



Small World Patterns in Food Webs

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The analysis of some species-rich, well-defined food webs shows that they display the so-called small world behavior shared by a number of disparate complex systems. The three systems analysed (Ythan estuary web, Silwood web and the Little Rock lake web) have different levels of taxonomic resolution, but all of them involve high clustering and short path lengths (near two degrees of separation) between species. Additionally, the distribution of connections $P(k)$ which is skewed in all the webs analysed shows long tails indicative of power-law scaling. These features suggest that communities might be self-organized in a non-random fashion that might have important consequences in their resistance to perturbations (such as species removal). The consequences for ecological theory are outlined.

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Introduction

The understanding of food web patterns in complex ecosystems is a central issue in ecology. As Stuart Pimm claims, food webs are the roadmaps through Darwin's entangled bank (Pimm *et al.*, 1991). Beyond the specific features of currently described food webs (such as the concrete species composition), a number of regularities have been observed suggestive of fundamental laws of ecosystem organization (see for example, Warren, 1994; Polis & Strong, 1996 and references therein).

One of the most successful approaches to real food webs deals with the graph patterns associated with the set of links between species. Specifically, a food web can be described in terms of a graph $G(V, E)$ consisting of a finite set V of vertices (nodes, species) and a finite set E of edges

such that each edge e is associated with a pair of vertices v and w . In spite of the fact that ecological graphs are directed (i.e. links go from one species to another and the reverse connection will be typically different in strength and sign), most theoretical studies deal with non-directed graphs. In other words, two species appear connected if they share a common edge, irrespective of its particular properties. This approach has been rather successful, since many reported regularities from field data are fully recovered from non-directed graph arguments of different nature (Cohen *et al.*, 1990; Pimm *et al.*, 1991; Williams & Martinez, 2000; see also Albert *et al.*, 2000). This observation is probably a consequence of fundamental laws constraining the basic topological arrangements of ecological networks that go beyond the specific rules of dynamical interaction (Brown, 1994; Solé & Bascompte, 2001).

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Recently, new theoretical approaches to graph complexity in nature have emerged. Two main results of these studies are: (a) the widespread presence of the so-called *small world* (SW) pattern of some economic, technologic and biological networks (Watts & Strogatz, 1998; Watts, 1999; Adamic, 1999) and (b) the presence of scale-free (SF) distributions $P(k)$ of connections (Barabási & Albert, 1999; Jeong *et al.*, 2000; Wagner & Fell, 2000; see also Lloyd & May, 2001). Specifically, in some cases the number of nodes with k links follows a power-law distribution $P(k) \sim k^{-\gamma}$ where most units are weakly connected and a few are highly linked to other nodes. This is, however, a non-universal feature: the graph of the neural network of *C. elegans*, for example, displays an exponential distribution of connections (Amaral *et al.*, 2000).

The SW pattern can be detected from the analysis of two basic statistical properties: the so-called *clustering coefficient* C_v and the *path length* L . Let us consider the set of links $\xi_{ij}(i, j = 1, \dots, S)$ where S is the number of species and let us assume that $\xi_{ij} = 1$ if a link exists and zero otherwise. Species will be labeled as s_i ($i = 1, \dots, S$). If a food web is considered, an additional parameter is the community matrix connectance C . Let us consider a given species (the i -th one) and the set of nearest neighbors $\Gamma_i = \{s_j | \xi_{ij} = 1\}$. Here we can calculate the clustering coefficient for this species as the number of connections between the species belonging to Γ_i . By defining

$$\mathcal{L}_i = \sum_{j=1}^S \xi_{ij} \left[\sum_{k \in \Gamma_i} \xi_{jk} \right] \quad (1)$$

and thus $c_v(i) = \mathcal{L}_i / (CS(CS - 1)/2)$ so that the clustering coefficient is the average over all species:

$$C_v = \frac{1}{S} \sum_{i=1}^S c_v(i) \quad (2)$$

and measures the average fraction of pairs of neighbors of a node that are also neighbors of each other.

The second measure is easily defined. Given two arbitrary species s_i and s_j , let $L_{min}(i, j)$ be the

minimum path length connecting these two species. The average path length L will be

$$L = \frac{2}{S(S-1)} \sum_{i=1}^S \sum_{j=1}^S L_{min}(i, j). \quad (3)$$

Small world graphs are highly clustered but the minimum path length between any two randomly chosen nodes in the graph is short. By comparison, random graphs (where nodes are randomly connected with some probability) are not clustered and have short L (Watts, 1999). At the other extreme, regular lattices are typically clustered and have long distances. It has been shown, however, that a regular lattice can be transformed into an SW if a small fraction of nodes are rewired to randomly chosen nodes. Thus, a small degree of disorder makes the lattice have short paths (as in the random case) but is still mostly regular (Watts & Strogatz, 1998).

