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Universality in food webs

D. Garlaschelli[a]

INFM and Dipartimento di Fisica, Università di Siena, Via Roma 56, 53100 Siena, Italy
and
Center for the Study of Complex Systems (CSC), Via T. Pendola 37, 53100 Siena, Italy

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Abstract. Among recently studied real-world networks, food webs are particularly interesting since they provide an example of biological organization at the largest scale, namely that of ecological communities. Quite surprisingly, recent results reveal that food webs do not display those properties which are observed in almost all other networks, such as a *scale-free* degree distribution and a large *clustering coefficient*. However, when food webs are regarded from the point of view of trasportation networks, it is possible to uncover very interesting scaling properties which are displayed by other trasportation systems, namely vascular and river networks. While other topological properties appear to vary across different webs depending on specific aspects, such scaling relations are universal. An interpretation of these results in terms of the interplay of universal and nonuniversal mechanisms in food web evolution is suggested.

PACS. 87.23.-n Ecology and evolution – 89.75.-k Complex systems – 05.65.+b Self-organized systems

1 Introduction

In the recent years, the scientific community has devoted great interest to the study of networks [1,2]. Systems which are very different in nature – such as groups of interacting proteins, socially related people and the Internet – can be described by means of the same graph-theoretic representation [1,2]. In such a picture, each unit of a system is represented by a *vertex* (denoted by an integer number $i = 1, \ldots, N$ where N is the total number of vertices) and each connection or relation between a pair of units is represented by a *link* (or *edge*) between the corresponding vertices.

Besides providing a unified description of different systems, graph theory can also help in characterizing their topological properties, such as the statistical distribution of the number of links (or *degree* k_i) of a vertex i. Remarkably, the analysis of a large variety of different real-world networks has highlighted the presence of common topological properties, some of which are the widespread power-law (or *scale-free*) form of the degree distribution $P(k) \propto k^{-\gamma}$ (where in most cases $2 \leq \gamma \leq 3$), the presence of correlations between vertex degrees, the small value of the *average distance* (minimum number of intermediate links) between pairs of vertices and a high level of *clustering* (presence of many links between neighbours of a given vertex).

These properties are highly nontrivial, in the sense that they are not observed in simple network structures such as regular lattices or completely random graphs, and can therefore be considered as the signature of some underlying mechanism shaping the observed complex topology of real networks [1,2]. This unexpected finding of structural similarities across different networks has stimulated a fascinating interdisplinary research, and in various scientific domains the tools of network theory have been used to characterize already well studied systems from a novel point of view.

In the present paper, we shall focus on a specific case study, namely the networks formed by predation relationships (*'who eats whom'*) in ecological communities, or *food webs* [3–5]. After a brief introduction to the subject, we clarify the importance of looking for universal features across different food webs. However, by reviewing some recent results [6–9] regarding the topological organization of food webs, we show that these systems look in some sense different from almost all other networks, and that no clear universal pattern appears to govern their topological properties. We then introduce the scenario proposed by the author, Caldarelli and Pietronero [10] suggesting that the controversial behaviour of food webs can be explained in terms of their specific functional role, namely the resource transfer in the ecosystem. When regarded within the framework of transportation networks [11–14], food webs appear to be very similar to other systems with analogous function, such as river basins [11,12] and vascular networks [13,14]. The qualitative analogy is the presence of nontrivial power-law relations describing the allometric scaling of transportation efficiency with system size,

[a] e-mail: garlaschelli@csc.unisi.it

characterized by universal scaling exponents [10]. We finally propose an interpretation of these results in terms of the underlying organizing aspects that could be responsible for the observed behaviour.

2 Controversial empirical results about food webs

In the ecological literature, the idea of defining a network representing the predation relationships among a set of species was first suggested by Elton in his pioneering work [15]. Generalizing the concept of *food chain* (a set of species feeding sequentially on each other in a resulting linear structure, see Fig. 1a), Elton introduced what he called a *food cycle* to provide a more complete and realistic description of real predator-prey (or *trophic*) interactions among species. In such a description (which is now referred to as *food web*), each species observed in a limited geographic area is represented by a vertex, and a directed link is drawn from each species to each of its predators [3–5] (see Fig. 1b). This defines a *directed network* reporting the trophic organization of ecological communities, whose understanding is clearly fundamental not only from a theoretical point of view, but also for practical reasons such as environmental policy and biodiversity preservation. More recently [16,17], it has been suggested that a less biased description is achieved when each group of functionally equivalent species (those sharing the same set of predators and the same set of prey) is aggregated in one *trophic species* and treated as a single vertex in the web. In the following, when addressing the properties of food webs, we shall always refer to the aggregated versions, or *trophic webs*.

