

Scaling relations in food webs

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In the last three decades, researchers have tried to identify universal patterns in the structure of food webs. It was recently proposed that the exponent η characterizing the efficiency of the transport of energy in large and small food webs might have a universal value ($\eta=1.13$). In this work we establish lower and upper bounds for this exponent in a general spanning tree with a fixed number of trophic species and levels. When the number of species is large, the lower and upper bounds are equal to 1, implying that the result $\eta=1.13$ is due to finite-size effects and that the value of this exponent depends on the size of the web. We also evaluate analytically and numerically the exponent η for hierarchical and random networks. In all cases the exponent η depends on the number of trophic species K , and when K is large we have that $\eta \rightarrow 1$. Moreover, this result holds for any fixed number M of trophic levels.

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I. INTRODUCTION

Understanding energy and material fluxes through ecosystems is a prime objective to answer many questions in ecology [1–3]. Ecological communities can be studied via resource transfer in food webs [4]. These webs are diagrams showing the predation relationships among species in a community. Usually, a group of species sharing the same set of predators and preys is aggregated in one trophic species [5,6]. So each trophic species is represented by a node and denoted by an integer number $i=1, \dots, K$, where K is the total number of trophic species. A relation between a pair of nodes is represented by a link directed from the prey to predator. There are several quantities introduced in the literature to characterize the food web structure, such as the fractions of the species in the trophic levels (basal, intermediates, and top), the fractions of links among them, the connectance, the average distance between two nodes, the clustering coefficient, and the degree distribution. It turns out that all these quantities are nonuniversal [7] and dependent on the size of the food web. Possibly, the only variable with common agreement in the literature is the maximum number of trophic levels ($M \leq 4$). Garlaschelli *et al.* [8] have considered food webs as transportation networks [10,11] whose function is to deliver resources from the environment to every species in the network. In this case, food webs appear to be very similar to other systems with an analogous function, such as river and vascular networks. In their work they have represented a real food web by spanning trees with minimal lengths. For each species i the number A_i of species feeding directly or indirectly on i plus itself, or plus 1, is computed. We can interpret A_i as the quantity of resources flowing through the only incoming link of species i in the food web, being independent of the topology of the network. They also

computed the sum of link weights within the branch $\gamma(i)$ rooted at i : namely, $C_i = \sum_{k \in \gamma(i)} A_k$. By analogy with river networks, Garlaschelli *et al.* [8] have interpreted C_i as the transportation cost and it is dependent on the network topology.

The shape of C_i as a function of A_i follows a power-law relation $C(A) \sim A^\eta$, where the scaling exponent η quantifies the degree of optimization of the transportation network. They found the same allometric scaling relation for different food webs. By plotting C_i versus A_i for each one of the seven largest food webs in the literature and by plotting C_0 versus A_0 for a set of different food webs, they found that the exponent varies between 1.13 and 1.16. Therefore, they concluded that the exponent η has a universal value ($\eta=1.13$) and it is one of the few known universal quantities in food webs. Nevertheless, this matter has been the subject of debates [13,14]. It is worth mentioning that the distribution of the number of prey (predator) is another universal quantity [12].

Observe that connecting structure to function, or structure to dynamics, has always been a primary aim of ecologists, but the tools for structural analysis are very poor compared to the arsenal of dynamics analysis [9]. We need to know how to link certain network properties to understanding and predicting the behavior of an ecosystem.

Here we establish upper (η_{max}) and lower (η_{min}) bounds for the exponent η in a general spanning tree network with M trophic levels and K trophic species, both fixed. In the limit $K \rightarrow \infty$, we have that $\eta_{max} = \eta_{min} \rightarrow 1$. We also evaluate analytically and numerically the exponent η for hierarchical and random networks. Our main conclusions are that (a) the result $\eta=1.13$ for food webs is due to finite-size effects (small K) and (b) the exponent η depends on K , so it is different for small and large food webs, and when K is large we have $\eta=1$. This last result implies that large food webs are efficient resource transportation networks. Moreover, these results hold for any number M of trophic levels.