In a graph with an average of $\langle k \rangle$ links per node, it can be shown for random graphs that $C_v^{rand} \approx \langle k \rangle / N$ and L^{rand} will be short. For large networks, an SW is present if L^{rand} is larger, but close to L and $C_v \gg C_v^{rand}$. When networks composed by a small number of units are analysed, the second condition is often replaced by $C_v > C_v^{rand}$. This is the case for the SW pattern in the neural network of the nematode worm *C. elegans* (ce) which has 282 neurons and $C_v^{ce} = 0.28$ and $L^{ce} = 2.65$, to be compared with the corresponding random graphs: $C_v^{rand} = 0.05$ and $L^{rand} = 2.25$. For the metabolic network of *E. coli*, Wagner and Fell obtained similar results, but with a much larger difference in the clustering.

The consequences of the SW and SF patterns are far from trivial and can be of great importance in recognizing evolutionary paths, the origins of homeostatic stability and the sensibility to perturbations in biological networks. Watts and Strogatz discuss some of these ideas in their seminal work, suggesting that SW architecture would play a relevant role in enhancing synchronization in the visual cortex. For metabolic networks, Wagner and Fell suggest that it might play a relevant role in allowing metabolism to react rapidly to perturbations thus displaying a very high homeostasis. What about ecological networks? Do food webs display these types of topological properties?

In this paper, we explore this question by analysing the statistical properties of a set of large ($S > 100$) ecological networks where a fine taxonomic resolution is available. For these webs, the SW property is shown to be present and a skewed distribution of links is also shown to be involved in most cases. The presence of these properties will be shown to have deep implications for theoretical and applied issues at different levels.

Ecological Small Worlds

It is interesting to see that, in fact, most static graph models of food webs involve features ranging from purely random nets (constant connectivity networks, see Martinez, 1991a) to purely hierarchical models (the cascade model, see Cohen *et al.*, 1990). Under the second class, a trophic species can only prey on a trophic species of lesser rank leading to a hierarchical structure sharing some features with some standard graphs patterns such as Cayley trees (Watts, 1999). For the constant connectance model (Martinez, 1991a), no such ranking is introduced and a trophic species preys on any other trophic species (including itself). However, ecological nets display both types of properties and some studies suggest that they also display clustering.

Evidence for clustering in food webs has been compiled in recent years (see Solow & Beet, 1998). A number of authors have shown that food webs are typically non-random but the effects of such topological properties on stability are far from clear (see Solow *et al.*, 1999, for a recent discussion).

The possible importance of clustering on the stability of ecological networks was already recognized from early statistical approaches (May, 1974; Pimm, 1982). Given the potential implications of the SW phenomenon for network homeostasis, the presence of such properties in real food webs would be of great interest in this discussion. We have found that, in fact, rich-species food webs with a good taxonomic resolution display the properties of small world behavior. In Fig. 1, we show the obtained results for the four large food webs analysed, which are known in the literature because they are the most detailed large community food webs available.

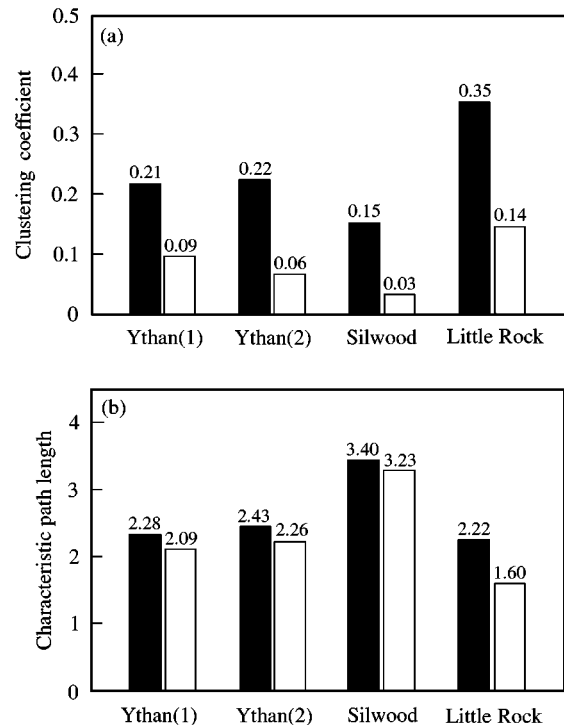


FIG. 1. (a) Clustering coefficient for the four analysed food webs (see text). Here the dark bars are real webs and the white bars correspond to randomly generated webs with the same average number of links per species (averaged over 200 generated samples). We can see that in all cases, the clustering is clearly larger than random; (b) characteristic path length L with random values. Except for Little Rock, the difference between the random and real case is very small. For the two Ythan webs, the improvement in resolution slightly modified the observed relations towards a better defined SW pattern.