Several quantities were introduced in the ecological literature in order to characterize food web structure, such as the fractions B, T, I of *basal* (with no prey), *top* (with no predators) and *intermediate* (with both predators and prey) species in the webs, the fractions of links between basal and top, intermediate and basal, top and intermediate species and the number of *trophic levels* (length of the shortest chain separating each species from the environment) [3–5]. Whether these properties are scale-invariant or instead display any trend with system size is a debated issue [16,18–20]. Moreover, patterns observed in smaller webs [5] do not seem to persist when more recent and larger webs [16,21–28] are considered. The only stable result seems to be the small value of the maximum trophic level l_{max} (typically $l_{max} \leq 4$) even when the total number of species is large [3–5].

2.1 Connectance

Another quantity introduced to describe food webs in a very simple fashion is the *connectance* (c), defined as the fraction of observed links (L) out of the N^2 possible ones [16,29]:

$$c \equiv \frac{L}{N^2}. \quad (1)$$

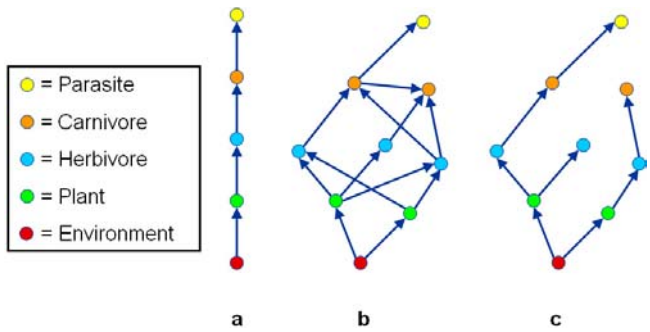

Fig. 1. Examples of the networks described in the text. a) Simple food chain with 4 species plus the environment. b) Food web with 8 species plus the environment and c) one possible corresponding spanning tree. The identity of the species is given in terms of the vertex colour and is explained in the legend.

Table 1. Properties of nine empirical food webs, in order of increasing number of trophic species N, and references to the original papers. The Ythan Estuary food web is present in two versions: with (2) and without (1) parasites. The values of η are obtained by plotting C_i versus A_i for each vertex in the corresponding web, except those marked with (*) which are inferred by plotting the value of C_0 versus A_0 for all webs in the table together (these values are therefore interpreted as 'expected' figures that could in principle differ from those computed directly on the individual webs, which on the other hand would be less reliable due to the small size of the webs, see Ref. [10]).

Food web [and reference]	N	c	D	C	η
Skipwith Pond [21]	25	0.31	1.33	0.33	1.13*
Coachella Valley [22]	29	0.31	1.42	0.43	1.13*
St Martin Island [23]	42	0.12	1.88	0.14	1.16
St Marks Seagrass [24]	48	0.10	2.04	0.14	1.16
Grassland [25]	63	0.02	3.74	0.11	1.15
Silwood Park [26]	81	0.03	3.11	0.12	1.13
Ythan Estuary 1 [27]	81	0.06	2.20	0.16	1.13
Little Rock Lake [16]	93	0.12	1.89	0.25	1.13
Ythan Estuary 2 [28]	123	0.04	2.34	0.15	1.13

Some early studies [18,19] suggested that a linear or non-linear scaling of connectance versus system size should hold: $c \propto N^{\alpha}$. By contrast, Martinez observed that, when trophic webs are considered, the connectance appears to display the almost constant value $c \approx 0.1$ [29]. While this 'constant connectance hypothesis' is confirmed by a range of empirical webs [16,23,24], other data deviate from this expectation and display either a larger [21,22] ($c \approx 0.3$) or a smaller [25–28] ($0.02 \leq c \leq 0.06$) value (see Tab. 1). While the former deviation can be traced back to the small size of some webs [21,22], the latter appears to be a genuine property, increasingly evident when the number of parasites in the webs increases. In any

case, there is no clear monotonous dependence of c on the number of species N. Therefore, like the other aforementioned quantities, the connectance does not show any clear trend across different webs. As a consequence, fundamental functional properties which depend on the connectance (such as food web stability under species removal [30]) also vary across different webs. We shall return on this point in the following.

2.2 Average distance

We now turn to 'more popular' topological quantities that, for theoretical reasons, have been intensively studied in many networks recently [1]. As we shall see, food webs are in some sense peculiar with respect to some of these properties.

