



View point

## Food web networks: Scaling relation revisited

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### Abstract

Food webs seem to possess scale invariant attributes among which efficiency has been recently included. Considering food webs as transportation networks it has been shown that minimum spanning trees, topologies that minimize cost for delivering medium, satisfy a universal scaling relation. It is not clear, however, whether resource distribution follows the criterion of minimum cost, because longer, less efficient routes are used as well. Because of this, instead of focusing on minimum length spanning trees (MLST) we consider directed acyclic graphs (DAGs) as better descriptors of food web hierarchies. Twenty well known empirical food webs have been transformed into DAGs and a scaling relation has been observed between number of nodes and their level of effective connectivity. Although we derived the scaling relation for DAGs using topological arguments, the exponent of the equation  $C \propto A^\eta$  shows same mathematical properties than its functional counterpart computed through flow analysis. This suggests that  $\eta$  can be used as a proxy for efficiency in food webs. The values of this coefficient for DAGs are lower than the ones obtained for minimum spanning trees, suggesting that food webs lie in the range of medium-to-low efficiency networks. This challenges the idea that these systems would be more efficient than other types of networks.

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### 1. Introduction

Scientists always look for invariant properties in the understanding that these attributes help to unveil organizing principles of nature (Rodríguez-Iturbe and Rinaldo, 1996; West et al., 1999). Ecologists are not

exceptions in this respect. Food web ecology, in particular, has become a particularly fertile arena for discussion about invariant properties. Several food web features, such as chain length, predator/prey ratio, fraction of species that occupy definite trophic positions, and number of connections per species, have been documented to be scale-invariant (Briand and Cohen, 1984, 1987; Sugihara et al., 1989). In parallel, however, other authors have cast doubts on the validity of these findings, inflating a debate whose

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most significant outcomes have populated scientific journals (Havens, 1992; Martinez, 1992, 1993, 1994; Deb, 1995; Bersier and Sugihara, 1997).

One recent study (Garlaschelli et al., 2003) states that the allometric equation  $C \propto A^\eta$  (universal scaling relation) that applies to transportation networks (rivers and metabolic networks, Banavar et al., 1999), holds also for food webs. Extending the original definitions,  $A$  would measure the amount of energy entering at any single node of the web and  $C$  would represent the total quantity of resource in the food web at any instant of time. The scaling exponent  $\eta$  would measure the efficiency of transfer, intended not as the usual trophic efficiency of transfer from one trophic level to another, but, rather, an overall measure of the extent at which the network optimizes resource delivery (Banavar et al., 1999, 2000; Garlaschelli et al., 2003).

The scaling exponent  $\eta$  ranges from 1 to 2 when there are no Euclidean dimensions to consider (e.g. this is not the case of river network or blood circulation) (West et al., 1999). These two extreme values pertain, respectively, a star-like structure, where all the nodes are directly connected to a central node (source) representing the external environment (maximum efficiency,  $\eta \approx 1$ ), and a chain-like structure, in which the nodes are sequentially linked with each other starting from the environment (minimum efficiency,  $\eta \approx 2$ ). The “source vertex”, or environment, represents the ultimate source of energy or resources for the network; it will be called “root” henceforth.

The allometric relation has been derived assuming that energy distributes to species in the web network

using minimum length spanning trees (MLST), topological architectures made of the minimum number of links necessary to keep the graph connected. In ecological terms, thus, a minimum spanning tree can be seen as the collection of pathways that allows energy (food) to reach all species at the minimum cost. When the magnitude associated with links is not specified, and there is no dissipation, this minimum cost exactly corresponds to the minimum distance from every node to the root, and the calculation of  $A$  and  $C$  is simplified. So  $A_i$  ( $i = 1, 2, 3, \dots, k$  nodes) becomes the number of species that feed directly or indirectly on  $i$  and  $C_i$  simply adds up the  $A$  values over the same set of nodes. This definition matches with the general one studied for other transportation networks only if the graph is tree.

If energy delivery in ecosystems was organized according to the criterion of minimum cost, the food webs would reduce to minimum spanning trees, with massive removal of links (see, for example, Table 1) and oversimplification of trophic hierarchies. Ecological consequences would be a null importance of omnivory and drastic changes in many species' trophic behavior. Studies on food web (Polis and Strong, 1996; Bondavalli and Ulanowicz, 1999), on the other hand, have revealed that matter and energy circulate in complex ways, longer pathways contribute to resource allocation in food webs as well, and trophic behaviors are not as simple as described by spanning trees. Thus, minimum spanning trees oversimplify the trophic portrait of ecological organization and one may ask whether food webs obey allometric scaling as predicted using spanning trees. To explore

Table 1  
The 20 ecological networks analyzed

System	# Nodes	# Edges	# MLST	# DAG	System	# Nodes	# Edges	# MLST	# DAG
Cone Spring	6	10	5	7	Upper Chesapeake	35	168	58	124
Cedar Bog Lake	10	22	13	15	Middle Chesapeake	35	160	66	113
Somme Estuary	10	27	17	19	Chesapeake Bay	37	126	54	101
Ythan Estuary	14	41	16	26	Lake Michigan	37	177	81	141
Baltic Sea	16	43	19	33	Mondego Estuary	44	357	133	227
Crystal River	22	64	28	45	St. Marks River	52	297	151	258
Charca de Maspalomas	22	61	31	48	Gramminoids Marshes	67	798	239	537
Lago Scuro	26	199	116	149	Cypress wet season	69	565	235	456
Narragansett	33	161	82	120	Mangrove	96	1367	368	1182
Lower Chesapeake	35	128	51	93	Florida Bay	126	1956	916	1730

# Nodes is the number of nodes (including the root); # edges is the number of edges before cycles are removed; # MLST is the number of edges remaining using MLST procedure; # DAG is the number of edges remaining using DAGs. See Supplement for complete data set and references.

this issue we thought that more appropriate descriptors for food web could be directed acyclic graphs (DAGs, henceforth).

Twenty selected food webs, obtained from energy flow networks pertaining to different ecosystems and that were described in literature, have been reduced to DAGs. While showing that these topologies are better representations of food webs than minimum spanning trees, we prove that a scaling relation for these structures can be found on a topological basis. Taking advantage of the properties of linear algebra, we propose a tentative ecological meaning for parameter  $C$  of the scaling relation, which has never been clearly defined for food webs (Garlaschelli et al., 2003). We show also that our scaling exponent has same mathematical properties than its original counterpart (Banavar et al., 1999).

This makes possible using it as a proxy for efficiency in food webs. The twenty DAGs we analyzed show lower efficiency than the corresponding minimum spanning trees, challenging the idea that food webs are more efficient than other types of networks (Garlaschelli et al., 2003).