These are:

1. *Ythan estuary*: This web is from a freshwater-marine interface. The number of species reported from two different studies are $S = 93$ (Hall & Raffaelli, 1991) and $S = 134$ (Huxham *et al.*, 1996). These studies differ in the taxonomic detail incorporated and we use them in order to verify the sensitivity in relation with the measurement of SW and scaling properties. This is the largest documented web in the U.K. and the average number of links per species are $\langle k \rangle = 8.75$ and 8.70 , respectively. The second web was expanded by adding 42 metazoan parasite species but their effect on $\langle k \rangle$ was weak. For this web most (88%) nodes correspond to real species. Some nodes involve lower resolution at

different levels (Nematodes, Acarina or Brown algae, for example, are lumped together).

2. *Silwood park web* (Memmott *et al.*, 2000): This is a sub-web obtained from a field site of 97 h in size. This is a very detailed community centered on the Scotch broom *Cytisus scoparius*, involving $S = 154$ species: one plant, 19 herbivores, 5 omnivores, 66 parasitoids, 60 predators and three pathogens. The average connectivity is $\langle k \rangle = 4.75$. All nodes of this (sub-) network are species (except node 122: immature spiders).

3. *Little Rock lake* (Martinez, 1991a, b): A web from a freshwater habitat, it includes $S = 182$

species. The Little Rock lake is a small lake with an area of 18 h. Here $\langle k \rangle = 26.05$. For this web, only 31% of nodes are associated to species. Most are genera-level nodes (63%) and the rest correspond to higher taxa (Bivalvia, Hirudinea, etc.).

We compared the observed values of C_v and L with the expected ones from the randomized webs with the same number of (total) links. As expected from an SW pattern, we see that all have very similar (and very short) distances L and clustering coefficient ratios from $C_v^{Yth1}/C_v^{rand} = 2.33$

