FOOD-WEB TOPOLOGY

Universal scaling in food-web structure?

Arising from: D. Garlaschelli, D. Caldarelli & L. Pietronero *Nature* 423, 165–168 (2003)

The statistical analysis of empirical food webs seeks to discover patterns in their structure. Garlaschelli *et al.*[1] describe food webs as transportation networks and show that the empirical webs used in their study have universal scaling exponents. Here we analyse 17 of the most comprehensive food webs — including the nine used by the authors[1] — but find no evidence for this universality. We also argue that the exponents that are observed are not a signature of food-web architecture but are a general property of networks that have few trophic levels, irrespective of their structure. We conclude that the short range of empirical exponents occurs because food webs contain only a few trophic levels and therefore that it does not add to our understanding of food-web topology.

For each empirical food web, Garlaschelli and colleagues build several spanning trees and, for every species i, compute the number A_i of species that directly or indirectly feed on i (plus itself), and the 'cost' function $C_i = \Sigma_k A_k$, where the sum extends over the same set as for A_i. The authors report scaling relations $C_i \propto A_i^{\eta}$, where the exponent η is in the range 1.13–1.16, and interpret this result as a universal property of food-web topology and a proof of self-similarity.

However, our analysis of plots of C_i against A_i for 17 food webs (Fig. 1) yields η values ranging from 1.09 to 1.26 (Table 1). The error is about 0.03 in all cases (95% confidence). The observed exponents therefore span a much larger range than the error and do not display universality, which would require the same value. The discrepancies observed between Table 1 and the values reported by Garlaschelli *et al.* are probably due to errors in their treatment of the raw data, which we have shown for the grassland empirical food web. Unlike Garlaschelli *et al.*[1], we used manipulated data sets supplied by N. D. Martínez's group that have been verified and used in their publications.

Table 1 | Exponents for empirical food webs

Name	η	Name	η
Little Rock	1.11	Canton	1.09
Ythan 91	1.11	El Verde	1.09
Ythan 96	1.12	Reef*	1.10
Coachella	1.14	Stony	1.10
Silwood	1.15	Shelf†	1.17
St Marks	1.18	Bridge Brook	1.20
St Martin	1.19	Benguela‡	1.20
Skipwith	1.22	Chesapeake	1.25
Grassland	1.26		

Details of the food webs are cited in ref. 5, except the *Caribbean Reef[3], †northeast US Shelf[4] and ‡Benguela[2].

Empirical food webs mostly have three levels and, when present, the number of species in the fourth level is very small[2–5] (the most is four species, in Ythan 96, as opposed to 124 species in the whole web). One can show that the 'cost' function C_i for the nodes of any three-level network is constrained to a narrow range, no matter what its internal structure, with exponents η that are compatible with the empirical range (Fig. 1a).

To prove this, we derive a general relationship between C_i and A_i. Let us start by considering a species i in the first level of a spanning tree of a three-level network. Species i sustains a sub-tree with n_2^i species in level 2 and n_3^i species in level 3, so that $A_i = 1 + n_2^i + n_3^i$, and C_i can be written as

$$C_i = A_i + \sum_{\text{level 2}}^{n_2^i} A_j + \sum_{\text{level 3}}^{n_3^i} A_j$$

All species in level 3 have $A_j = 1$, so the last sum yields n_3^i. The second sum provides the number of species sustained by all the n_2^i species (including them); that is, $n_2^i + n_3^i$. By introducing the average topological distance to species i of the species above i, namely $d_i = (n_2^i + 2n_3^i)/(n_2^i + n_3^i)$, then

$$C_i = A_i(d_i + 1) - d_i \qquad (1)$$

This reasoning can be directly generalized to any network, so equation (1) is completely general.

For a three-level network, equation (1) provides narrow bounds for C_i. For a given value A_i, the smallest (or largest) C_i corresponds to the smallest (or largest) d_i. The shortest d_i occurs when all species above i are in the closest upper level, so that $d_i = 1$ and $C_i = 2A_i - 1$. The largest d_i corresponds to i in the first level, one species in level 2 and $A_i - 2$ species in level 3, yielding $C_i = 3A_i - 3$.

C_i is therefore bounded by two straight lines: $2A_i - 1 \leqslant C_i \leqslant 3A_i - 3$.

Figure 1a shows that the 17 empirical food webs studied actually fall within this narrow region. The short range of empirical exponents (Table 1) is therefore simply a consequence of the small number of trophic levels in food webs. We have confirmed this by extensive analysis of three-level networks, for instance for random networks (Fig. 1b). Notice also that the concept of self-similarity is difficult to apply to networks with only three levels.

Garlaschelli *et al.* attempt to confirm their claim of universality by plotting C_0 versus A_0. However, in our plot of C_0 against A_0 for the 17 food webs (Fig. 1c), we find a scaling with exponent 0.97 ± 0.10 (95% confidence), which

