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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FOOD-WEB TOPOLOGY

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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