Robust Patterns in Food Web Structure

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We analyze the properties of seven community food webs from a variety of environments—including freshwater, marine-freshwater interfaces and terrestrial environments. We uncover quantitative unifying patterns that describe the properties of the diverse trophic webs considered and suggest that statistical physics concepts such as scaling and universality may be useful in the description of ecosystems. Specifically, we find that several quantities characterizing these diverse food webs obey functional forms that are universal across the different environments considered. The empirical results are in remarkable agreement with the analytical solution of a recently proposed model for food webs.

In natural ecosystems species are connected through trophic relationships defining intricate networks, the so-called food webs. Understanding the structure and mechanisms underlying the formation of these webs is of great importance in ecology. For this reason, much research has been done in constructing empirical webs and uncovering unifying patterns describing their structure. However, in the last decade the construction of larger and more complete food webs clearly indicated that the previously reported unifying patterns do not hold for the new webs. Indeed, the complexity of the new webs has rendered quite difficult the challenge to obtain quantitative patterns that substitute the old ones.

Here, we analyze the properties of seven detailed community food webs from a variety of environments—including freshwater habitats, marine-freshwater interfaces and terrestrial environments. Remarkably, we uncover quantitative unifying patterns that describe the properties of the diverse trophic webs considered and capture the random and non-random aspects of their structure. Specifically, we find that several quantities—such as the distributions of number of prey, number of predators, and number of trophic links—characterizing these diverse food webs obey robust functional forms that depend on a single parameter, the linkage density $z$.

In our analysis, we use results obtained for complex networks and for a recent model of food web formation, the “niche model” of Ref. [1]. We first describe the theoretical model and its predictions: An ecosystem with $S$ species and $L$ trophic interactions between these species, defines a network with $S$ nodes and $L$ directed links. In the niche model, one first randomly assigns species $i = 1, \ldots, S$ to “trophic niches” $n_i$, which are mapped into the interval $[0,1]$. A species $i$ is characterized by its niche parameter $n_i$ and by its list of prey. Prey are chosen according to the following procedure: species $i$ preys on the species $j$ with niche parameters $n_j$, inside a segment of length $x n_i$ centered in a position chosen randomly inside the interval $[x n_i/2, n_i]$. Here, $0 < x < 1$ is a random variable with probability density function $p_x(x) = b(1-x)^{(b-1)}$. The values of the parameters $b \equiv (S^2/2L-1)$ and $S$ determine the linkage density $z \equiv L/S$ of the food web, and the directed connectance $L/S^2$, which is a measure of the fraction of the actual number of trophic links as compared to the maximum possible number $S(S-1)/2$.

In the limit of large web sizes ($S \gg 1$) and small connectances ($L/S^2 \ll 1$), one can derive analytical expressions for the distribution of number of prey $k$. We consider the cumulative distribution $P_{\text{ prerey}}(k) = \sum_{k' \geq k} P_{\text{ prerey}}(k')$ because it is less noisy than the probability function $p_{\text{ prerey}}(k)$. We obtain

$$P_{\text{ prerey}}(k) = \exp \left( \frac{k}{2z} - \frac{k}{2z} E_1 \left( \frac{k}{2z} \right) \right),$$

where $E_1(x)$ is the so-called exponential-integral function. Equation (1) predicts that the distribution of number of prey decays exponentially for large $k$.

Also in the limit of large web sizes and small connectances, one can derive analytical expressions for the distribution of number of predators $m$. We obtain,

$$P_{\text{ pred}}(m) = \frac{1}{2z} \sum_{m' = m}^{\infty} \gamma(m' + 1, 2z),$$

where $\gamma(m + 1, z)$ is the so-called “incomplete gamma function”. To gain intuition about the functional form, note that $p_{\text{ pred}}(m)$ is approximately a step function: It is constant for $m < z$, and then it decays with a Gaussian tail for $m \approx 2z$. We observe that the cumulative distribution $P_{\text{ pred}}(m)$ decreases linearly as $1 - m/z$ for $m < z$ and decays as the error function for $m \approx 2z$.

