs to that of counterpart random webs (Table 2: Cl/Cl_{ran}) gives ratios ranging from 0.3 to 3.8. Only four food webs, the three very low connectance Scotch Broom and Ythan Estuary 1 & 2 webs, plus Little Rock Lake, display clustering that is twice or more that of random webs (Cl/Cl_{ran} = 2.1 to 3.8). Eleven webs have Cl/Cl_{ran} < 1.5, with six of those webs displaying equal or lower clustering than random webs (Cl/Cl_{ran} = 0.3 to 1.0). The largest clustering coefficient ratio, 3.8 for the large version of the Ythan Estuary web, is lower than ratios for other biological networks. The substrate and reaction graphs for *Escherichia coli* display clustering coefficient ratios of 12.3 and 6.6 (Wagner and Fell 2001) and the *C. elegans* neural network has a ratio of 5.6 (Watts and Strogatz 1998). Looking across 33 real-world networks including biological and non-biological networks, the clustering coefficient ratio increases as an approximate power-law function, specifically a linear function, of the

size of the network, with an exponent of ~ 1 (Figure 1). A 1:1 ratio occurs in networks with ~ 43 nodes. The non-biological networks displayed, which range in size from 4941 to 1,520,251 nodes (Albert and Barabási 2002) have clustering ratios that range from 16 for the power grid (Watts and Strogatz 1998) to $\sim 14,000$ for neuroscience coauthorship (Barabási et al. 2001). Biological networks, especially ecological networks, have relatively few nodes compared to non-biological networks and clustering coefficients that are much closer to random.

The linear relationship of the clustering ratio to network size arises because clustering in random networks should be equal to connectance ($C = L/S^2$), since the likelihood that one node is connected to another node is the same as the likelihood that two neighbors of a node are connected. This is demonstrated by the near identity of Cl_{ran} with C for the 33 networks of Figure 1 ($Cl_{ran} = 1.0425C + 0.00089$, $P < 0.001$, $r^2 = 0.996$). However, observed clustering appears to scale linearly with L/S for the same networks ($Cl = 0.0033L/S + 0.2332$, $P = 0.006$, $r^2 = 0.219$). Thus, the ratio of observed to random clustering should increase approximately linearly with S , since $(L/S)/(L/S^2) = S$.

Following Amaral et al. (2000), we analyzed cumulative rather than density distributions of food web degree data. Previously published food-web density degree distributions include degree bins with a frequency of 0 that were not included when scale-free functions were fit to the data (Montoya and Solé 2001). The use of cumulative distributions avoids the problem of arbitrary exclusion of null bins and gives a more accurate picture of the shape of the distribution in small, noisy data sets. All 16 of the trophic food webs display cumulative degree distributions that differ from a Poisson distribution expected in random networks (Fig. 2). Non-random density distributions were also reported for the taxonomic food web versions of Scotch Broom (referred to as “Silwood

Park”), Ythan Estuary 1 & 2, and Little Rock Lake (Montoya and Solé 2001).

The two least connected food webs display scale-free or broad-scale degree distributions, with power-law behavior over the whole range of the Grassland web (exponent = 1.71) and part of the range of the Scotch Broom web (exponent = 0.92) (Fig. 2). The Scotch Broom web displays an exponential drop-off in the tail. The remaining 14 food webs display single-scale distributions. Eight food webs have data consistent with an exponential distribution (Ythan Estuary 1 & 2, El Verde Rainforest, Canton Creek, Chesapeake Bay, St. Martin Island, Little Rock Lake, Mirror Lake) and six webs, generally those with relatively high connectance, have data consistent with a uniform distribution (Stony Stream, St. Marks Seagrass, Lake Tahoe, Bridge Brook Lake, Coachella Valley, Skipwith Pond). One of the uniform distribution food webs, Lake Tahoe, displays a tail well fit by a Gaussian distribution. An overlay of normalized food web data from all 16 webs clearly demonstrates the general trend that distribution tails drop off faster than expected for scale-free networks (Fig. 3).