The *average distance* (D) of an undirected network is defined as the minimum number of links separating two vertices, averaged over all vertex pairs. This quantity is always found to be small in real networks, and its typical dependence on the number of vertices N is logarithmic [1]:

$$D \propto \log N. \tag{2}$$

By contrast, note that in a regular d-dimensional lattice one has $D \propto N^{1/d}$. The average distance of food webs has been studied independently by Montoya and Solé [6] and by Williams et al. [7], with similar results showing that its value is always $D \leq 3$. In both cases food webs were treated as undirected, since from an ecological point of view one is mainly interested in the propagation of perturbations in the webs, which are likely to 'travel' in both directions along each link. The values of D computed on a set of real webs are reported in Table 1. Due to the small size ($N < 200$) of recorded food webs, it is however difficult to check whether the observed values of D do show a logarithmic dependence on N. Some hints in this direction come from a recent food web model [17] that reproduces well the empirical values of D in the observed range and is found to predict [9] a logarithmic dependence of the form (2) for large web sizes. In any case, the small value of the average distance is one of the few clear properties of real food webs together with the aforementioned (and obviously related) small value of l_{max}. In the literature, this property is sometimes referred to as the *small-world* behaviour [1,31] in a 'weak' sense, as we clarify below.

2.3 Clustering coefficient

Another simple but relevant quantity that sheds light on the local wiring properties of networks is the *clustering coefficient* (C), defined as the fraction of observed links between neighbours of a vertex (out of the total possible neighbour pairs) averaged over all vertices.

In real networks, this quantity is always found to be larger than expected in a random graph [1,31]. If the network displays simultaneously a large clustering coefficient *and* a small average distance, it is said to display a *small-world* behaviour in a 'strong' sense [31].

The clustering coefficient of real food webs has been independently addressed by Montoya and Solé [6] and by Dunne, Williams and Martinez [8]. Table 1 reports the values of C for a set of webs. While in some cases the value of C is unambiguously larger than random [6,8], in others it is even smaller [8]. In their analysis, Dunne, Williams and Martinez suggest that the reason for this ambiguous behaviour is again the small size of food webs. They show that the ratio of observed to random clustering increases roughly linearly with network size in a large number of real networks:

$$C_{observed}/C_{random} \propto N. \tag{3}$$

However the value of the intercept is such that, when N is sufficiently small such as in food webs, $C_{observed}/C_{random}$ can display values smaller than one [8]. As a consequence, food webs cannot be considered as small-world networks in the aforementioned 'strong' sense. Interestingly, as for the average distance, a recent model [17] reproduces the empirical values of C in the observed range and predicts [9] that indeed $C \propto 1/N$ for large food webs.

2.4 Degree distribution

We now turn to the degree distribution $P(k)$, which is probably considered as the most important topological property characterizing a network. In almost all studied real-world networks, the functional form of the degree distribution is a power law [1]:

$$P(k) \propto k^{-\gamma} \qquad 2 \leq \gamma \leq 3. \tag{4}$$

In the case of food webs, however, the behaviour is quite irregular [6,8,9]. First note that, since food webs are directed networks, one can distinguish between the *in-degree* k^{in} (number of incoming links) and the *out-degree* k^{out} (number of outgoing links) of a vertex. The degree distribution was studied both in its 'undirected' version $P(k)$, where $k = k^{in} + k^{out}$ [6,8], and in the two possible 'directed' forms $P^{in}(k^{in})$ and $P^{out}(k^{out})$ [9].

Montoya and Solé [6] suggested that in few isolated cases $P(k)$ can be fitted by a power law, while in others it has an irregular behaviour. However, their study was based on the analysis of the probability density $P(k)$, and not of the cumulative one $P_>(k) \equiv \int_k^\infty P(k')dk'$. Since the size of food webs is very small (generally less than 200 species), the resulting data are very noisy and the analysis cannot be considered as conclusive.

A more statistically reliable analysis by Camacho, Guimerà and Amaral [9] showed that for the food webs in their study the cumulative distributions $P_>^{in}(k^{in})$ and $P_>^{out}(k^{out})$ have distinct functional forms, which are however universal across different webs, and that none of them is scale-free.

Finally, Dunne, Williams and Martinez [8] studied the behaviour of $P_>(k)$ on more food webs and showed that the functional form of the distribution is not universal, and that it seems to depend on the connectance of the webs. In

a couple of webs with extremely low connectance $P(k)$ is consistent with a power-law distribution (although it can be fitted by an exponential one as well), while as the connectance increases the webs tend to display exponential and then uniform degree distributions.