It is worth mentioning that this problem is related to river and vascular networks [10]. Consider K sites uniformly distributed in a d -dimensional volume. The network is con-

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structured by linking the sites in such way that there is at least one path connecting each site to the source (a central site). Since each site is feed at steady rate $F_i=F$, the metabolic rate B clearly is given by $B=\sum_i F_i=FK$. Let I_b represent the magnitude of flow on the b th link. Then, the total quantity of nutrients in the network, at a particular time, is given by $V=\sum_b I_b$. Banavar *et al.* [10] define the most efficient class of network as that for which V is as small as possible. Using this procedure they found $V\sim B^{(d+1/d)}$. For river basins, $d=2$ and $V\sim B^{3/2}$. In vascular systems $V\sim B^{4/3}$ since $d=3$. The variables A_0 and C_0 of the food webs are related, respectively, to the number of transfer sites K and the total volume of nutrients V by the following equations: $K=A_0-1$ and $V=C_0-A_0$. Then we have that $C_0\approx A_0^{(d+1/d)}$ if A_0 is large enough. The value of the exponent η for a food web can be smaller than the one of rivers ($\eta=3/2$) or the one of vascular systems ($\eta=4/3$) because the spanning tree of a food web is not embedded in a Euclidean space.

II. GENERAL HIERARCHICAL MODEL

Let us consider a hierarchical network with M trophic levels. The network is constructed in the following way. We begin with a node representing the environment, node 0. Then we connect n_1 nodes to it. Since these nodes are feeding directly on the environment, they constitute the first trophic level. Obviously, the number of species in this level is $N_1=n_1$. The second level is constructed by connecting n_2 nodes to each node of the first level. Now, in this level, we have $N_2=n_1n_2$ species. This procedure is repeated until level M .

Since A_i is the number of species feeding directly or indirectly on node i , plus itself, we have that

$$\begin{aligned} A_M &= 1, \\ A_{M-1} &= n_M A_M + 1 = n_M + 1, \\ A_{M-2} &= n_{M-1} A_{M-1} + 1 = n_M n_{M-1} + n_{M-1} + 1, \\ &\vdots \\ A_0 &= 1 + \sum_{\alpha=1}^M N_\alpha = K + 1. \end{aligned}$$

The cost of resource transfer, defined by $C_i=\sum_k A_k$, where k runs over the set of direct and indirect predators of i plus itself, is given by

$$\begin{aligned} C_M &= 1, \\ C_{M-1} &= n_M C_M + A_{M-1} = 2n_M + 1, \\ C_{M-2} &= n_{M-1} C_{M-1} + A_{M-2} = 3n_M n_{M-1} + 2n_{M-1} + 1, \\ &\vdots \\ C_0 &= 1 + \sum_{\alpha=1}^M (\alpha + 1) \prod_{i=1}^{\alpha} n_i = 1 + \sum_{\beta=1}^M (1 + \beta) N_\beta. \end{aligned}$$

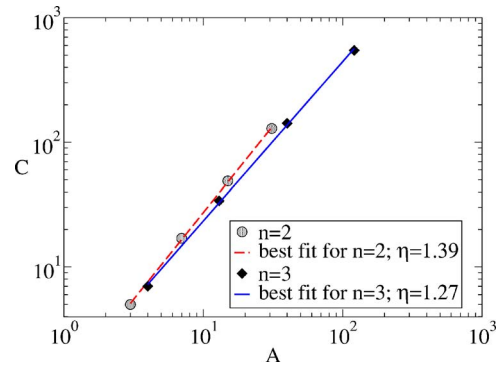


FIG. 1. (Color online) Log-log plots of C_i versus A_i for networks with constant ramification ratio $n=2$ and $n=3$. Note that the exponent decreases when n grows.

The exponent η , as was proposed in the literature [8], can be found by (a) plotting C_i as a function of A_i for a network with number of trophic levels M , and total species number K fixed. Usually, the point (1,1) is neglected due to finite-size effects. It can be also found by (b) plotting C_0 as a function of A_0 for several networks with different trophic species number K . This last procedure determines the large-scale exponent [14]. Note that in hierarchical spanning tree networks, C_i and A_i for species in the same trophic level are equal, implying that we have only $M+1$ points in a $C_i \times A_i$ plot. Let us first use procedure (a) for networks with constant ramification ratio $n_i=n$ and constant number of trophic levels $M=4$. We find $\eta=1.39$ for $n=2$ and $K=30$ and $\eta=1.27$ for $n=3$ and $K=120$, as is shown in Fig. 1. Clearly, the exponent η depends on value of K and decreases as long as K grows. In the limit that $n\rightarrow\infty$, the total number of species K is unlimited and the exponent η approaches the value 1.