Recent investigations (Dodds et al., 2001; Kozłowski and Konarzewski, 2004; Makarieva et al., 2003, 2005) highlighted some controversial aspects inherent in the distributive network models proposed by West et al. (1999) and Banavar et al. (1999). Such inconsistency concerned the value of the scaling exponents that the former authors calculated as multiple of  $1/4$  instead of the expected  $1/3$ . In this work, we do not consider the Banavar exponent as a reference value for food webs; rather, in developing our argument we are only interested in comparing mathematical properties for the new exponent we calculate for food webs: in doing so we will be able to propose an ecological meaning for it.

## 2. Food webs: a comparison between minimum length spanning tree (MLST) and directed acyclic graph (DAG)

Rooted spanning trees (the notion of tree comes from Cayley, 1891) are collections of  $N - 1$  nodes, which are attached, directly or indirectly, to an origin node called root.  $N - 1$  edges (directed links) make these structures connected. In particular, in these

topologies a single path connects each node to the root. Main steps of the algorithm used in searching for spanning trees are detailed in Appendix A. Spanning trees can be identified in any connected graph. The minimum length spanning tree of a graph defines the subset of edges that minimize the length of the paths from the root to every node and yet maintain the graph connected.

Graphs are used to represent ecological food webs. Nodes and edges are, respectively, the trophospecies and their feeding interactions. The root here represents the external environment, the ultimate provider of energy to the whole web. Searching for MLST in a food web graph means identifying the shortest pathway that connects every species to the environment. An example of minimum length spanning tree is depicted in Fig. 1b, in which the root is the black vertex. This graph originates from the hypothetical food web of Fig. 1a.

Banavar et al. (1999, 2000) derived an allometric relation between the quantity of resource exchanged at node  $i$  ( $A_i$ ) and the cost of its transfer ( $C_i$ ) for the most efficient class of transportation networks in a wide variety of systems. Garlaschelli et al. (2003) extended this allometric relation to food webs, once reduced to MLST.

The two parameters,  $A$  and  $C$ , are like fingerprints for every node. For food webs ( $A_i$ ) is the number of species that directly or indirectly feed on the  $i$ th node plus the node itself; adding up these values for the  $i$ th node (i.e. summing all the values of  $A$  pertaining its direct or indirect predators) yields  $C_i$ . It has to be noted that for food webs the two parameters have been calculated on a pure topological basis, whereas

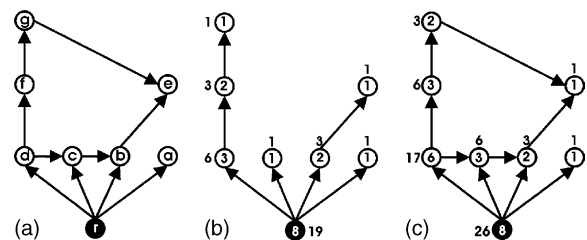


Fig. 1. A hypothetical food web (a) and its sub-graphs corresponding to a minimum spanning tree (b) and the directed acyclic graph (c) (in this case no edge has been removed because the original network was already acyclic).  $A$  and  $C$  are given inside and outside each node, respectively. The filled circle designates the root node (modified from Garlaschelli et al., 2003).

Banavar et al. (1999) approached the question in a functional way. Only the particular structure of MLST allows extending the theoretical results known for the general definition of  $A$  and  $C$  (including the theorem yielding the limits  $1 > \eta > 2$ , Banavar et al., 1999) to the results obtained by Garlaschelli and colleagues. In fact, when the link magnitude is not specified, and there is no dissipation, the minimum cost corresponds exactly to the minimum distance calculated from every node to the root: the functional approach and the topological one matches with one another.

Here, we face some problems. First, a clear ecological meaning for  $C$  has never been introduced. In the flow-based approach each node in the tree is assumed to consume one unit of currency; it follows that what enters node  $i$ , that is  $(A_i)$ , must be sufficient to satisfy the requirement of that node and that of all the nodes that depend on it for their requisite medium. In this case  $C$  is obviously a cost function because it computes the whole amount of currency needed to maintain that set of nodes at any instant of time. When  $A$  is computed as the number of direct and indirect predator feeding on every node, the meaning of  $C$  as cost function remains somehow vague.

Second, there is a problem regarding food web representation. As a first step in the MLST search species are assigned to integer levels (Appendix A) that are calculated as the minimum possible distance from the root, which occupies conventionally level 0. All the nodes that are linked directly to it belong to level 1; those directly connected with the latter occupy level 2, and so forth. Thus, a minimum length spanning tree ordines species along the energy route in a similar way that Lindemann's (1942) trophic hierarchy does. If a species feeds both as a primary carnivore and a secondary carnivore it will be assigned to primary carnivores in the MLST, as this role implies a shorter connection to the root in terms of trophic steps. With reference to Fig. 1a the top-right node, which behaves partially as a top predator, is reduced to a primary consumer in the corresponding MLST (Fig. 1b). Thus, from an ecological point of view, ecosystems becomes oversimplified when described by MLST (Polis, 1991; Abrams et al., 1996; Raffaelli et al., 2002).

By using integer trophic levels in the way the MLST does, a variety of different trophic hierarchies are reduced to the same one because species with

different discrete trophic positions are assigned to the same trophic level. It is like whether a high number of species, say  $n = 100$ , were ordered in a lesser number of trophic levels, say  $l = 6$ . The maximum number of trophic hierarchies (ordered sequences of trophic levels), ranging from the linear chain ( $n$  trophic levels with one species each) to a uniform community (a single level containing all species) is:

$$H_{l,n} = \sum_{j=1}^l (S(j,n)j!) \rightarrow H_{6,100} = \sum_{j=1}^6 (S(j,100)j!) \\ = 6.53E + 77,$$

where  $S(j,n)$  is the corresponding Stirling number of the second kind (Appendix B). Although this number is very high the fraction of hierarchies (with no bias) that can be formed by grouping 100 species in 6 trophic levels is  $(H_{6,100}/H_{100,100}) = 1.17 \times 10^{-96}$ . This means that many food webs are represented by the same structure/hierarchy, even if they were different before applying MLST: an over-simplification of food web hierarchy.