3 Transportation properties of food webs

The results reported so far show that food webs display a nonuniversal behaviour with respect to the most commonly used quantities characterizing network topology. As compared with the robust trends displayed by a large number of networks of different kind, this is a surprising behaviour. However, according to a recent study [10], a possible explanation to this puzzle is the inability of the above quantities to capture any fundamental functional role of food webs. Clearly, when looking for universal structural properties of real networks, the natural candidates are those quantities which reflect the *function* that the networks stably have, despite possible differences due to specific conditions. The idea explored by the author, Caldarelli and Pietronero [10] is therefore to consider food webs as transportation networks [11,12,14] whose function is to deliver resources, starting from the abiotic environment, to every species in the web. In this framework, it is possible to use tools borrowed from the statistical physics of river networks [11,12] and fractal vascular systems [13,14] to characterize food webs as well.

3.1 Food webs as transportation systems

A trasportation system is composed by a *source* and a set of N points to be reached. The natural biological example is that of a vascular system delivering blood from the heart to the various parts of the organisms. The inverse problem where there are N sources draining into one final point or sink is simply obtained by reversing the direction of the flow. The prototypic example, well studied by physicists in the recent years [11], is that of river networks, where the rain collected by the sites of the basin is transferred through channels to a final outlet where the main stream of the river originates.

In the ecological case, all species living in an ecosystem need resources to survive. These resources are obtained by feeding on other species, or by directly exploiting the abiotic environmental resources (in the case of primary producers) such as water, light and chemicals. Food webs can therefore be treated as ecological transportation networks. More explicitly, if the set of abiotic resources is considered as a formal 'species' and represented as the *environment vertex* in a food web, one obtains a connected structure such that, starting from the environment, every species can be reached by following the direction of the links (see Figs. 1a and b). In the language of graph theory, this warrants that every food web admits a *spanning tree*, defined as a loopless subset of the network such that each vertex can be reached from the source (see Fig. 1c). As we now show, the topological properties of suitably chosen spanning trees are tightly related to the efficiency of a transportation network.

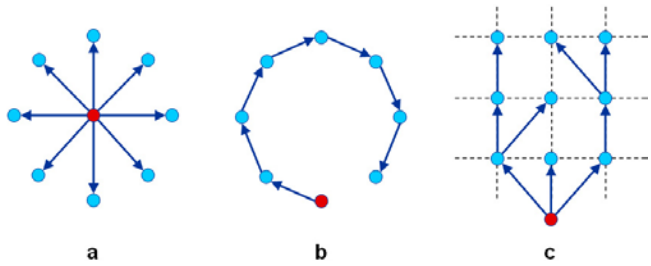

Fig. 2. Examples of possible tree-like transportation systems. The red vertex always indicates the source. a) Star-like configuration (maximum efficiency), allowed if there are no geometric constraints. b) Chain-like configuration (minimum efficiency), always allowed. c) Spanning tree of a bidimensional lattice with nearest-neighbours connections (geometric constraint). By reversing the direction of the flow, this is a schematic representation of a river network.

Before proceeding further, we note that a fundamental property of transportation systems is that each of the N sites needs to receive (or to deliver, in the case of rivers) a certain amount of resources per unit time. The excess resources can then be delivered to neighbouring sites. The resulting picture is that each vertex in a transportation network 'dissipates energy' and therefore transfers only a part of its resources to other vertices through its outgoing links. In a food web, part of the energy reaching a species is transferred (in the form of prey) to its predators, but a nonvanishing part is necessarily kept in the form of the equilibrium population size of the species (food webs are always assumed to be the snapshot of an equilibrium state of the population dynamics). If this were not the case, the species would be left with no individuals and clearly go extinct.

3.2 Free and geometrically constrained topology

The function of resource transfer, when associated to some optimization criterion, shapes the topology of transportation networks in a nontrivial way [12,14]. The system can in fact deliver resources in a more or less efficient way, and if it is subject to some evolutionary process its structure may change until an optimized configuration is reached. This optimized state is usually a trade-off obtained maximizing the transportation efficiency while being subject to the constraints limiting the system's possible configurations.

To clarify the above concept, let us consider two extreme opposite cases: the *star-like* (see Fig. 2a) and the *chain-like* (see Fig. 2b) networks. In the former case the source is at the center and the points are all directly connected to it, while in the latter all vertices have only one incoming and one outgoing link, except the source and the most distant vertex. Let us assume that all vertices require resources at the same rate and, as explained above, 'keep' a certain fraction of the incoming resources. As a consequence, if the number N of vertices to be nourished is