Let us return to the more general case of hierarchical models. The large-scale exponent η can be evaluated by

$$\eta = \frac{\ln C_0}{\ln A_0} = \frac{\ln \left[1 + \sum_{\alpha=1}^M (\alpha + 1) \prod_{i=1}^{\alpha} n_i \right]}{\ln \left(1 + \sum_{\alpha=1}^M \prod_{i=1}^{\alpha} n_i \right)}. \tag{1}$$

If at least one ramification ratio is large, $n_\beta\rightarrow\infty$, we have that $\ln A_0 \approx \ln n_\beta$ and $\ln C_0 \approx \ln n_\beta$. Therefore we find $\eta\rightarrow 1$ when the number of species is large. We can also use Eq. (1) to evaluate the exponent η for hierarchical networks with constant ramification ratio. We found for this networks $\eta=1.41$ ($n=2$ and $K=30$) and $\eta=1.31$ ($n=3$ and $K=120$). These values can be compared with the ones obtained previously with procedure (a) (see Fig. 1).

In Eq. (1) the exponent η depends on the value of K , decreasing as long as K grows. For example, consider the hypothetical food web with total species trophic number $K=146$ and the species trophic numbers in each level given by $N_1=38$, $N_2=63$, $N_3=43$, and $N_4=2$. We find the exponent $\eta=1.22$. But if we double the number of trophic species in each trophic level $N_i=2N_i$, the exponent is now $\eta\approx 1.19$. In that equation the exponent η also depends on the relative

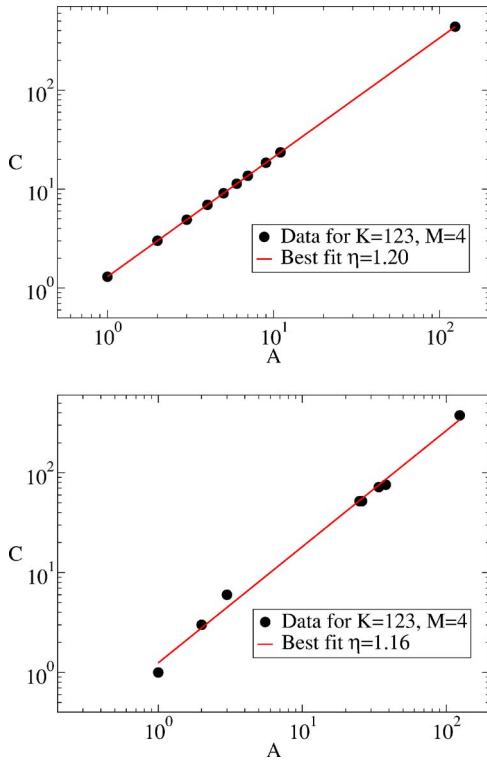


FIG. 2. (Color online) Log-log plots of C_i versus A_i for two different random networks.

distribution of the species in each level, for a given total species number K . For the hypothetical food web described above with 146 trophic species we change the distributions of species in each level to $N_1=114$, $N_2=20$, $N_3=10$, and $N_4=2$. We find the exponent $\eta=1.16$. The exponent has changed from $\eta=1.22$ to $\eta=1.16$.

III. RANDOM NETWORKS

Now, let us consider a random network with M trophic levels and K trophic species. The network is constructed in the following way. First, we determine randomly the population in each level N_α ($\alpha=1, 2, \dots, M$), obeying the restrictions M fixed and K fixed. Then, the N_1 nodes are connected to the environment, constituting the first trophic level. The second level is constructed by randomly connecting the N_2 nodes to the N_1 nodes of the first level. This procedure is repeated until level M is constructed. In Fig. 2 the $C_i \times A_i$ graph is shown for two different random networks with $K=123$ and $M=4$.