Directed acyclic graphs overcome these difficulties. They preserve multiple links, pruning away only those necessary to close directed cycles (feedback arcs). In the MLST procedure any edge from a node  $j$  to a node  $k$  is removed if the level assigned to  $j$  is greater or equal than  $k$ 's. This produces a drastic reduction in the number of links with respect to the original food web. In a DAG only the feedback edges in the depth first search tree of the root node vanish (Appendix C). In other words, only those edges that point back to a node that has been already visited are removed when food webs are explored starting from the root. In summary, the MLST simply excludes all closed structures (compare Fig. 1a with its MLST in Fig. 1b). Whereas the DAG retains any closed structure that is not a circuit, being the latter a sequence of links that leaves a node and return to it by following the direction of links.<sup>1</sup> Because there are no true circuits in the web of Fig. 1a its structure is preserved in the corresponding DAG (Fig. 1c). In a MLST the maximum number of links is  $N - 1$  ( $N$ ,

<sup>1</sup> While there is no problem in computing  $A$  in the presence of closed structures that are not circuits, the presence of directed cycles complicate the computation because they form pathways of an infinite length.

number of nodes) whereas in a DAG it is higher, and equal to  $N(N - 1)/2$ .

Because multiple pathways are retained in DAGs also the trophic identity of the species remains unaltered, as shown by the top-left node of the web of Fig. 1a. It follows that DAGs do not alter the structure of the hierarchies. Because they are more conservative in terms of trophic structure than MLST, DAGs are plausible representations of the trophic complexity of food webs (Polis and Strong, 1996).

Another virtue of these structures is that there exists only one DAG for any food web graph, once the root node has been specified. On the contrary many spanning trees can be traced in a food web, and, to find a relationship between  $A$  and  $C$ , each value of  $A$  must be compared with the average of the corresponding values of  $C$  (Garlaschelli et al., 2003).

The computation of  $A$  and  $C$  for a DAG is the same as for MLST:  $A_i$  counts the number of reachable nodes (direct and indirect predators) from node  $i$ ;  $C_i$ , the sum of the  $A$  values for the same set of nodes plus  $A_i$ . However, when computed for a DAG,  $A$  and  $C$  do not match with their flow-based counterparts (Banavar et al., 1999). Consistency holds only for MLST. To make this point clearer, consider node  $d$  in Fig. 1c.  $C_d$ , computed by adding up the  $A$  values of the nodes that receive food from  $d$ , is equal to 17. Recalling the original definition for  $C$  this value would equal the amount of flow units necessary to keep alive this group of nodes, if each of them needs one flow unit, as it is usually assumed. However, because the pathway  $d \rightarrow f \rightarrow g \rightarrow e$  provides the unit flow necessary to sustain  $e$ , what comes to it via the other path  $d \rightarrow c \rightarrow b \rightarrow e$  gives rise to an excess energy to this node. In synthesis,  $C = 17$  would overestimate the flow requirements of the group of nodes that depends on  $d$ . That is to say, using  $A$  and  $C$  values computed as we have done as synonymous of flow units, would yield systematic over estimations. This is due to the presence of multiple links that point to the same node. In the case of MLST such overestimation does not occur as there is only one link pointing to any node.

So, in this analysis while  $A_i$  is the number of nodes reachable from node  $i$ ,  $C_i$  computes the number of all pairs “origin-destination” that can be identified in the set of nodes that depend on node  $i$  and that can be identified in the graph following the direction of links.

Using linear algebra (see Appendix D for details) this calculation is facilitated because it is simply the number of non-zero coefficients of the matrix  $P^{\text{DAG}} = [I - T^{\text{DAG}}]^{-1}$ , where  $I$  is the identity matrix and  $T^{\text{DAG}}$ , the adjacency matrix of the sub-graph formed by the  $i$ th node and all its predators. In this matrix, every non-zero coefficient witnesses that a pathway exists between the row node and the column node. Thus,  $C_i$  measures the overall number of effective connections between nodes belonging to the subset that depends on node  $i$ . We call these connections “effective” because they include indirect linkages, whereas in food webs usually two node are said to be connected if there is a direct junction between them. Although any coefficient in matrix  $P^{\text{DAG}}$  shows the number of pathways between any two nodes,  $C$  is equal to the number of these non-zero terms: only the fact that the row node sees somehow the column node matters, independently from how many paths make their connection possible. While  $C_i$  quantifies the level of connectedness of the subsystem that depend on node  $i$  through both direct and indirect paths, it also gives a perception of how extended are the branches in a DAG (and in the food web).

We derived the bounds for  $C$  and  $A$  values for a generic DAG, and found that they do coincide with the ones for MLSTs (Appendix D). In particular,  $C$  values are bounded to the maximum possible number of couples of nodes origin-destination that in theory can exist in the food web. We also demonstrate that it is still possible to compare  $A$  and  $C$  for DAGs and MLSTs and they have the same topological (and ecological) significance. We stress that, although a DAG is usually not a tree, a tree is always a DAG. The procedure presented here can therefore be seen as the generalized case of the one presented by Garlaschelli et al. (2003).

The level a certain node belongs to in a spanning tree depends on where the root is positioned. Although the literature is full with examples of food web structures (Cohen et al., 1990; Menge, 1995, and see references in Montoya and Solé, 2003) in many of these, however, the environment is not explicitly considered and its position has to be imposed. Common sense intuition would suggest linking the root to basal species, those having no incoming edges. The main point here is that root position affects the trophic level a certain species is assigned to, and ambiguities about which species import resource from



outside the system render trophic hierarchies in MLST extremely uncertain.

Searching for a DAG does not require assigning each variable a level, but root's position must be defined anyway because also its structure depends on where the source vertex is positioned. To avoid ambiguities with respect to this we derived our food webs from energy flow networks, in which the root position is determined by input flows (Ulanowicz, 1997; Ulanowicz et al., 1998). To perform this study we used 19 published and 1 unpublished networks (see Table 1) in which the number of species ranges from 5 to 125 ( $\mu = 38.5$ ,  $\sigma = 30$ ). We point out here that in these energy flow networks most species are trophic species, that is taxa organized to represent living compartments based on probable diet and life history characteristics. Only a few nodes of the networks are representative of taxonomic species.

### 3. Results

Main features of the 20 selected food webs are described in Table 1. They have been investigated using both MLST and DAG procedure.  $A$  and  $C$  values were then computed for minimum spanning trees and DAGs according to the definition given in the preceding section. When the number of spanning trees exceeded  $10^6$  (Appendix B) we considered only the first  $10^5$  trees, assuming this set as a good sample of the entire population.

To test the existence of the allometric property  $C \propto A^\eta$  we plotted  $\log(C)$  versus  $\log(A)$ . We obtained the 40 linear regressions (20 systems, 2 algorithms) that are presented in Fig. 2.