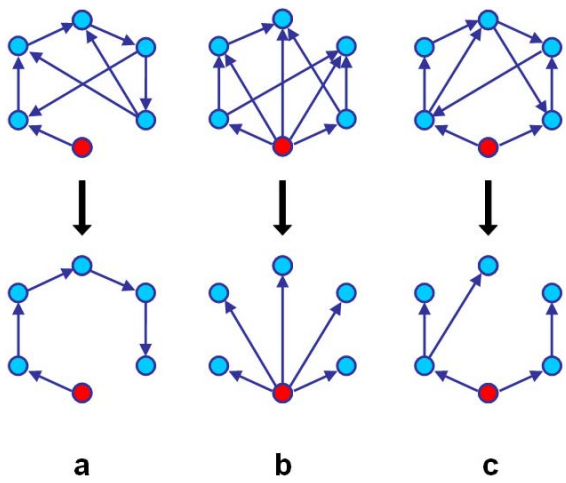

Fig. 3. Possible transportation networks (top) in the case of no geometric constraints and corresponding spanning trees (bottom) using the method of chain length minimization. a) Maximally inefficient network: the spanning tree is chain-like. b) Maximally efficient network: the spanning tree is star-like. c) Intermediate case with a nontrivial spanning tree.

doubled, in the star-like network the amount of resources to be provided by the source per unit time doubles, while in the chain-like case this quantity becomes even larger since, before reaching the most distant vertex, the flow of resources undergoes dissipation through many successive links.

Note that, by adding links to the star and the chain in such a way that the shortest paths from the source to all vertices are unchanged (see for instance Figs. 3a and b), in both cases the efficiency is not increased significantly, since the additional amount of resources reaching each vertex is much less than the already incoming quantity. This means that the efficiency of the network is essentially determined by the topology of its *spanning tree* obtained by minimizing the distance of each vertex from the source. The presence of additional links determines other properties such as the stability under vertex removal, but does not affect the transportation efficiency qualitatively (this is a crucial point in the following analysis). Also note that the presence of a link is usually associated to a 'cost' for the system: in the vascular case, the formation of unnecessary tissues such as additional blood vessels is clearly discouraged. Therefore, unless other factors make loops necessary, the least expensive choice is a tree-like network.

It can be shown that the star and the chain are indeed the most and the least efficient tree-like transportation networks respectively [12,14]. If there is no constraint on the topology of the network, the spanning tree can be chain-like, star-like or something in between (see Fig. 3). Since the star-like configuration is allowed, the system can reach the most efficient state. But if there is some constraint limiting the range of possibilities, the star-like configuration is in general not allowed and there will be a different optimal topology for the system. For instance, consider the case of a network embedded in a bidimensional space where only nearest-neighbour connections are allowed. In such a case, the optimal transportation system looks like that shown in Figure 2c, where each vertex is reached by one of the possible shortest chains originating at the source. In general, every spanning tree of a d-dimensional lattice obtained by minimizing the distance of each vertex from the source is an optimal (geometrically constrained) transportation network in d dimensions. Note that the least efficient chain-like topology can be realized also in presence of geometric constraints, and looks like a spiral or S-like structure starting at the source and spanning the whole lattice. In this case too, adding loops such that the shortest chains are unchanged does not affect the efficiency of the network significantly.

3.3 Allometric scaling

The above results can be rephrased quantitatively by exploiting the tools of river networks theory [11]. For each vertex i in a length-minimizing spanning tree of a transportation network, it is possible to define the number A_i of vertices in the subtree (or *branch*) $\gamma(i)$ rooted at i (hereafter we assume that such branch also includes the vertex i itself). In a river basin, this counts the number of sites 'uphill' point i (*drained area*), and by assuming unit rainfall rate at each site this gives the total rate (expressed in unit time) at which the site i transfers water downhill. In vascular systems A_i is instead the 'metabolic rate' at point i, or the blood quantity needed per unit time by the part of the organism reached by the branch of i.

In general, in unit time A_i can be viewed as the quantity of resources flowing through (or *weight* of) the only incoming (outgoing, for rivers) link of vertex i in a tree-like transportation network. Note that A_i is completely independent on the topology of the tree, being simply equal to the size of the branch irrespectively of its internal structure. However, depending on how links are arranged within each branch, the quantity of resources flowing through all the links in the branch can change significantly. Indeed, the sum of link weights within the branch $\gamma(i)$ rooted at i can be computed as

$$C_i \equiv \sum_{j\in\gamma(i)} A_j \tag{5}$$

and regarded as the *trasportation cost* at i. If the source is labeled by $i = 0$, the quantities A_0 and C_0 represent the 'total metabolic rate' (which simply equals $N+1$) and the total transportation cost (amount of resources flowing in the whole network per unit time) respectively. By plotting C_i versus A_i for each vertex i in the network, or by plotting C_0 versus A_0 for several networks of the same type, one obtains the so-called *allometric* scaling relations [12–14]

$$C(A) \propto A^{\eta} \tag{6}$$

where the scaling exponent η quantifies the transportation efficiency. Clearly, the larger the value of η the less efficient the transportation system. It is easy to show that,