IV. DISCUSSION

An increasingly wide array of information, social, physical, and biological networks (Albert and Barabási *in press*) including food webs (Montoya and Solé 2001) have been described as small-world networks with short path lengths and high clustering. Our analyses suggest that most food webs do not display typical small world topology. Characteristic path lengths of food webs are short and only slightly longer than random, consistent with small world topology and observations for most real-world networks (Montoya and Solé 2001, Williams et al. 2001, Albert and Barabási 2002). However, only four of fifteen trophic food webs analyzed, including two that are different versions of the same web, unambiguously display the much greater than random clustering expected for

small-world topology, as also reported for the taxonomic versions of the same four webs (Montoya and Solé 2001). The apparent deviation of most food webs from small-world topology is related to the small size of food webs (10^1 to 10^2 nodes) compared to most other networks (10^2 to 10^7 nodes) examined for small-world properties. When network size is taken into account, food webs fit into a predictable continuum of clustering, with increasingly greater than random clustering observed in larger networks. In general, observed clustering coefficients tend to increase as a linear function of links per species. These findings suggest that the expectation of high clustering in small-world topology (Watts and Strogatz 1998) is generally inapplicable to small networks with relatively few links per species.

As with small-world topology, the degree distributions of food webs appear similar to other real-world networks in some respects and different in others. We observed degree distributions that deviated from random (see also Montoya and Solé 2001), as observed in other networks (Albert and Barabási 2002). Williams and Martinez (2000) reported the deviation of food web degree distributions from distributions in random networks for prey and predator links considered separately (“generality” and “vulnerability,” Schoener 1989) in a set of seven trophic food webs reanalyzed in this study for non-directed degree distributions. A simple one-dimensional “niche model” was found to successfully predict those non-random distributions and other topological properties (Williams and Martinez 2000), including characteristic path length (Williams et al. 2001).

While the shapes of food-web degree distributions deviate from random, they also differ from scale-free, power-law distributions observed in many other networks (Albert and Barabási 2002). Our comprehensive analysis of 16 food webs, including reanalysis of the four previously studied webs (Montoya and Solé 2001), shows that food webs are generally single-scale networks (Amaral et al. 2000), displaying either exponential or uniform distributions. To our knowledge,

uniform distributions have not been previously reported for real-world networks. We found a partial exponential distribution in the Scotch Broom trophic web and exponential distributions in the Ythan Estuary 1 & 2 trophic webs ($r^2 = 0.97$ to 0.98) that differ from the less explanatory ($r^2 = 0.79$ to 0.83) scale-free patterns previously reported for the taxonomic versions of those webs (Montoya and Solé 2000). This is likely due to our use of cumulative rather than density distributions for analysis in order to incorporate empty bin data, and not due to differences in resolution of taxa in trophic versus taxonomic webs. An analysis of cumulative distributions for the taxonomic versions of the 16 food webs did not substantively alter our results (data not shown).

We find that food webs with relatively high connectance typically display uniform distributions while webs with very low connectance display power-law or partial power-law distributions. The tendency towards a uniform degree distribution in high connectance food webs may occur because networks with relatively few nodes and high connectance have relatively high average degree. This minimizes the difference between the average ($2L/S$) and the maximum possible ($2S$) degree, cutting off distribution tails that would include nodes with much higher than average degree, as often seen in large, low connectance, small-world networks (e.g., Figure 1 non-food web networks have mean nodes = 140,000, $C = 0.01$, and $L/S = 1400$). Conversely, sparsely connected food webs with very low average degree can display power-law distributions as seen in many real-world networks. The lowest connectance food web, Grassland ($C = 0.026$), displays a power-law distribution and has $S = 61$ and $L/S = 1.59$, which differ by a factor of $C^{-1} = 38.4$. In contrast, the highest connectance food web, Skipwith Pond ($C = 0.315$), displays a uniform distribution and has $S = 25$ and $L/S = 7.88$, which differ by a factor of only 3.2.

Both low and high connectance food webs are unusual, and their more extreme connectances appear to be artifacts of particular food web collection or assembly procedures. The two lowest connectance webs ($C \approx 0.03$), Grassland

and Scotch Broom, the only webs that display complete or partial power-law degree distributions, are “source webs” constructed by following food chains upward from one or a few basal species. In addition, these webs ignore co-occurring generalists such as spiders and birds and focus on specialist parasitoid insects whose immature stages develop on or within a single insect host, ultimately killing the host. Such parasitoids tend to be linked to very few other species, resulting in webs with low C (Martinez et al. 1999). The two highest connectance webs ($C \approx 0.3$), Coachella Valley and Skipwith Pond, which display uniform distributions, are small webs dominated by omnivores, taxa that feed at multiple trophic levels. Such taxa tend to be generalists with links to many other species, resulting in high C . In Coachella Valley, the high levels of omnivory are an artifact of high node aggregation (only 1 of 30 taxa are identified at the species level). Most food webs are less skewed towards specialists or generalists and thus have connectances closer to 0.1 and are more likely to display exponential degree distributions.