Considering how  $A$  and  $C$  have been defined it is not clear whether the slope of these regression lines accounts for efficiency ( $\eta$ ) as it has been defined in the flow-based approach (Banavar et al., 1999). However, in Appendix D, we demonstrate that our  $\eta$  shows the same mathematical behavior than the one originally computed by Banavar et al. (1999). In fact, its value ranges from 1 (star like structure) to 2 (maximally connected DAG). In all cases, for the same system, DAG produced higher slope than MLST. The two sets of slopes do not overlap: MLST-slopes range from 1.136 to 1.140, whereas DAG-based range from 1.592 to 1.995. A one-tailed paired  $t$ -test showed that the

differences were significant ( $t = 15.827$ , d.f. = 19,  $P < 0.001$ ).

Once established that the two algorithms produced different outcomes, we pooled all  $\log(C)$  and  $\log(A)$  values and performed an ANOVA to test for a common slope the dependent variable  $\log(A)$  with the type of algorithm and system size. Both interactions ( $\log(A)$ :size and  $\log(A)$ :algorithm) yielded significant differences ( $F_{1,707} = 21.511$ ,  $P < 0.001$  and  $F_{1,707} = 1242.557$ ,  $P < 0.001$ , respectively); that is to say when all the coefficients are considered a size effect can be observed.

This size effect somehow contradicts the hypothesis that a scaling relation exists in MLST and DAG. However, when we used only the 10 larger networks (# of nodes  $> 35$ ) among those considered in this study we found that this effect vanishes ( $F_{1,531} = 3.080$ ,  $P < 0.079$ ; note that although the number of networks is halved, the overall number of nodes, that is the degrees of freedom in the  $F$ -test, remains quite high). This can be explained by the fact that every time  $A = 2$  then  $C$  is equal to 3. For  $A$  greater than 2,  $C$  may assume different values depending on the structure of MLST and DAG. Small size networks produce MLST and DAG in which a high proportion of vertices share the fixed combination  $A = 2$  and  $C = 3$ , and this forces the slope of the regression lines to higher values (Garlaschelli et al., 2003). It must be added, however, that this effect is due mainly to MLST, whereas in DAG this problem is less pronounced.

Plotting the root values ( $A_0C_0$ ) for all systems (Fig. 3), however, we found that, while the effect of the algorithm is still strong ( $F_{1,34} = 345.7195$ ,  $P < 0.001$ ), that due to size vanishes ( $F_{1,34} = 0.0928$ ,  $P = 0.7625$ ). If we consider that the value of the root node summarizes the contribution of all other nodes in the graph, we can state that allometry is maintained.

Also Fig. 3 highlights the generality of our results. The significant regression line suggests that the allometric relation found between size of food webs ( $A$ , number of nodes) and overall connectedness ( $C$ , realized or effective connections) holds across different ecosystems.

### 4. Discussion

In this paper, we reconsider the allometric relation  $C \propto A^\eta$  that was derived considering food webs as

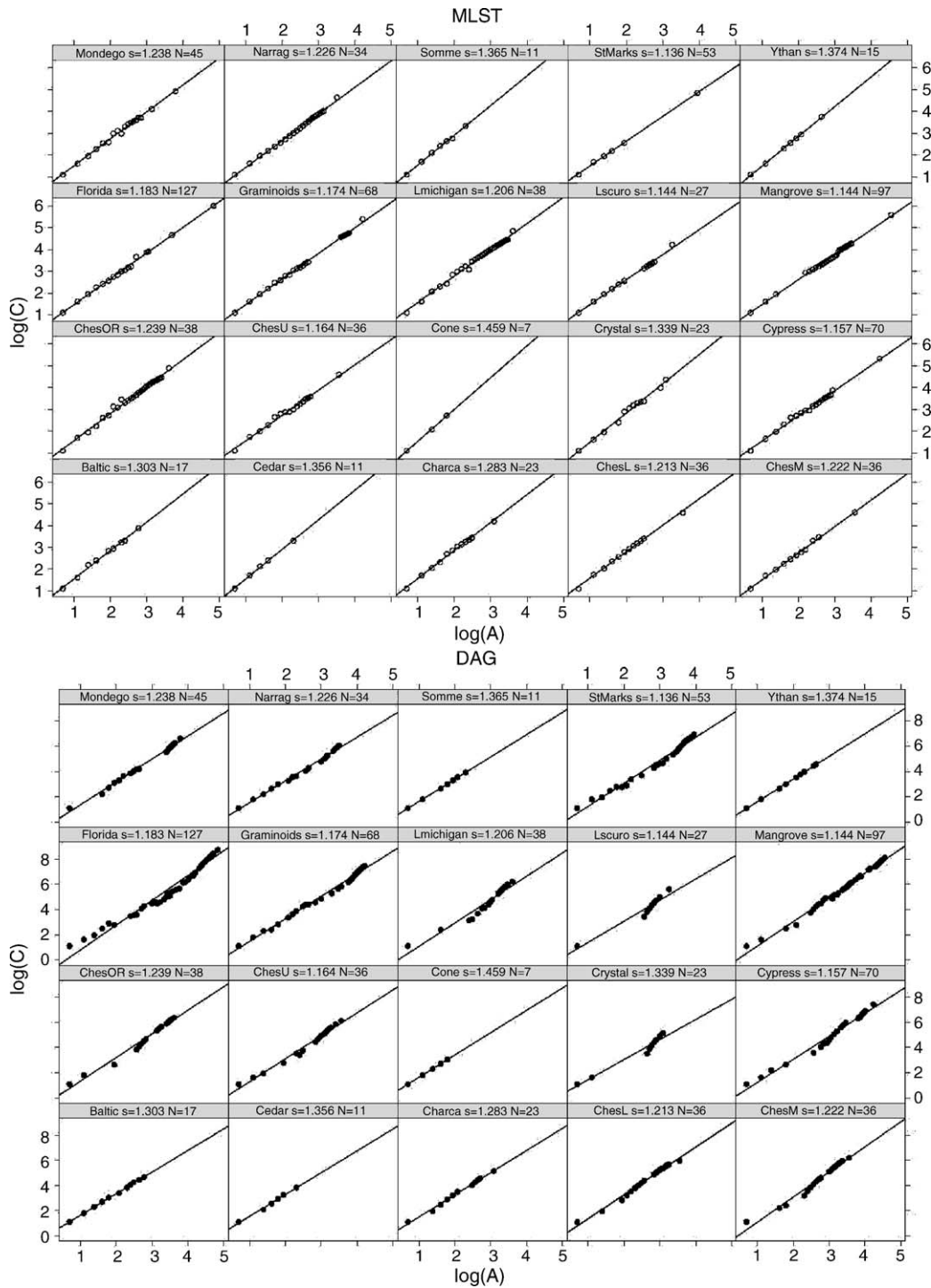


Fig. 2. Regression lines of  $\log(C)$  versus  $\log(A)$  for minimum length spanning trees (upper) and directed acyclic graphs (lower) obtained from the 20 food webs listed in Table 1. For each line the slope ( $s$ ) and the number of points ( $N$ ) is given. Terminal nodes ( $A = 1$ ,  $C = 1$ ) have been excluded because they can force the exponents toward artificially high values.