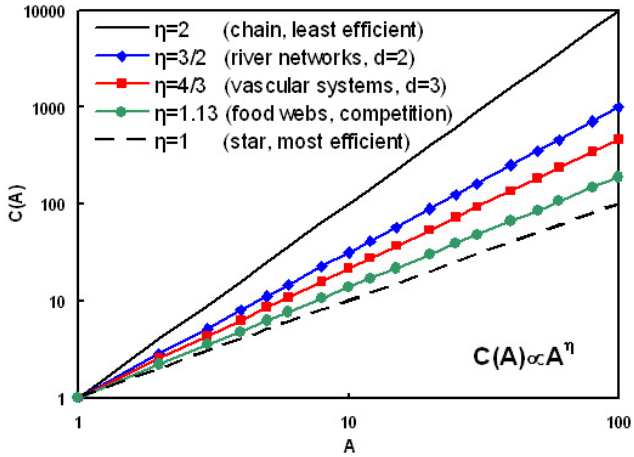

Fig. 4. Plot of the transportation cost (C) versus system or subsystem size (A) in different networks. The optimal case corresponds to $\eta = 1$ (star-like spanning tree), and the least efficient to $\eta = 2$ (chain-like spanning tree). Real transportation systems display intermediate values of the exponent: in the optimized d-dimensional geometrically constrained case $\eta = (d+1)/d$, while in food webs the observed value is $\eta = 1.13$ (competition-like constraint).

for star-like networks, $\eta = 1$ and one recovers the expected linear scaling of cost with system size. For chain-like networks, $\eta = 2$ confirming a much worse efficiency. In the case of length-minimizing spanning trees in a d-dimensional space, it can be proved [12,14] that

$$\eta_d = \frac{d+1}{d} \tag{7}$$

which clearly reduces to the previous cases $\eta_1 = 2$ (chain) and $\eta_\infty = 1$ (star), where $d = \infty$ formally indicates no geometric constraint. All the above trends are shown in Figure 4.

Remarkably, real river basins always display the value $\eta = 3/2$ [11], while for vascular systems the value $\eta = 4/3$ is observed [13,14] (see Fig. 4). This means that the evolution of these networks shaped them in order to span their embedding space ($d = 2$ and $d = 3$ respectively) in an optimal (length-minimizing) way [12,14], independently of other specific conditions of the system. Moreover, the value of η in both cases is different from what expected by simple scaling arguments based on Euclidean geometry, such as quadratic scaling of embedding area (or cubic scaling of embedding volume) with the fundamental length in the network [12,14]. In other words, the scaling is not isometric (hence *allometric*). By contrast, the observed values are those predicted by fractal geometry [14,32], confirming that self-similar structures are often obtained as a result of optimization processes driving the evolution of complex systems [32].

3.4 Spanning trees of food webs

We finally turn to food webs. In this case, there is clearly no geometric constraint and in principle all the outcomes presented in Figure 3 are possible. If one assumes biological evolution to drive ecological communities towards an optimization of the resource transfer, the natural expectation is the tendency of the spanning trees to be closer to a star than to a chain. However, in principle each food web could display a spanning tree with specific properties, different from that of any other food web, due to particular environmental and evolutionary conditions.

However, a recent analysis [10] of the allometric scaling relation of equation (6) in length-minimizing spanning trees of food webs shows that, remarkably, $\eta \approx 1.13$ on a large set of real webs, independently of the properties of the corresponding habitat and surrounding environment (see Tab. 1). Due to the absence of an embedding geometric space, in food webs η is smaller than in river or vascular networks, as expected. However, it also deviates from the most efficient value $\eta = 1$ in a systematic way. The same value of the exponent is observed both within each analysed web, highlighting self-similar branching properties, and across all webs, revealing an invariant scaling of total transportation cost C_0 with network size $A_0 = N + 1$ [10] (see Tab. 1 and the corresponding caption). Marine, terrestrial, desertic, freshwater and island food webs fall therefore within the same 'universality class'.

We also note that the self-similarity of the spanning trees (or in other words the statistical equivalence of the whole tree and of its branches) is confirmed by noticing that a *source web* (that is, a web reporting only species 'sustained' by a reference one playing the role of the environment vertex) like Silwood Park, centered on the Scotch Broom *Cytisus scoparium* [26], displays the same value of the allometric exponent. This is consistent with the interpretation that the spanning tree of a source web, being a branch of the larger (undocumented) spanning tree of the whole community food web, is described by the same statistics of the whole web (self-similarity) and of the other webs (universality). As compared to the 'irregular' behaviour of food webs with respect to other important topological quantities (see Sect. 2), this is really an encouraging result.