The lack of power-law degree distributions in food webs also may relate to how ecosystems assemble and evolve compared to other networks. Networks that display scale-free degree distributions probably emerge via a set of mechanisms that differ from those that produce networks with broad- and single-scale distributions (Amaral et al. 2000). Barabási and Albert (1999) developed a simple “scale-free model” that produces networks with power-law degree distributions. This model incorporates two generic mechanisms that they argue are common to real-world networks: 1) growth of the network by addition of nodes and links at each time step and 2) preferential attachment of new nodes to existing nodes with a high number of links. While these assumptions may be useful for describing evolution of the WWW or citation networks (but see Kleinberg et al. 1999, Adamic and Huberman 2000), they appear less appropriate for ecosystems and some other types of networks. Alternate models that remove either of the assumptions (Barabási and Albert 1999, Barabási et al. 1999) or

incorporate “aging” (some nodes cannot accept new links) or “cost” (a maximum number of links per node) eliminate scale-free topology and produce broad- or single-scale degree distributions (Amaral et al. 2000).

In ecosystems, both assumptions of the scale-free model may be problematic. In particular, the simple growth assumption is violated since there are both additions and losses of nodes (species) at ecological and evolutionary time scales via immigration, emigration, evolution, and extinction. The net effect of such changes can be expansion, contraction, or no change of species richness (as well as trophic links) within an ecosystem over time. Whether new species preferentially link to highly connected species already in the food web is less clear. Data from a wide range of studies suggest that generalist consumers (species with a large number of links to prey) are more likely to prey on invasive species than specialist consumers, as observed for insect herbivores of invasive plants (Connor et al. 1980, Strong et al. 1984) and parasitoids of invasive insect herbivores (Cornell and Hawkins 1993). This supports the preferential attachment hypothesis. However, we can also hypothesize that an invasive species will be more likely to establish successfully if it has few consumers. Initial data from some Hawaiian food webs suggests that there are more successfully established alien parasitoids than alien herbivores or plants, which may be attributable to parasitoids typically having fewer consumers than species at lower trophic levels (J. Memmott, pers. com.). Regarding predation links to resource species, there is little data to suggest whether invasive consumers have any tendency to prey on species that already have a large number of consumers. Theoretically, competitive exclusion causes overlapping niches to repulse each other (Begon et al. 1996), reducing the average number of consumers preying upon resource species. However, a species may have many consumers because it is relatively abundant, which may make it more likely to be preyed upon by new species. Empirically, a balance of these two mechanisms is suggested by the success of the niche model, which randomly distributes niches free of

repulsion or attraction. The niche model successfully predicts a wide range of observed food-web properties (Williams and Martinez 2000, Williams et al. 2001) but has yet to be tested against clustering and degree distribution.

A clear understanding of the structure of food webs from a variety of ecosystems is useful for developing a more general understanding of biological and non-biological network topology. In particular, while food webs display far less clustering than expected in small world networks, we have shown how low clustering in food webs represents an extreme in a continuum of clustering dependent on the size of networks. Also, the small size and relatively high connectance of most food webs compared to other real-world networks has provided insight into what types of networks can be expected to display various kinds of degree distributions. From a more applied, conservation-minded perspective, an understanding of food web topology can help us to explore and predict functional responses of ecosystems to structural changes. The most dramatic structural change that many ecosystems face is human-driven biodiversity loss. Structural analyses can provide another tool for exploring how robust or fragile ecosystems are to species loss (Solé and Montoya 2002, Dunne et al. 2002), as assessed for Internet and WWW topology (Albert et al. 2000) and metabolic and protein networks (Jeong et al. 2000, 2001). Such analyses can also more generally provide evidence of whether and what aspects of topology and network complexity drive robustness (Dunne et al. 2002).

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Table 1. Food webs examined for network topology, listed in order of increasing connectance (links/species²).