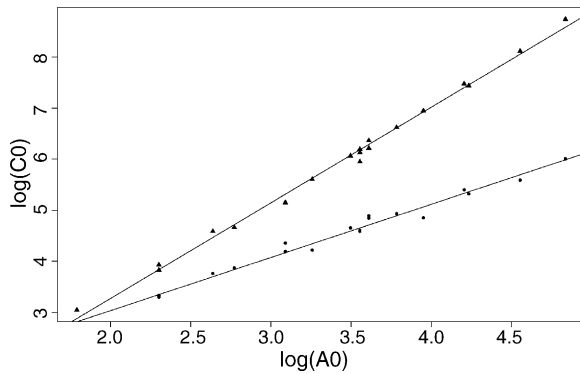


Fig. 3. Regression lines obtained by plotting  $\log(C_0)$  versus  $\log(A_0)$  values for MLST ( $R^2 = 0.9834$ ,  $F_{1,18} = 1127$ ,  $P < 2.2E - 16$ ) and DAG ( $R^2 = 0.9945$ ,  $F_{1,34} = 3426$ ,  $P < 2.2E - 16$ ).

transportation networks, reducible to minimum spanning trees (Garlaschelli et al., 2003). The gross simplifications that spanning trees operate on the original food webs (Polis and Strong, 1996) cast doubts about the validity of these structures as adequate descriptors.

We used directed acyclic graphs as more adequate proxies for food webs and extended to them the topological approach used by Garlaschelli and colleagues on MLST. Although an ecological meaning for  $C$  has never been proposed, the way we used to compute the  $C$  values (using linear algebra) suggest that this parameter is a measure of the effective connections that are established in the food web ( $C_{\text{root}}$ ) or in that part of the web whose node are all rooted in node  $i$  ( $C_i$ ). This effective connectivity scale with the size of the food web and this allometric relation has the usual form  $C \propto A^\eta$ . However, due to the different definition we used for  $A$  and  $C$  one may wonder whether the scaling exponent obtained in this study holds the same meaning than the one obtained by Banavar and colleagues using flow analysis.

The ranges of variation for our exponent coincide with that of Banavar's. The fact that the value Banavar et al. (1999) obtained was mathematically controversial does not affect the limits of variations for the scaling exponent in connected food webs as the transitive closure matrix cannot have less than  $N$  edges (where  $N - 1$  is the number of species in the food web) and more than  $N^2$  edges.

We found that the ranges of values for  $\eta$  (see Appendix D) in the two cases coincide: because of

this, reasonably, our scaling exponent can be used as a proxy for efficiency in food webs. On the other hand it is widely recognized that a close relation exists between the anatomy of networks and their functions (Strogatz, 2001); according to this, food web efficiency in delivering the resources must be related to topological extension of their branching structure, measured through the level of effective connectivity in any part of the web.

Taking our scaling relation as a proxy for efficiency we expect food webs to be less efficient than expected, as the slope of the regression lines is higher for DAGs in comparison with MLST (the higher the slope the lower the efficiency). Accordingly, energy delivery in ecosystems would not be organized according to the criterion of optimal efficiency. In fact whether delivering at a minimum cost would represent the optimal solution, a suite of interacting constraints such as food preference (Chesson, 1983), size effect in predator-prey interactions (Hastings and Conrad, 1979; Cousins, 1987), dynamical features (Pimm and Lawton, 1977; Sterner et al., 1997), and efficiency in energy transfer between trophic levels (Hairston and Hairston, 1993) determine which flow patterns really govern resource distribution in ecosystems. These evidences challenge the idea of ecosystems as more efficient than river and vascular networks in delivering medium (Garlaschelli et al., 2003; Banavar et al., 1999). In this respect, we averaged the slopes calculated for DAGs and MLSTs for each of the 20 selected networks, and we obtained values in the range 1.41–1.61. On average, thus, we expect that if our scaling exponent could measure efficiency the food webs considered in this study would be classified as medium-to-low efficiency systems.

Perhaps the allometric relation described here suggests further thoughts. Consider the root node: it holds that  $C_{\text{root}} = A_{\text{root}}^\eta$  and because  $A_{\text{root}} = V$  then  $C_{\text{root}} = V^\eta$ . As shown in Appendix D, however,  $C_{\text{root}}$  is the number of non zero coefficients of the adjacency matrix coupled with the transitive closure of the food web, that is the number of effective connections between any pair of nodes. Recalling that  $E/V^2$  is a general definition for connectance (Martinez, 1992) we can state that  $C_{\text{root}}/V^2$  is the connectance computed on the transitive closure. Compared with the usual connectance, which is based on the number of direct links in the web, this of the transitive closure, we



reiterate, consider connections established through either direct links or indirect paths. We propose to call the connectance of the transitive closure  $\chi$ . It is easy to show that an allometric relation between  $\chi$  and the number of nodes exists. In fact

$$\chi = \frac{C_{\text{root}}}{V^2} = \frac{A_{\text{root}}^\eta}{V^2} = \frac{V^\eta}{V^2} = V^{\eta-2}$$

Parameter  $\chi$  would range between 0 (star-like structure,  $V \rightarrow \infty$ ) and 1 (chain-like graph or completely connected DAG,  $V \rightarrow \infty$ ).

Results of this study are based upon a topological investigation of unweighted networks. This approach has limitations. The most significant one, in the context of this paper, is that unweighted edges lead to overemphasize rare interactions (Hairston and Hairston, 1993). The implicit assumption that the links are equal in value does not allow identifying those pathways that play a major role in energy distribution. By assigning the magnitude to interaction links, topologies that actually govern resource delivery would be identifiable. They, in turn, could be explored in search of allometric relations. This topic will be examined in further investigations.

When confronted with the structure of minimum spanning trees one may wonder whether they are mathematical/topological abstractions without any real counterpart. In minimum length spanning trees resource moves in a completely determined fashion, in the sense that there are no redundant pathways to reach a given node from the root and from any other node. According to this one may recognize in this structure something similar to the maximally constrained configuration in which an ecosystem would be expected to evolve in the absence of major external driving forces (Ulanowicz, 1997).