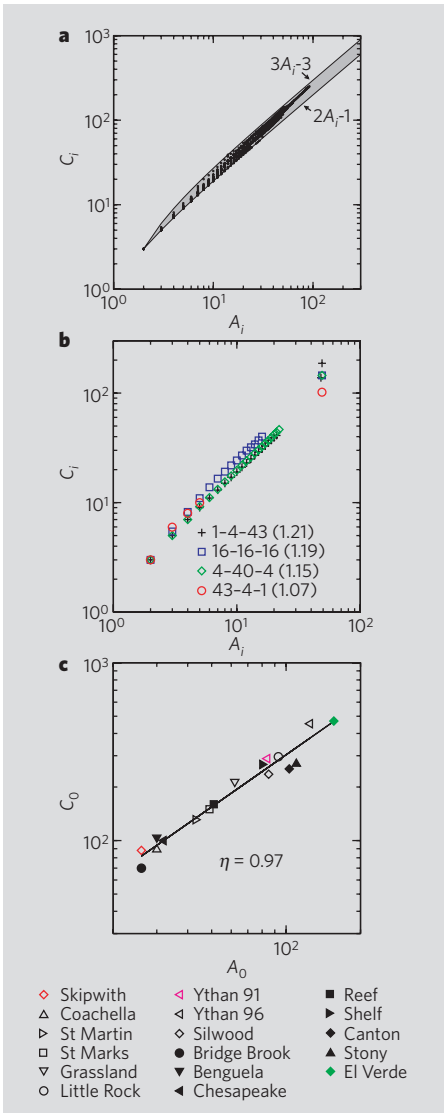

Figure 1 | Cost of energy transfer. The 'cost' function C plotted against A, the number of species that directly or indirectly feed on species i. **a,** C_i versus A_i plots for 17 empirical food webs (listed in Table 1), excluding the environment. All of them fall between the two limit cases (see text), showing that the exponent η is constrained to a small range close to unity for networks of any architecture, provided that they have only a few levels. **b,** Four random networks (designated by different symbols) with the same parameters as the St Marks food web (which has 3 trophic levels and 48 species) for various distributions of species within levels (as indicated by dashes in the key). Their exponents (in parentheses) are compatible with the empirical range. **c,** C_0 versus A_0 for the empirical food webs. The scaling is close to $\eta = 1$, as expected for networks with only a few trophic levels (see text). Plots in **a** and **b** were obtained after averaging C_i over 1,000 spanning trees chosen at random.

is significantly different from 1.13. We can show that an exponent very close to unity is expected for networks with only a few levels. In effect, equation (1) can be applied to the environment (node 0), yielding $C_0 = A_0(1 + d_0) - d_0$, where d_0 is the average distance of the species in the food web to the environment. Note that when d_0 is constant, one obtains a scaling $C_0 \propto A_0^{\eta}$, with $\eta = 1$. As empirical food webs mostly have three levels, the average distance has very little room to change, so it is expected to be roughly constant at $d_0 \approx 2$. The dispersion of data points around the straight line in Fig. 1c simply shows the variability of the average distances around $d_0 \approx 2$.

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Garlaschelli et al. *reply*

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Although Camacho and Arenas[1] raise potentially interesting points, we believe that some of their arguments are flawed or undermined by poor statistics, and therefore that they do not invalidate our results[2].

Even though the two limiting curves shown in their Fig. 1a for three-level food webs define a 'narrow' region[1], several power laws can be drawn between them. The authors show for the randomized St Marks web (their Fig. 1b) that different distributions of species between levels yield different exponents, but they do not explain why the empirical web should display the particular value $\eta = 1.18$, which is only one of its allowed values. Moreover, as the (A_0, C_0) points in Fig. 1b are the most affected by the randomization, the allowed range for the C_0 versus A_0 curve in Fig. 1c must be even wider. In our opinion, the claim of Camacho and Arenas[1] that the observed values of η (including that for the C_0 versus A_0 curve) are due merely to the number of trophic levels is incorrect.

This means that our claim that allometric scaling adds information on food-web structure still stands, in particular with regard to the distribution of species between levels: for example, the distribution (6–31–11) for the real St Marks web is 'in between' two of the randomized distributions (4–40–4 and 16–16–16) considered in Fig. 1b of Camacho and Arenas[1], and so the observed value ($\eta = 1.18$) lies between those for the two randomizations ($\eta = 1.15$, $\eta = 1.19$), but far from the other values. Randomized webs must therefore be forced to have a distribution of species between levels very similar to the empirical one in order to display (approximately) the same exponent.

What is more interesting is the broader range of exponents measured by Camacho and Arenas, suggesting that our results might be subject to variation if different webs are considered. However, we believe that the statistics are not strong enough for new conclusions to be drawn. The discrepancy between our results for some webs highlights the extreme sensitivity of η to small variations in the data, such as the presence or absence of even a single link, which can significantly affect the trophic-level structure.

The reason for this sensitivity is the small size of food webs, which is known to obscure the assessment of various other properties, such as the clustering coefficient and the degree distribution[3]. In this situation, the large-scale behaviour is best captured by the C_0 versus A_0 curve (Fig. 1c in ref. 1). However, equation (1) of Camacho and Arenas[1] shows that, for $i = 0$, the leading term is $C_0 \propto A_0 d_0$, implying that, for the sublinear trend ($\eta = 0.97$) to hold, d_0 should decrease with the number of species. This is an unrealistic situation, again due to the small size of the webs, confirming that the statistics still yield no reliable result.

In the absence of data for larger webs, we can address only the expected dependence of d_0 on A_0 (or, equivalently, on N). In real webs[3], d_0 is always very similar to the average distance l_{av}, which was shown[4] to scale as $l_{av} \propto \ln(N)$ in empirical and model webs (including many of those considered by Camacho and Arenas). Then their equation (1) indicates that $C_0 \propto A_0 \ln(A_0)$, a curve that could be used as an alternative fit to the plots shown by Camacho and Arenas and by us; this corresponds to a different 'universality class', defined by the formal limit of infinite dimension D (logarithmic corrections naturally arise in such a limit) and representing an even more efficient topology.

Alternatively, it is possible — given that chain-length minimization reflects minimization of energy dissipation[2] — that d_0 is also related to the length l_{opt} of the optimal minimum-dissipation chain[5]. Depending on the system details, l_{opt} scales as $\ln(N)$, as $N^{1/3}$, or as a more general power law[5].

The claims of Camacho and Arenas are therefore entirely based on the assumption that d_0 remains fixed as N increases, which in our view is an unrealistic hypothesis that disregards the wide range of possibilities described here.

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