Food Web	Citation	Habitat
Grassland	Martinez et al. 1999	Grassland
Scotch Broom	Memmott et al. 2000	Shrubland
Ythan Estuary 1	Huxham et al. 1996	Estuary
Ythan Estuary 2	Hall and Raffaelli 1991	Estuary
El Verde Rainforest	Waide and Reagan 1996	Rainforest
Canton Creek	Townsend et al. 1998	Stream
Stony Stream	Townsend et al. 1998	Stream
Chesapeake Bay	Baird and Ulanowicz 1989	Estuary
St. Marks Seagrass	Christian and Luczkovich 1999	Estuary
St. Martin Island	Goldwasser and Roughgarden 1993	Island
Little Rock Lake	Martinez 1991	Lake
Lake Tahoe	Martinez unpublished data	Lake
Mirror Lake	Martinez unpublished data	Lake
Bridge Brook Lake	Havens 1992	Lake
Coachella Valley	Polis 1991	Desert
Skipwith Pond	Warren 1989	Pond

Table 2. Topological properties of empirical and random food webs networks.

	Taxa	S	$C (L/S^2)$	L/S	D	D_{ran}	Cl	Cl_{ran}	Cl/Cl_{ran}
Grassland	75	61	0.026	1.59	3.74	--	0.11	--	--
Scotch Broom	154	85	0.031	2.62	3.11	2.82	0.12	0.04	3.0
Ythan Estuary 1	134	124	0.038	4.67	2.34	2.39	0.15	0.04	3.8
Ythan Estuary 2	92	83	0.057	4.76	2.20	2.19	0.16	0.06	2.7
El Verde Rainforest	156	155	0.063	9.74	2.20	1.95	0.12	0.07	1.4
Canton Creek	108	102	0.067	6.83	2.27	2.01	0.02	0.07	0.3
Stony Stream	112	109	0.070	7.61	2.31	1.96	0.03	0.07	0.4
Chesapeake Bay	33	31	0.071	2.19	2.65	2.40	0.09	0.09	1.0
St. Marks Seagrass	48	48	0.096	4.60	2.04	1.94	0.14	0.11	1.3
St. Martin Island	44	42	0.116	4.88	1.88	1.85	0.14	0.13	1.1
Little Rock Lake	182	92	0.118	10.84	1.89	1.77	0.25	0.12	2.1
Lake Tahoe	800	172	0.131	22.59	1.81	1.74	0.14	0.13	1.1
Mirror Lake	586	172	0.146	25.13	1.76	1.72	0.14	0.15	0.9
Bridge Brook Lake	75	25	0.171	4.28	1.85	1.68	0.16	0.19	0.8
Coachella Valley	30	29	0.312	9.03	1.42	1.43	0.43	0.32	1.3
Skipwith Pond	35	25	0.315	7.88	1.33	1.41	0.33	0.33	1.0

Table 2 footnotes: “Taxa” refers to the number of compartments in the original food web, which can range from ontogenetic stages (e.g., largemouth bass juveniles) to non-phylogenetic categories (e.g., detritus, seeds) to highly aggregated taxa (e.g., microbes). S refers to trophic species, C refers to connectance, L refers to trophic links. D refers to characteristic path length, and Cl refers to the clustering coefficient. D_{ran} and Cl_{ran} refer to the mean D and Cl for 100 random webs. D_{ran} and Cl_{ran} could not be calculated for the Grassland web due to the difficulty of assembling non-fragmented random webs with very low average node degree ($2L/S < \sim 4$).