In addition to this topological correspondence, a functional analogy can be found between minimum spanning trees and maximally constrained networks. According to Ulanowicz (1990), the latter would emerge from a process wherein those pathways that foster more efficient transfers flourish at the expenses of less effective routes, so that the network will tend to become dominated by a few, intense flows. Minimum length spanning trees, on the other hand, maximize efficiency of transportation (Garlaschelli et al., 2003). As such they seem to be ideal

candidates to give a shape to the maximally efficient flow patterns that would emerge under the selective pressure of internal processes during ecosystem succession (Ulanowicz, 1990).

The tendency to select few, efficient connections, however, would be balanced by the need to maintain resilience, for which a certain degree of redundancy is necessary (Mac Arthur, 1955; Mageau et al., 1995). DAG, with their redundancy, would be intermediate topologies between two extremes: those in which redundancy is maximized, and the mostly constrained, highly efficient minimum spanning trees. These two extremes correspond to the initial and final states in Ulanowicz' model of ecosystem growth and development (Ulanowicz, 1990, 1997). We believe that this scenario is intriguing and deserves further attention.

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## Appendix A. Minimum length spanning trees

Garlaschelli et al. (2003) proposed a method for removing “weak” edges from food webs, obtaining a subgraph that can embed one or more spanning trees.

Here, we summarize this procedure for a better understanding of the technique.

We define a food web  $G$  as a digraph with  $V$  nodes (trophospecies) and  $E$  edges (trophic relations). A special node represents the “environment” (source of all spanning trees).

The procedure can be sketched in four steps:

- (a) assign a trophic level to every node;
- (b) remove the “weak” edges;
- (c) seek for spanning trees;
- (d) for each spanning tree compute the  $A$  and  $C$  values.

### A.1. Assigning the trophic level

In a food web, every node-species is connected, directly or indirectly, with the environment, that supplies the required energy. Thus, the food web is said to be rooted in  $r$  (the root node). From a graph theory point of view the underlying undirected graph of the food web digraph is surely connected and a simple path linking every species to the environment ( $r$  node) can be identified. Garlaschelli et al. assign to the first node ( $r$ ) the level  $L_0$ . Then recursively,  $L_1$  is assigned to all predators of the first node;  $L_2$  to all predators of  $L_1$ -nodes and so forth. Because the maximum distance between any node and the environment is somehow bounded (Post, 2002), there will be maximum four to six different levels no matter how big the system is.

### A.2. Removing “weak” edges

Thermodynamic constraints make longer trophic pathways weaker than the shorter one. Accordingly, every edge that goes from a node belonging to level  $L_i$  to a node belonging to level  $L_j$  with  $i \geq j$  is a “weak” link because the shorter way to go from the root to node  $j$  does not include the link in question. These “loop forming” edges, take part in undirected cycles (cycles of the underlying undirected graph).

### A.3. Seeking for spanning trees

There are many ways for listing all the spanning trees of a given digraph. We implemented the one based on DFS-search and backtracking (Read and Tarjan, 1975), because it is the simplest one. Note that the number of spanning trees of the simplified digraph (after removal of the “weak” edges) still could be very high (Appendix E; e.g. we found more than  $10^{25}$  spanning trees for the Cypress Wet ecosystem). In these cases we computed “only” the first 10,000 spanning trees, assuming that this would be a good sample of the entire population.

### A.4. Computing $A$ and $C$ values

The last step consists in computing the  $A$  and  $C$  values for each node in every spanning tree. The  $A_i$  value associated with a node  $V_i$  is the number of nodes

reachable from  $V_i$  plus the node itself. That is  $A_i$  is the number of predators (direct or indirect) of the  $i$ th trophospecies plus 1. The  $C_i$  value assigned to node  $V_i$  is the sum of all the  $A_j$  values of the predators of  $V_i$  plus  $A_i$ . Probing whether a graph possesses an allometric relation is possible by plotting  $\log(C)$  versus  $\log(A)$  for all nodes.

## Appendix B. Stirling numbers of the second kind

The number of ways to partition  $n$  elements into  $j$  nonempty boxes is given by the Stirling number of the second kind  $S(n, j)$  (Stirling, 1730) The notation used is the one proposed by Riordan (1980). The set  $[A, B, C]$  can be partitioned into three boxes in one way  $S(3, 3) = 1(\{A\}\{B\}\{C\})$ ; into two boxes in three ways  $S(3, 2) = 3(\{A\}\{BC\}, \{AB\}\{C\}, \{AC\}\{B\})$ ; in one box in one way  $S(3, 1) = 1(\{ABC\})$ .

Stirling numbers of the second kind can be recursively computed using the formula:

$$S(n, k) = S(n - 1, k - 1) + kS(n - 1, k)$$

This formula can be used to originate the so-called Stirling triangle (Table A1):

## Appendix C. Depth first search (DFS) and feedback edges: building a rooted DAG

DFS (Tarjan, 1972) is one of the most important graph-search algorithms. DFS visits all nodes that are connected to an initial node (root of the DFS-tree); it uses a recursive algorithm to go deeper into the graph.

Table A1  
Stirling numbers of the second kind: ways to partition  $n$  objects (row numbers) into  $j$  nonempty boxes (column numbers)

	1	2	3	4	5	6	7
1	1						
2	1	1					
3	1	3	1				
4	1	7	6	1			
5	1	15	25	10	1		
6	1	31	90	65	15	1	
7	1	63	301	350	140	21	1

In particular, DFS is carried out on the first node by carrying out DFS on its neighbours.

This algorithm can be quickly written assigning different colours to the various nodes according to the following specifications:

- white: node to be visited;
- grey: discovered node;
- black: visited node.

Nodes that during the search are encountered for the first time become grey. Returning to a node once it has been discovered makes it black. This occurs when there are edges that point back to a grey node (“feedback edges”). Those arcs form directed cycles in the graph.

In pseudo-code, the procedure can be written as:

```
DFS_Visit(A: node) {
  mark A grey
  for every node B
  if an edge connecting A to B exists {
    if B is white then DFS_Visit(B)
    if B is grey then the edge AB is a feedback edge:
      remove AB edge
  }
  mark A black
}

Main {
  mark all nodes white
  DFS_Visit(root)
}
```

See [Cormen et al. \(1989\)](#) for a complete analysis of DFS algorithm and examples.

## Appendix D. Allometry in spanning trees and directed acyclic graphs: deriving bounds and properties

### D.1. Definitions

A directed graph  $G(V, E)$  is a collection of  $V$  nodes and  $E$  oriented edges connecting them. In a Spanning Tree, the  $V$  nodes are connected by  $V - 1$  edges; every node has one incoming edge and may have more than

one outgoing edges. A directed acyclic graph (DAG) is a directed graph where no closed pathways can be formed following the direction of links. In every DAG there is at least a source (node with no incoming edges) and a sink (node with no outgoing edges). For every DAG there exists at least a way of disposing nodes so that, for every pair of nodes  $a$  and  $b$ , if  $a$  comes before  $b$  in the ordering then there cannot be any edge going from  $b$  to  $a$  (this way of ordering nodes is called topological sorting).