Next, we analyze the empirical data for seven food webs with 25 to 92 trophic species. These webs have linkage densities $2.2 < z < 10.8$, and connectances in the interval $0.06-0.31$. We first investigate the distributions of number of prey and number of predators. Figures 1a,b compare the cumulative distributions of the number of prey and number of predators for species in...
the St. Martin Island web with our analytical predictions, and suggest that these distributions are well approximated by Eqs. (1)–(2) without any free parameters for fitting. Equations (1) and (2) indicate that $P_{\text{prey}}(k)$ depends only on $k/2^z$. So, we plot in Figs. 2a,c the cumulative distributions $P_{\text{prey}}(k)$ versus the scaled variable $k/2^z$ for the food webs and find that the data collapse onto a single curve, supporting the possibility that $P_{\text{prey}}$ obeys a universal functional form.

The scaling of $P_{\text{pred}}(m)$ is not as straightforward. Equation (3) indicates that “true” scaling holds only for $m/2^z < 1/2$, while for larger values of $m/2^z$ there is a Gaussian decay of the probability function with an explicit dependence on $z$. However, the decay for $m > 2^z$ is quite fast and, to first approximation, not very relevant. Thus, we plot $P_{\text{pred}}(m)$ versus the scaled variable $m/2^z$ for the food webs and indeed find a collapse of the data onto a single curve for $m/2^z < 0.7$ (Figs. 2b,d).

Figure 2 supports the strong new hypothesis that the distributions of number of prey and number of predators follow universal functional forms. To improve statistics and better determine the specific functional form of these distributions, one may pool the scaled variables, $k/2^z$ and $m/2^z$, from the different webs into single distributions, $P_{\text{prey}}$ and $P_{\text{pred}}$, respectively. Figures 3a,b show the cumulative distributions of scaled number of prey and scaled number of predators. Note that the distributions are well approximated by Eqs. (1)–(2) even though there are no free parameters to fit in the analytical curves. These results are analogous to the finding of scaling and universality in physical, chemical and social systems.

Figure 3 plots the probability densities for the distribution of number of prey and number of predators. It is visually apparent that both distributions are different. This is confirmed by the Kolmogorov-Smirnov test which rejects the null hypothesis at the $p < 0.001$ level. The distribution of number of prey decays exponentially, and the distribution of number of predators is essentially a step function with a fast decay.

One can perform a similar analysis for the distribution $p_{\text{link}}$ of the number of trophic links $r \equiv k + m$. As for number of prey or number of predators, the data from the different webs, upon the scaling $r/2^z$, collapse onto a single curve, further supporting the hypothesis that scaling holds for web structure. To better determine the specific functional form of $p_{\text{link}}(r)$, we pool the scaled variables, $r/2^z$, from all webs except Ythan into a single distribution (Fig. 3d). We find that $p_{\text{link}}(r)$ has an exponential decay for $r/2^z \gg 1$, in agreement with our theoretical calculations. Therefore, there is a characteristic scale for the linkage density, e.g. food webs do not have a scale-free structure, in contrast to reports in recent studies of food-web fragility.