4 Discussion: structure and function

The results reported so far suggest that, while other commonly used topological quantities do not capture robust properties of food webs, the allometric scaling relation of equation (6) appears to highlight an invariant functional property, namely the resource transportation across the ecosystem. Such *function* seems to shape the *structure* of food webs in a universal fashion.

This is instructive in general, since the choice of the relevant topological quantities characterizing a network often ignores whether they capture a true underlying functional aspect. If they do not, they may display no clear behaviour across different networks of the same type, especially if the boundary conditions change from case to case.

The above results have interesting evolutionary implications as well. Ecological communities are known to

evolve due to immigration, speciation and extinction of species [33,34]. This clearly changes the topology of food webs, however different snapshots of such evolution at different places suggests that allometric scaling is quantitatively invariant in time and space. The resulting picture is that further evolution of the food webs would not result in a greater efficiency. In some sense, the observed property is already the 'asymptotic' one. The deviation from the star-like case $\eta = 1$ is therefore not due to transient factors, and has to be interpreted as the result of an ecological mechanism which is constantly at work.

4.1 Competition

A natural candidate for this mechanism is *interspecific competition* [10]. A star-like spanning tree corresponds to maximum competition for the same resource, unless there is an infinite amount of the latter. With finite resources, if the number of competing species is large the gain associated to feeding directly on the environment may become less than the competitive effort it requires. When this occurs, species tend to differentiate their 'diet' in such a way that some of them do not feed directly on the environment, causing the spanning tree to deviate from being star-like. The argument can then be generalized, so that each species realizes a trade-off between maximizing its resource input (by minimizing its trophic level) and minimizing its competitive effort (by maximizing its trophic level). This results in the universal structure of the spanning trees. Note that the finding is consistent with the observed small number of trophic levels mentioned in Section 2, and at the same time it is far more general since it also reveals, as we pointed out, the self-similar and universal character of more detailed properties of food web topology.

4.2 Recovering the role of loops

Besides resource transportation, there is another functional aspect of food webs which was recently shown to be tightly related to a structural property, namely the *robustness* under species removal. An analysis by Dunne, Williams and Martinez [30] showed that the fraction of species to be eliminated in order to induce the simulated secondary loss of half the initial number of species increases monotonically (with an approximately logarithmic dependence) with the connectance c defined in equation (1). The connectance is therefore a simple topological quantity determining the stability of food webs, much like the scaling exponent η is a simple way to characterize their efficiency.

Now, note that c can also be regarded as a measure of the number of loops in the web. More specifically, if $L_{tree} = N$ denotes the number of links in the spanning tree of a food web, the remaining $L_{loops} = L - L_{tree}$ are those responsible for the presence of loops in the original web. The connectance can then be written as

$$c = \frac{L}{N^2} = \frac{L_{tree} + L_{loops}}{N^2} = \frac{1}{N} + \frac{L_{loops}}{N^2}. \qquad (8)$$

Therefore the results in reference [30] show that, when the number of loop-forming links in a food web increases, the robustness of the web also increases.

Note that in the spanning tree analysis presented in Section 3.4 all loops are clearly ignored. In other words, while in order to characterize food web efficiency loops are irrelevant, their are of fundamental importance in determining web stability. This observation allows us to recover the role of loops that was ignored so far in the spanning tree analysis.

4.3 Food web structure decomposition

The puzzling behaviour of food webs appears now clearer. Food web structure can be decomposed in suitably defined (length-minimizing) spanning trees and the remaining loop-forming links. The former determine the transportation properties of the webs, and can be simply characterized by the value of the allometric exponent η. The latter instead determine the robustness under species removal, and are simply related to the connectance c. In this picture, spanning trees and loops are complementary ingredients of food web topology as well as of food web function. As we mentioned in Section 2, the connectance is one of the properties that vary across food webs in an unclear fashion. As a consequence, food web stability is a highly varying property as well, whereas transportation efficiency appears universal.