Any digraph can be represented by a  $V \times V$  adjacency matrix. In it every coefficient specifies if there is an edge going from the row-node to the column-one. Once topological sorting has been performed on a DAG the adjacency matrix takes the form of a strictly upper triangular matrix (that is to say a matrix where  $M[i, j] = 0$  if  $i \geq j$ ).

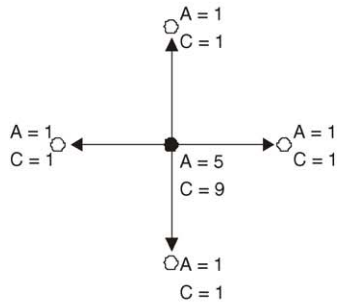
### D.2. Allometry in spanning trees

We define two quantities  $A$  and  $C$  associated with every node. From a graph-theory point of view  $A_i$  is the number of nodes reachable from the  $i$ th node.  $C_i$  is the sum of the  $A_j$ s of the nodes reachable from the  $i$ th node. An allometric relation between  $A$  and  $C$  is defined when  $\log(C_i)/\log(A_i) = \eta$  for all nodes.

The maximum value of  $\eta$  for a spanning tree is obtained when the nodes are sequentially connected to form a chain-like structure ([Fig. 4](#)). By disposing this linear chain made of, say,  $V$  nodes from left (root as the initial node) to right (terminal node, sink) and starting

MLST Maximal Efficiency

Configuration - STAR



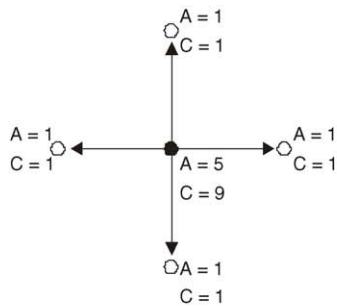
MLST Minimal Efficiency

Configuration - CHAIN



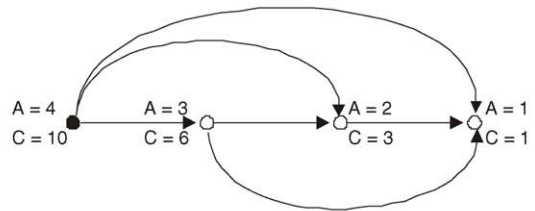
DAG Maximal Efficiency

Configuration - STAR



DAG Minimal Efficiency

Configuration - Maximally connected DAG



Maximally connected DAGs

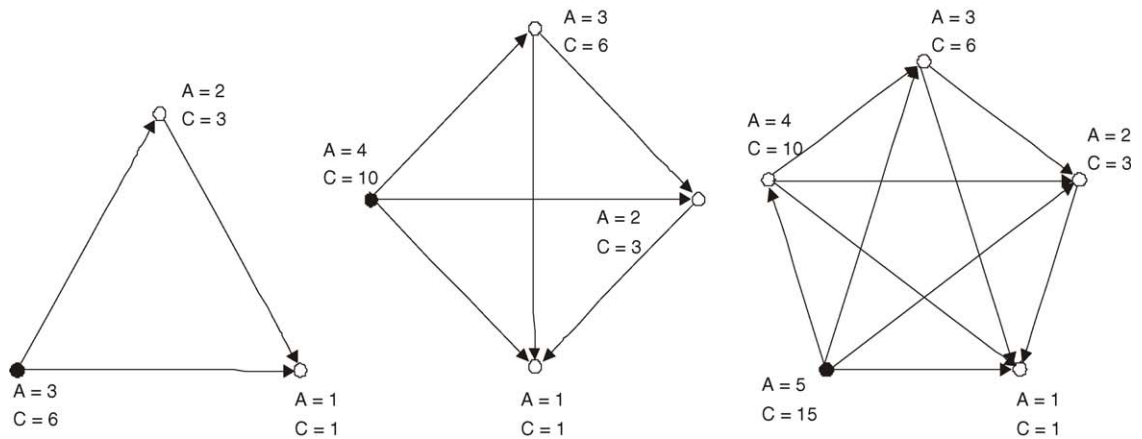


Fig. 4. Extreme configurations for MLST (top) and DAGs (middle); maximally connected DAGs (3–5 nodes) and their relation with geometry (bottom).

computing  $A$  values the other way around (from right to left) one obtains 1, 2, 3, . . . ,  $V$ . The  $C$  values are 1, 3, 6, 10, . . . (triangular numbers). This means that the  $C$  value of the root will be  $C_{\text{root}} = V(V + 1)/2$ .

For an infinite chain the value for  $\eta$  would be:

$$\eta = \lim_{V \rightarrow \infty} \frac{\log((V(V + 1))/2)}{\log(V)}$$

that, after applying l' Hospital's rule twice, yields  $\eta = 2$ .

The lower bound for  $\eta$  is obtained when the spanning trees possess a star-like configuration (Fig. 4). In this case, the  $A$  values will be 1 for all the nodes but the root, whose value still equals the number of nodes  $V$ . All the nodes will have  $C = 1$  except for the root whose value will be  $C = 2V - 1$ .

The minimum value of  $\eta$  for an infinite star is expressed by the limit

$$\eta = \lim_{V \rightarrow \infty} \frac{\log(2V - 1)}{\log(V)}$$

that, applying l' Hospital's rule yields to  $\eta = 1$ .

These properties of  $\eta$  have been obtained by Banavar et al. (1999) using flows-based considerations.

### D.3. Allometry in DAGs

In a DAG every node can have more than one incoming edges and the maximum number of edges is  $V(V - 1)/2$ . The maximally connected DAG is the one in which every node is directly connected to all the nodes that follows it. Such ordering sequences can be highlighted by a topological sorting, as the one represented in Fig. 4. In this sequence the last node reaches itself only, its immediate antecedent points to it and itself, and so forth. Finally the root reaches all the nodes.

As one can easily see, the values for  $A$  and  $C$  are the same computed for the chain-like spanning tree. Because  $A$  counts the number of reachable nodes its value does not change no matter how many pathways connect two nodes. As  $C$  is computed as a summation of  $A$  values it comes out that also the  $C$  values are the same. Thus, the scaling parameter  $\eta$  for a maximally connected DAG composed by  $V$  nodes is the same obtained for a  $V$  nodes chain. Because every spanning

tree is also a DAG, we can state that the minimum  $\eta$  for a DAG is obtained for a star-like structure as well.