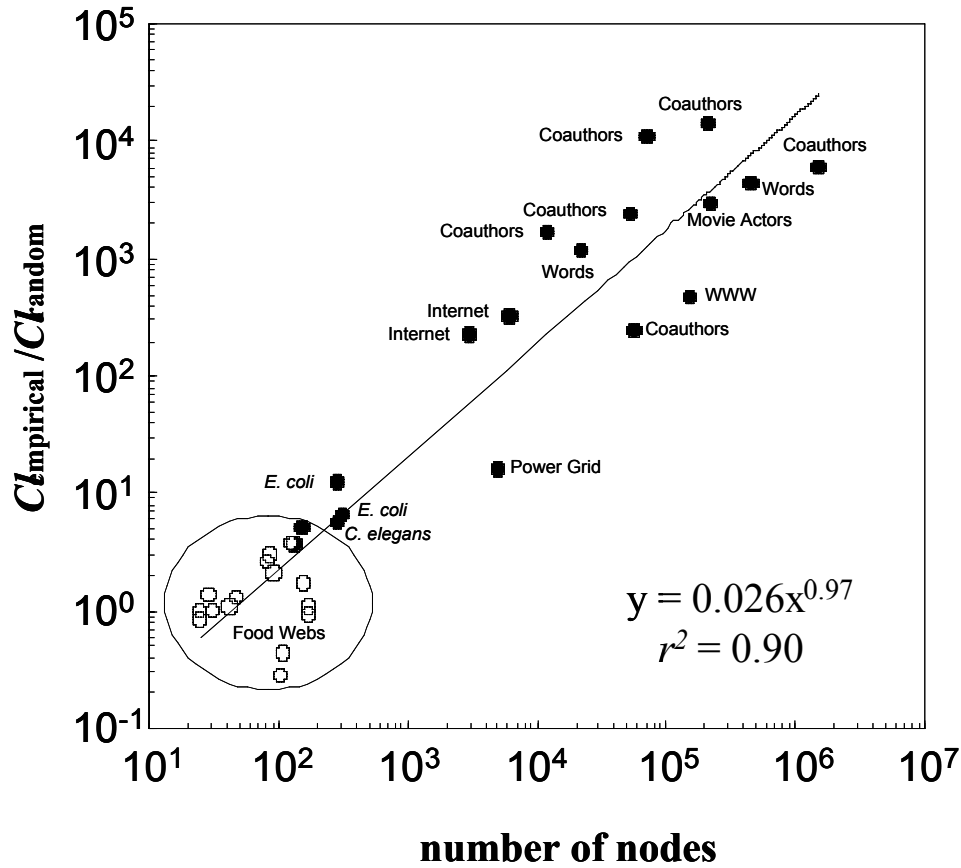


Figure 1. Log-log plot of the clustering coefficient ratios (empirical:random web values) as a function of size of the network. Open circles represent data from 15 trophic food webs (all but the Grassland web, Table 2) from the current analysis. Dark circles represent data from previous studies of 18 scale-free small-world networks summarized in Albert and Barabási (2002): 2 taxonomic food webs (Montoya and Solé 2001); *E. coli* substrate and reaction graphs (Wagner and Fell 2001); *C. elegans* neural network, movie actors, and power grid (Watts and Strogatz 1998); 4 science coauthorship data sets (Newman 2001a,b); 2 math and science coauthorship data sets (Barabási et al. 2001); low and high estimates for Internet domains (Yook et al. 2001, Pastor-Satorras et al. 2001); WWW sites (Adamic 1999); and concurrence and synonymy of words (Cancho and Solé 2001, Yook et al. 2001). If the current set of 15 food webs are excluded, the power-law exponent is 0.89 and $r^2 = 0.83$.