Note that the exponent η depends on the relative distribution of species in each level. Therefore, a mean value for this exponent can give us a better description. We can evaluate the mean value of A_i and C_i in each level by

$$\bar{A}_\alpha = \frac{1}{N_\alpha} \sum_{j \in \alpha} A_j,$$

$$\bar{C}_\alpha = \frac{1}{N_\alpha} \sum_{j \in \alpha} C_j.$$

Here α specifies the trophic level ($\alpha=1, \dots, M$). These quantities are averaged on several random configurations.

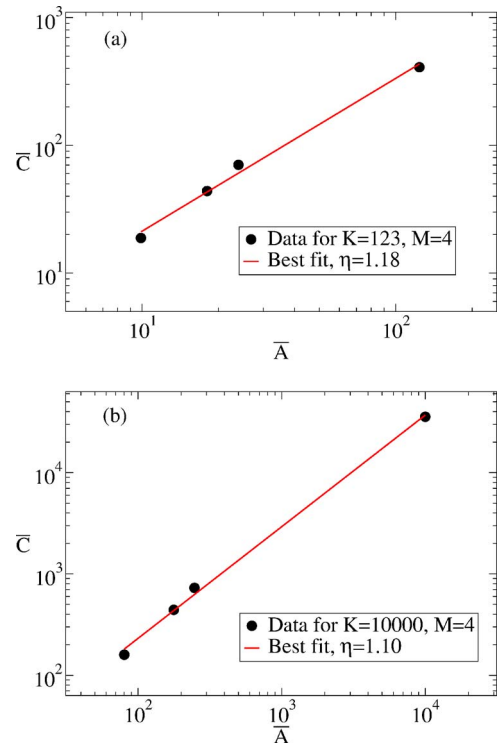


FIG. 3. (Color online) Log-log plots for random networks. (a) $\bar{C}_\alpha \times \bar{A}_\alpha$ for a network with $K=123$ and $M=4$. (b) $\bar{C}_\alpha \times \bar{A}_\alpha$ graph for a random network with $K=10\,000$ and $M=4$. Note that when K is large enough the exponent is $\eta \approx 1$.

In Fig. 3(a) the $\bar{C}_\alpha \times \bar{A}_\alpha$ graph is shown for random networks with $K=123$ (the number of trophic species of the Ythan Estuary web with parasites [8]) and $M=4$. A best fit furnishes $\eta=1.18$. A similar fit for $K=93$ (the number of trophic species of the Little Rock Lake food web [8]) and $M=4$ gives us $\eta=1.21$. Note that the exponent decreases when K increases. Clearly, our exponent is larger than that found by Ref. [8] for the same trophic species number K . But when K grows our exponent becomes smaller than theirs. Obviously, if $\eta=1.13$ represents a universal value for food webs of all sizes, then random spanning trees networks with the same number of trophic levels M are more efficient than food webs. In Fig. 3(b) the $\bar{C}_\alpha \times \bar{A}_\alpha$ graph is shown for a random network with $K=10\,000$ and $M=4$. Note that when K is large enough we have that $\eta \approx 1$.

The exponent η can also be computed by procedure (b). For each value of K we evaluate an average for several configurations and find the mean value of C_0 . In Fig. 4(a), the $C_0 \times A_0$ plot is shown for random networks with $M=4$ and K varying from 50 up to 1000. Now we have that $\eta=1.00$. It is worth mentioning that $C_0 \times A_0$ always furnishes $\eta=1$ independently of the range of K . We have also simulated random networks with $M=10$ trophic levels. In Fig. 4(b) the $C_0 \times A_0$ plot is shown. The results are similar.