The upper and lower bounds for  $\eta$ , therefore, do coincide and the values of  $\eta$  obtained for spanning trees and DAGs are directly comparable.

### D.4. Derivation of $\eta$ using linear algebra:

The values for  $A$  and  $C$  can be computed using linear algebra; in this way one also can have a perception of the ecological meaning of these two coefficients. In the case of a four-node linear chain, the Adjacency matrix would be:

$$T^{\text{ST}} = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

The transitive closure  $\text{Cl}(G)$  of a graph  $G$  is a graph which contains an edge  $E_{u,v}$  whenever there is a directed path from  $u$  to  $v$  (Skiena, 1990, p. 203). The  $T^{\text{Cl}}$  matrix associated with the transitive closure of the four-node chain can be obtained as  $T^{\text{Cl}} = [I - T^{\text{ST}}]^{-1}$ , where  $I$  is the identity matrix.

$$T^{\text{Cl}} = \begin{bmatrix} 1 & 1 & 1 & 1 \\ 0 & 1 & 1 & 1 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

This matrix renders automatically  $A$  and  $C$  values for every node:  $A_i$  will be the  $i$ th row sum;  $C_i$  will be sum of all coefficients of the sub-matrix obtained excluding the rows and columns belonging to nodes that are non reachable from the  $i$ th node. The first row sum is the  $A_{\text{root}}$  value and the summation across the whole matrix yields to the  $C_{\text{root}}$  value.

For a spanning tree, the matrix  $[I - T^{\text{ST}}]^{-1}$  includes coefficients with values 1 or 0, because in a spanning tree there can be just a pathway connecting any two nodes. This does not hold for DAGs. Consider a maximally connected four-node DAG like the one in Fig. 4. Its adjacency matrix would be:

$$T^{\text{DAG}} = \begin{bmatrix} 0 & 1 & 1 & 1 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$



the matrix  $P = [I - T^{\text{DAG}}]^{-1}$  will take the following form:

$$P^{\text{DAG}} = \begin{bmatrix} 1 & 1 & 2 & 4 \\ 0 & 1 & 1 & 2 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

Any coefficient computes the number of pathways linking row nodes with column node. To transform the matrix  $P$  into the Adjacency matrix of the transitive closure associated with the DAG we should build a matrix where a coefficient takes value 1 if the corresponding coefficient in  $P > 0$ , and 0 elsewhere, that is:

$$T_{\text{Cl}}^{\text{DAG}}[i, j] = \begin{cases} 1 & \text{if } P[i, j] > 0 \\ 0 & \text{elsewhere} \end{cases}$$

$$T_{\text{Cl}}^{\text{DAG}} = \begin{bmatrix} 1 & 1 & 1 & 1 \\ 0 & 1 & 1 & 1 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \end{bmatrix} = T_{\text{Cl}}^{\text{ST}}$$

This matrix is exactly the same than the one obtained for a chain-like tree (see before). Thus, a chain-like tree and a maximally connected DAG possess the same transitive closure. Because this matrix has been obtained for a maximally connected four-node DAG, one soon recognizes that the maximum value for  $A$ , which is  $V$  (number of nodes in the graph) can be computed by counting the number of 1s in the first row of the matrix, that pertaining the root node. Accordingly the maximum value for  $C$  will be  $V(V + 1)/2$ . The value  $\eta = 2$  when  $V \rightarrow \infty$  thus holds in both the cases of spanning tree and DAG.

#### D.5. Allometry and connectance

Considering the root node, the universal scaling relation found for DAGs takes the form  $C_{\text{root}} = A_{\text{root}}^\eta$ . Because  $A_{\text{root}} = V$  then  $C_{\text{root}} = V^\eta$ . As shown before, however,  $C_{\text{root}}$  is the number of edges of the adjacency matrix coupled with the transitive closure of the food web, that is it shows whether a connection exist between any pair of nodes (that can be either direct or indirect) of the graph. Recalling the general definition for the connectance  $E/V^2$  we can state that  $C_{\text{root}}/V^2$  is the connectance of the transitive closure, which is the connectance made of both direct and indirect

contributions. This highlights the ecological meaning of  $C$ . We propose to call the connectance of the transitive closure  $\chi$ . It is easy to show that an allometric relation between the connectance of the transitive closure and the number of nodes exists. In fact:

$$\chi = \frac{C_{\text{root}}}{V^2} = \frac{A_{\text{root}}^\eta}{V^2} = \frac{V^\eta}{V^2} = V^{\eta-2}$$

$\chi$  would range between 0 (star-like structure,  $V \rightarrow \infty$ ) and 1 (chain-like graph or completely connected DAG,  $V \rightarrow \infty$ ).

#### Appendix E. The matrix tree theorem

Given a digraph  $G(V, E)$ , with no self-loops, one can easily compute the number of spanning trees of the graph with the node  $V_i$  as a source (Harary, 1994). We define  $A[a_{i,j}]$  the adjacency matrix of the graph  $G$ . We construct a new matrix  $M^{\text{id}}[m_{i,j}^{\text{id}}]$  where:

- $m_{i,j}^{\text{id}} = -a_{i,j}$  if  $i \neq j$
- $m_{i,i}^{\text{id}} = \text{InDeg}(V_i)$

$\text{InDeg}(V_i)$  is the in-degree (number of edges incident to) of  $V_i$ .

The number of spanning trees starting from  $V_i$  is the value of any  $i$ th column entry of the cofactor matrix computed from  $M^{\text{id}}$ .

Given a  $4 \times 4$  adjacency matrix

$$A \equiv \begin{bmatrix} 0 & 1 & 1 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

the matrix  $M^{\text{id}}$  will become:

$$M^{\text{id}} \equiv \begin{bmatrix} 1 & -1 & -1 & -1 \\ -1 & 2 & 0 & -1 \\ 0 & -1 & 1 & 0 \\ 0 & 0 & 0 & 2 \end{bmatrix}$$

and the cofactor matrix where  $C_{i,j} = (-1)^{i+j} \text{Minor}_{i,j}$  where  $\text{Minor}_{i,j}$  is the determinant of the matrix

obtained by eliminating the  $i$ th row and the  $j$ th column:

$$C \equiv \begin{bmatrix} 4 & 0 & 0 & 0 \\ 4 & 0 & 0 & 0 \\ 4 & 0 & 0 & 0 \\ 4 & 0 & 0 & 0 \end{bmatrix}$$

In this case, the graph has four spanning trees starting from the first node. This theorem was proved by Tutte (1948).

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