Next, we test if the scaling hypothesis suggested by the analysis of distribution of trophic links also applies to other quantities characterizing food web structure. We consider two quantities with ecologic implications: (i) the average trophic distance $d$ between species (which is the number of species needed to trophically connect two given species), and (ii) the clustering coefficient $C$ (which counts the fraction of species’ triplets that form fully-connected triangles). The latter relates to the compartmentalization in an ecosystem while the former relates to typical food-chain length.
FIG. 3: (a) Cumulative distribution $P_{\text{prey}}$ of the scaled number of prey $k/2z$ for the pooled webs (all except Ythan). The solid line is the analytical prediction (3), and the dashed line is a numerical simulation of the niche model \[1\] with $S = 244$ (the size of the pooled data) and $z = 7.5$ (the average degree for the pooled webs). (b) Cumulative distribution $P_{\text{pred}}$ of the scaled number of predators $m/2z$ for the pooled webs. The solid line is the analytical prediction (3) for the case $z = 7.5$, and the dashed line is a numerical simulation of the niche model \[1\] with $S = 244$ and $z = 7.5$. (c) Comparison of the probability density functions of the scaled number of prey and number of predators. It is visually apparent that the two distributions have distinct functional forms. (d) Probability density function of the number of trophic interactions per species $r = k + m$ pooled for all webs except Ythan. The solid line is obtained by numerically convolving the distributions (3)–(5) while the dashed line is obtained by numerical simulations of the niche model in the limit of large web sizes and small connectances (we use $S = 1000$ and $z = 5$)—the same limit for which the analytical curves where derived \[1\].

The tail of the distribution decays exponentially, indicating that food webs do not have a scale-free structure.

In Fig. 4a, we compare our numerical results for the average trophic distance $d$ for the niche model \[1\] with the values calculated for the food webs analyzed. We find that $d$ increases with web size as $\log S$ both for the model and for the data. This logarithmic increase is the expected behavior for a random graph; however, the slopes measured for the data and the model are different from the value predicted for a random graph \[1\], suggesting that there is a degree of “order” to the connectivity of the food web which may encode the mechanisms of food web assembly. Remarkably, this characteristic of the empirical food webs appears to be captured by the niche model \[1\]. The results of Fig. 4a also support the scaling hypothesis and suggest that the average distance in a food web may also follow a unique functional form for different food webs.

Figure 4b shows our results for the clustering $C$ of the food webs studied and for the niche model \[1\]. We find that the data is well approximated by the model predictions, and that $C$ decreases to zero as $1/S$ as web size $S$ increases.

The major finding of this study is the uncovering of unifying quantitative patterns characterizing the structure of food webs from diverse environments. Specifically, we find that the distributions of the number of prey, number of predators and number of links of most of the best studied food webs seem to collapse onto the same curve after rescaling the number of links by its average $z$. Remarkably, the corresponding curves are in agreement with the analytical predictions of the niche model. Therefore, these distributions can be theoretically predicted merely by knowing the food web’s linkage density $z$, a parameter readily accessible empirically. Regularities such as these are interesting as descriptors
of trophic interactions inside communities because they may enable us to make predictions in the absence of high-quality data, and provide insight into how communities function and are assembled.

Our results are of interest for a number of other reasons. First, food webs do not have a scale free distribution of number of links (total, incoming or outgoing). This is surprising since one could expect most species to try to prey on the most abundant species in the ecosystem (an “abundant-get-eaten” kind of mechanism). Such a preferential attachment would lead to a scale-free distribution of links; instead, we find a single-scale distribution, suggesting that species specialize and prey on a small set of other species. Second, the results of Figs. 4a,b support the scaling hypothesis and indicate that there is very little, if any, compartmentalization in ecosystems suggesting the possibility that ecosystems are highly interconnected and that the removal of any species may induce large disturbances. Third, the structure of food webs is different from many other biological networks in two important aspects: the links are uni-directional and the in- and out-degrees are different. These two facts are a result of the directed character of the trophic interactions and of the asymmetry it creates. Interestingly, the niche model captures this asymmetry in its rules, which may explain its success in explaining the empirical results.

Our findings are surprising for two reasons: (i) they hold for the most complete food webs studied, in contrast to previously reported patterns [8], and (ii) they support the possibility that fundamental concepts of modern statistical physics such as scaling and universality [13]—which were developed for the study of inanimate systems—may also be applied in the study of food webs—which comprise animate beings. Indeed, our results are consistent with the underlying hypothesis of scaling theory [13], i.e., food webs display universal patterns in the way trophic relations are established despite apparently “fundamental” differences in factors such as the environment (e.g. marine versus terrestrial), ecosystem assembly, and past history.

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