IV. UPPER AND LOWER BOUNDS FOR THE EXPONENT

The main point of this paper is to develop a general argument to demonstrate that the large-scale exponent is $\eta=1$ for

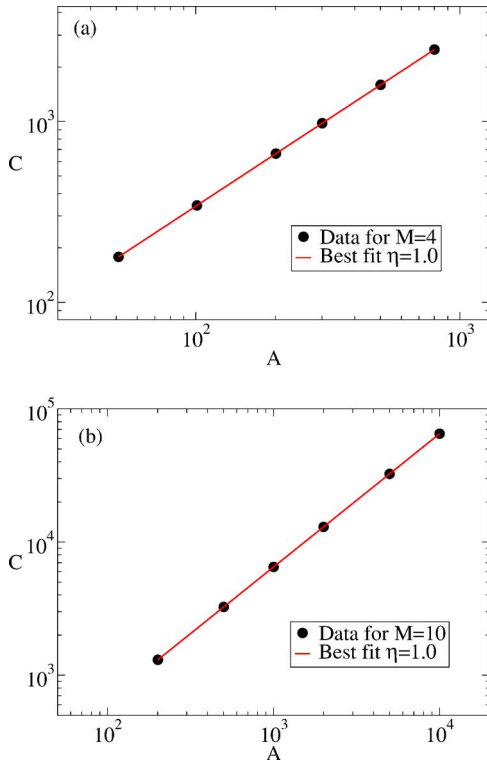


FIG. 4. (Color online) Log-log plots for random networks. (a) $C_0 \times A_0$ for $M=4$ and K varying from 50 up to 1000 and (b) $C_0 \times A_0$ for $M=10$ and K varying from 200 up to 5000. Note that the large-scale exponent has the same value $\eta=1.00$ and is independent of M .

large K and for a fixed value of M . Let us consider a spanning tree with M and K , both fixed. To obey the constraint of M fixed, we put one node in each level. Now we must put in the levels each one of the remainder $K-M$ nodes. Since C_0 is cumulative, a node that is put as near as possible of the environment has a minimal contribution to the global cost. On the other hand, a node put as far as possible of the environment has a maximal contribution to C_0 . To construct the network with maximum value of cost, $C_{0,max}$, we must link all $K-M$ nodes to the node of the last level. In this network we have $N_1=N_2=\dots=N_{M-1}=1$ and $N_M=K-M+1$. $C_{0,min}$ is obtained by linking the $K-M$ nodes directly to the node representing the environment. In this case, we have that $N_1=K-M+1$ and $N_2=N_3=\dots=N_M=1$. Note that these constructions are the closest networks to the starlike and chainlike ones, respectively, that obey the constraints of M and K fixed. Using Eq. (1) we have that

$$C_{0,min} = 1 + 2K + \frac{M}{2}(M-1),$$

$$C_{0,max} = 1 + K(M+1) + \frac{M}{2}(1-M).$$

Then, the lower and the upper bounds for the exponent η are

$$\eta_{max} = \frac{\ln C_{0,max}}{\ln(K+1)} = \frac{\ln \left[1 + K(M+1) + \frac{M}{2}(1-M) \right]}{\ln(K+1)},$$

$$\eta_{min} = \frac{\ln C_{0,min}}{\ln(K+1)} = \frac{\ln \left[1 + 2K + \frac{M}{2}(M-1) \right]}{\ln(K+1)}.$$

When M is fixed and $K \rightarrow \infty$, we have that $\eta_{max} = \eta_{min} \rightarrow 1$.

Consider again the simulation of random networks. We verified that the constructions with minimum and maximum C_0 are the ones just described. Moreover, the result above explains why we find that $\eta \rightarrow 1$ when K is large in the simulations of random networks.

V. SUMMARY

In summary, we studied the transportation properties of several networks that represent spanning trees of food webs. First, we analyzed and idealized a hierarchical model that can be solved analytically. Then we showed that the exponent η depends on the value of K and, when K is large enough, the exponent η approaches the value 1. We constructed random networks that represent more realistically a spanning tree formed by food webs. We evaluated numerically the exponent η by several procedures. For all the cases we observed that the exponent depends on the size of the web and, if K is large, we have that $\eta \rightarrow 1$. An important mark is that all the results are independent of the number of trophic levels, M . Moreover, we establish maximum and minimum values for the exponent η in a general spanning tree with K and M fixed. When M is fixed and the number of species is large these values became equal to 1. Therefore, we can conclude that $\eta=1$ for a large food web and that large food webs are efficient resource transportation systems, in the sense that they have smaller cost to transport resources than networks with $\eta > 1$.

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