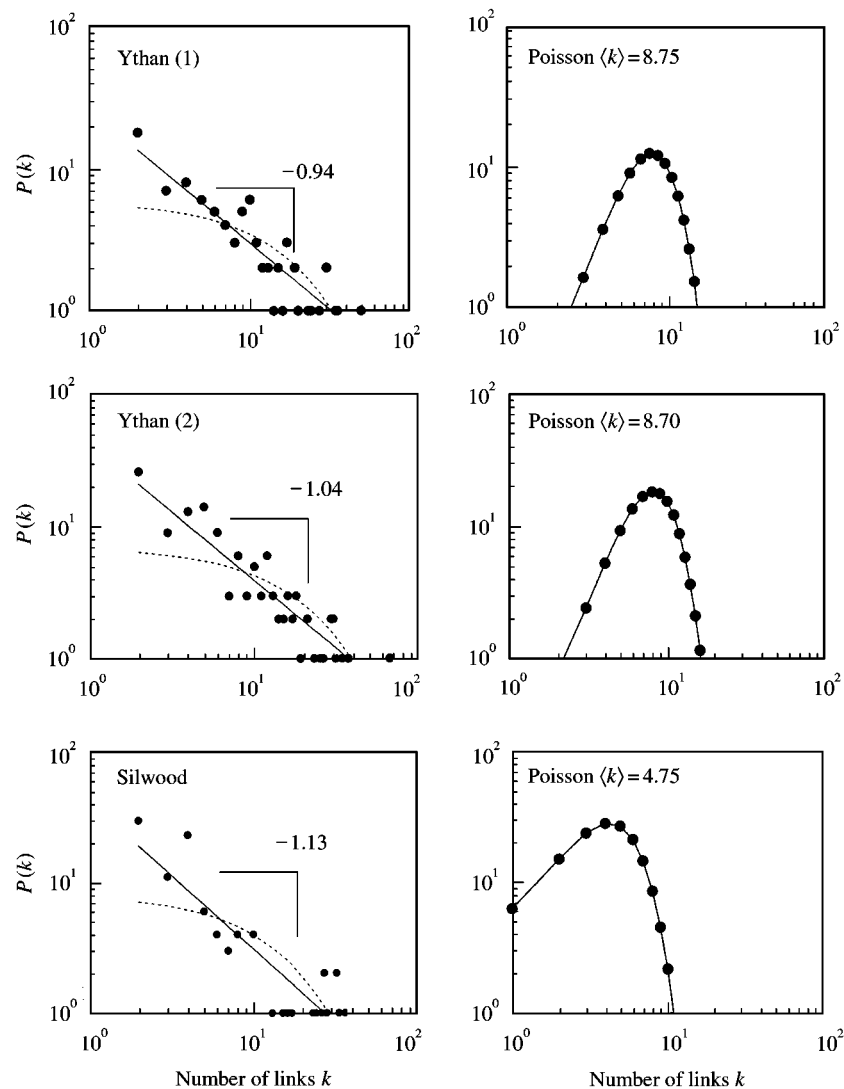


FIG. 2. Frequency distributions of links $P(k)$ for the analysed webs. Left column: actual data, which fit quite well a power law for the Ythan and Silwood cases (the exponential fit is also shown as a dotted line). The improvement in taxonomic resolution for Ythan (2) only modifies the exponent slightly. Right column: Expected distributions from the random graph approximation, predicting Poissonian behavior. None of the analysed food webs can be approached by the random case.

to $C_v^{Silw}/C_v^{rand} = 5.0$ (numerically close to the *C. elegans* data), i. e. clearly larger than expected from random webs. For the average path length, we found that the values are very close except for the Little Rock case, where notable differences are present.

An additional and surprising feature of the observed distributions of connections $P(k)$ is that they show strongly non-Poissonian behavior (which would be expected from random wiring). The classic result by Erdős and Rényi (ER) on random graphs (see Bollobás, 1985) and S nodes shows that the probability that a vertex has k edges follows a Poisson distribution $P(k) = e^{-\langle k \rangle} \lambda^k / k!$. Here

$$\langle k \rangle = \binom{S-1}{k} P_r^k (1 - P_r)^{S-k-1}, \quad (2)$$

where P_r is the probability that two nodes are connected. The observed distributions for Ythan webs and the Silwood example are shown in Fig. 2 (left column). In both webs, the distribution was found to be strongly skewed with a good agreement with a power-law fit. The observed values for a regression of the log-transformed data are:

$$\gamma^{Yth1} = 0.94 \pm 0.06 \quad (r^2 = 0.79, p < 0.01),$$

$$\gamma^{Yth2} = 1.04 \pm 0.05 \quad (r^2 = 0.83, p < 0.01),$$

$$\gamma^{Silw} = 1.13 \pm 0.06 \quad (r^2 = 0.79, p < 0.01).$$

For comparison, the expected connectivity distributions from a random, Poissonian net are also shown in Fig. 2 (right column). Here, the average number of links per species in each web was used.

The Little Rock web (Fig. 3) shows a fluctuating distribution of connections with a very high variance, but no obvious recognizable standard shape, although it is also skewed, with a prominent peak of 21 species (involving a coarse-grained cluster of cyanobacteria and green algae predated by pelagic cladocera, copepods and rotifers) with $k = 26$ links. These anomalies are likely to be due

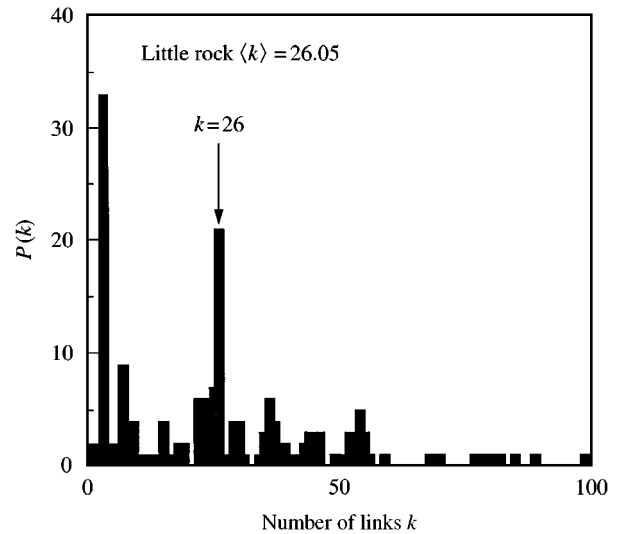


FIG. 3. Little Rock lake link distribution. Here $P(k)$ is clearly skewed but strong fluctuations are observable as scattered peaks, in particular a large peak at $k = 26$ involving a large cluster of interacting species (see text). Other peaks are observable, revealing strong deviations from a monotonous power-law tail.

to the taxonomic resolution used (mostly at genera or higher levels).