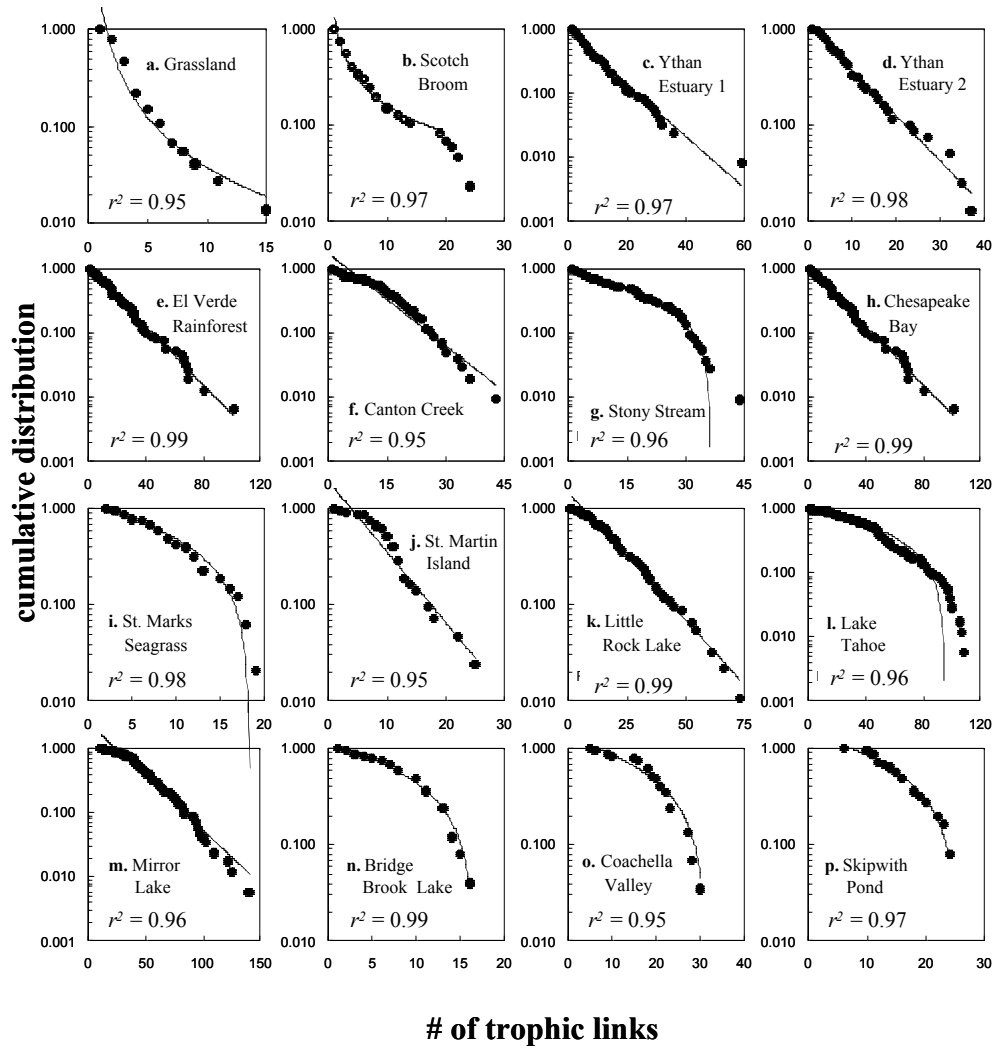


Figure 2. Linear-log plots of the cumulative distributions of links per species (both incoming links from predators plus outgoing links to prey) in 16 food webs. Webs are ordered by increasing connectance (see Table 1). Lines and r^2 values show the fit to the data of the best of three simple models: 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.

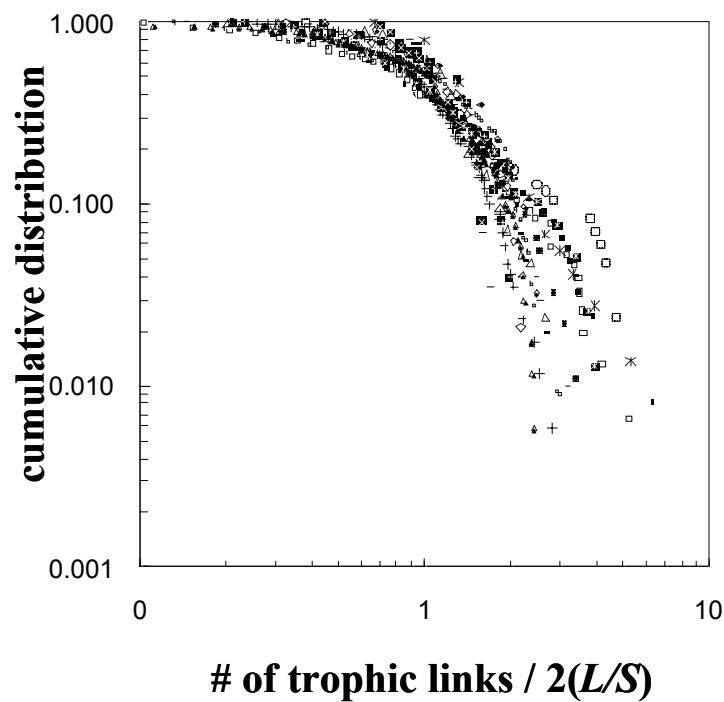


Figure 3. Log-log overlay plot of the cumulative distributions of links per species (both incoming links from predators plus outgoing links to prey) in 16 food webs. The link data are normalized by the average number of links/species in each web. If the distributions followed a power law, the data would tend to follow a straight line.