The reason for the nonuniversal behaviour of connectance is not completely clear yet. However, an argument proposed by Cousins [36] can be used to provide a simple possible explanation in terms of the different compositions of food webs. Cousins argued that when the energy flows from large to small organisms (such as in host-parasite interactions) the consumer tends to specialize and to feed on only one or few species [36]. By contrast, when the energy flows from small to large organisms (such as in most ordinary prey-predator interactions) the consumer has to face weaker constraints and can therefore have more different prey species. As a consequence, food webs with a large fraction of host-parasite interactions will tend to have smaller connectance than webs with few or no parasites. This expectation is rigorously verified in real food webs [10]. For example, in the lowest-connectance food web (Grassland [25]) almost all links are from large to small species. Similarly, adding parasites [28] to the Ythan Estuary food web [27] decreases the connectance. The value of the scaling exponent η is however unchanged in all these cases (see Tab. 1).

Whether the high variability of the fraction of host-parasite interactions in food webs is due to a systematic subjective bias in the data is an interesting but unanswered question. Therefore it is not clear whether the connectance varies due to either intrinsic or experimentally induced reasons. However, it is straightforward to note that the variability of c accounts for the nonuniversal behaviour of related quantities such as the clustering coefficient C and, as mentioned in Section 2, the degree distribution $P(k)$ [8]. By contrast, note that even if in

principle the abundance of loops also affects the average distance D (see for instance the relatively large value of D in the lowest-connectance web in Tab. 1), in food webs the effect is suppressed since, due to the efficient shape of the spanning tree, the distances from the environment (or in other words the number l_{max} of trophic levels) are always small independently of the connectance. This suggests that C and $P(k)$ vary due to the nonuniversal behaviour of c, whereas D and l_{max} are always small due to the universal small value of η.

4.4 Food web models

We finally compare the empirical results to the outcomes of various models [5,33,17] and show how our interpretation can help to improve some aspect of food web modelling.

The *Cascade Model* [5] and the more recent *Niche Model* [17] generate food webs in a static fashion, by assigning each species i a variable x_i and by drawing a link from species i to species j according to some rule depending on the variables x_i and x_j. Both models introduce a single tuning parameter which implicitly determines the connectance of the webs [5,17]. Although the *Niche Model* improves the predictions of the *Cascade Model* by successfully reproducing a wider range of observed properties [17] (see also the discussion regarding the average distance and clustering coefficient), both models do not reproduce the empirical value $\eta \approx 1.13$ of the scaling exponent. The spanning trees of the model webs display values of η systematically smaller than the observed one [10]. However, due to the static character of the models, the high degree of efficiency has not to be interpreted as the result of some optimization process, but simply as a particular property of the randomly generated webs [5,17].

By contrast, the *Webworld Model* [33–35] is an example of a dynamic model where food webs are first generated in a random initial state and then evolve through speciation and extinction of species. This is accomplished by assigning each species a (time-dependent) set of features determining their trophic abilities and therefore food web topology. The topology can now range from a fully connected to a chain-like web as in Figure 3. In any intermediate case, many quantities (including η and c) undergo an initial transient evolution and then fluctuate about a stable 'asymptotic' value [33]. Interestingly, during the evolution c increases and η decreases from the corresponding initial values [10] (therefore both efficiency and stability increase). For a suitable parameter choice, the asymptotic webs display the empirical value of η. However, this parameter choice yields an asymptotic value of the connectance $c \approx 0.12$ [10], therefore only the webs consistent with the 'constant connectance hypothesis' [29] mentioned in Section 2 are correctly reproduced. This means that the model webs are close to the empirical ones dominated by ordinary prey-predator interactions, but are significantly different from those including many host-parasite interactions. This argument is consistent with the hypotheses of the model, since when species evolve they can develop 'new' features (and hence additional incoming links) irrespective of whether their body size is larger or smaller than their resource. In other words, the aforementioned stronger evolutionary constraints limiting the number of incoming links of parasites are not taken into account.

In summary, our observation of a possible 'decoupling' of the spanning tree topology from the loop structure strongly suggests that, in order to reproduce both features, static and dynamic food web models need at least two independent parameters tuning network topology, each accounting for the properties of one subset of the network.

5 Conclusions

Food web ecology has recently benefited from the advances in the theory of complex networks. However, several studies show that most topological properties which are ubiquitously found in many real-word networks display an 'anomalous' behaviour in food webs, denoting a seemingly problematic or irregular structural organization. Our results reveal that, when the fundamental functional aspects of resource transportation is properly characterized, interesting universal food web properties emerge. Our findings allow for an interpretation of food web topology as the result of the interplay of universal mechanisms (trade-off between maximizing resource input and minimizing interspecific competition) shaping the topology of the spanning trees and of nonuniversal mechanisms (development of more or less links in food web evolution depending on the abundance of host-parasite interactions) determining their loop structure. The variability of many quantities and the relative stability of others can be simply reconciled within such disassembling of food web structure. As we showed, these results are also helpful in suggesting how to improve current food web modelling.

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