The exponent derived from our study is rather different from the estimations obtained for Internet or the metabolic graphs suggesting that, in spite of the fact that the SW pattern together with the scaling law might be common to many different types of networks, the ecological webs belong to some different class of complex phenomena (Solé *et al.*, 1996) to be defined in future theoretical studies.

Discussion

In this paper, we have presented evidence for SW patterns in ecological networks. The aim of our study was to see to what extent such evidence was strong enough by analysing a small number of large, taxonomically well-defined food webs from the ecological literature. The webs analysed have different origins but all of them share the SW pattern in their graphs and are clearly away from their random counterparts. As far as we know, this is the first reported evidence for such a property in ecology. It reveals, by means of a new measure, the existence of clustering in food webs associated to short path lengths and opens

a number of questions not previously formulated in previous theoretical studies.

Although some food web analyses found evidence for the existence of compartments (Solow & Beet, 1998), such species clusters were established in terms of the trophic similarity between pairs of species (see also Pimm & Lawton, 1980, for a similar measure). In contrast, the aim of the clustering coefficient as a measure of compartmentalization is to find out as to what extent groups of species are more connected internally than they are with another species or groups of species. In other words, this new measure goes beyond by looking not only for resource use guilds (see Wilson, 1999) but also for sub-webs with higher internal connectance than the rest of the community.

The use of the clustering coefficient is supported by the fact that groups of species with diets of similar species do not occur, especially in species-rich systems, such as those analysed in this article (Winemiller, 1990; Polis & Strong, 1996). In this respect, this measure of compartmentalization minimizes the importance of discrete and homogeneous trophic-level dynamics in complex food webs, an issue widely considered as an artifact by many ecologists (see Polis & Strong, 1996, for a review). The clustering coefficient does not consider the trophic position of the species in the food web, focusing only on the presence or absence of the interactions.

Two of the webs analysed correspond to the same system: the Ythan estuary food web. These two webs involve different taxonomic resolution but the exponents and indices remained basically the same for the two cases. This agreement suggests that the SW property and the scaling law are rather robust and that no completely detailed description of the species-level graph needs to be defined in order to detect these properties. For the best-defined web (Silwood), where all nodes belong to species, we obtain the best evidence of SW, suggesting that less-detailed webs introduce a coarse-grained resolution that might hide a higher degree of clustering (this seems to be confirmed by the Ythan example). The worst result is given by Little Rock lake, where the resolution is mainly at the genus level and strong deviations from the power law are observable.

On comparing the food webs analysed here with those compiled in the Ecoweb database (1989) and with some food webs recently described (Chesapeake bay, Baird & Wanowicz, 1989; Coachella Valley, Polis, 1991; Benguela ecosystem, Yodzis, 1998), all of them clearly less detailed, we can also see that despite the fact that SW properties are present in almost every food web, a higher level of taxonomic resolution provides higher evidence of these topological properties. Therefore, an increase in sampling effort on those food webs with less-detailed description might result in a higher evidence of SW properties.

The SW phenomenon appears to be associated with highly non-random, fat-tailed distributions of links. The plots of $P(k)$ show that all food webs (and others not explored here due to their lower taxonomic resolution) involve strong deviations from the Poissonian behavior and confirm the presence of clustering in ecological interactions. These properties reveal that some new features of ecological graphs have to be considered by future models in order to explain their origin and meaning.

In general, SW webs have been shown to provide fast responses to perturbations, therefore providing a great source of homeostasis (Watts & Strogatz, 1998; Lago-Fernández *et al.*, 2000). In this context, the presence of these types of web patterns might have important consequences for the fragility and resilience of ecological communities. The food webs reported here have an extremely high resistance in terms of the number of secondary extinctions (that is, species that become extinct due to the removal of other species on whom their survival depends) when random removal of species is simulated. Random food webs with the same number of links, number of species and average number of links per species have shown a higher sensitivity when species are removed at random from the web (Solé & Montoya, 2001). In this sense, classic studies on ecosystem resilience and resistance might benefit from considering these topological properties. Some enlightening theoretical studies based on the analysis of small-species models show this trend (Pimm & Lawton, 1977) where some simple topological arrangements between species are predefined. But perhaps some other regularities will emerge from our results

when rich-species models are taken into account.

Another important question emerging from our study is how these food webs with SW topologies are constructed through community assembly rules, that is, how they are built dynamically. Even if a community is assembled by random addition of species through a process of biological invasions, interactions can lead to non-random webs (Drake, 1990a, b). The SW topology might be related to underlying community level constraints and might help in understanding as to how biodiversity emerges and persists through time.

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