

## 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.

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In natural ecosystems species are connected through trophic relationships [1,2] defining intricate networks [3–6], the so-called food webs. Understanding the structure and mechanisms underlying the formation of these webs is of great importance in ecology [7]. For this reason, much research has been done in constructing empirical webs and uncovering unifying patterns describing their structure [7,8]. However, in the past 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 [9,10]. 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 nonrandom aspects of their structure. Specifically, we find that several quantities—such as the distributions of the 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 [6] 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  $i = 1, \dots, S$  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  $xn_i$  centered in a position chosen randomly inside the inter-

val  $[xn_i/2, n_i]$ . Here,  $0 \leq x \leq 1$  is a random variable with probability density function  $p_x(x) = b(1-x)^{b-1}$  [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 [1].

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 the number of prey  $k$  [11]. We consider the cumulative distribution  $P_{\text{prey}}(k) = \sum_{k' \geq k} p_{\text{prey}}(k')$  because it is less noisy than the probability function  $p_{\text{prey}}(k)$ . We obtain

$$P_{\text{prey}}(k) = \exp\left(-\frac{k}{2z}\right) - \frac{k}{2z} E_1\left(\frac{k}{2z}\right), \quad (1)$$

where  $E_1(x)$  is the so-called exponential-integral function [12]. Equation (1) predicts that the distribution of the 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 the number of predators  $m$  [11]. We obtain

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

where  $\gamma(m + 1, z)$  is the so-called “incomplete gamma function” [12]. To gain intuition about the functional form (2), 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  $m \approx 2z$  [11]. It follows then that the cumulative distribution  $P_{\text{pred}}(m)$  decreases linearly as  $1 - m/z$  for  $m < z$  and decays as the error function [12] 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  $0.06-0.31$  [1]. We first investigate the distributions of the number of prey and number of predators. Figures 1a and 1b compare the cumulative distributions of the number of prey and number of predators for species in the

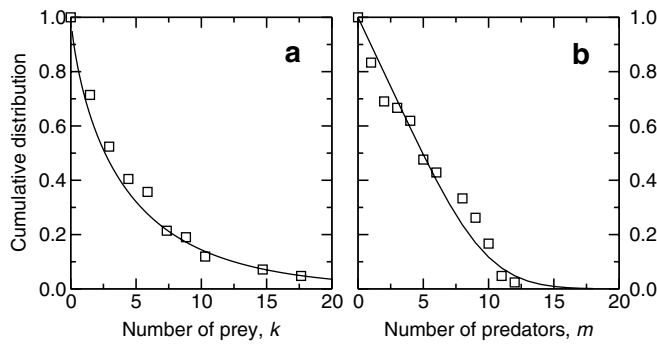


FIG. 1. Cumulative distribution (a)  $P_{\text{prey}}$  of the number of prey  $k$ , and (b)  $P_{\text{pred}}$  of the number of predators  $m$  for the St. Martin Island web. The data agree well with the analytical predictions of Eqs. (1) and (2) (indicated by the solid lines), without any free parameters for fitting as  $z$  is determined empirically.

St. Martin Island web [13] with our analytical predictions, and suggest that these distributions are well approximated by Eqs. (1) and (2) without any free parameters for fitting. Equations (1) and (2) and the results of Fig. 1 suggest the possibility that  $P_{\text{prey}}$  and  $P_{\text{pred}}$  obey universal functional forms that depend only on  $z$ .

Indeed, Eq. (1) predicts that  $P_{\text{prey}}(k)$  depends only on  $k/2z$ . So, we plot in Figs. 2a and 2c the cumulative distributions  $P_{\text{prey}}(k)$  versus the scaled variable  $k/2z$  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 [14].

The scaling of  $P_{\text{pred}}(m)$  is not as straightforward. Equation (2) indicates that “true” scaling holds only for  $m/2z < 1/2$ , while for larger values of  $m/2z$  there is a Gaussian decay of the probability function with an explicit dependence on  $z$ . However, the decay for  $m > 2z$  is quite fast and, to first approximation, not very relevant. Thus, we plot  $P_{\text{pred}}(m)$  versus the scaled variable  $m/2z$  for the food webs and indeed find a collapse of the data onto a single curve for  $m/2z < 0.7$  (Figs. 2b and 2d) [15].

Figure 2 supports the strong new hypothesis that the distributions of the number of prey and the 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,  $k/2z$  and  $m/2z$ , from the different webs [14,15] into single distributions,  $p_{\text{prey}}$  and  $p_{\text{pred}}$ , respectively. Figures 3a and 3b show the cumulative distributions of the scaled number of prey and scaled number of predators. Note that the distributions are well approximated by Eqs. (1) and (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 3c plots the probability densities for the distribution of the 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 the number of prey decays exponentially, and the distribution of the 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 the number of prey or number of predators, the data from the different webs, upon the scaling  $r/2z$ , collapse onto a single curve, further supporting the hypothesis that scaling holds for food web structure. To better determine the specific functional form of  $p_{\text{link}}(r)$ , we pool the scaled variables,  $r/2z$ , from all webs except Ythan into a single distribution (Fig. 3d). We find that  $p_{\text{link}}(r)$  has an exponential decay for  $r/2z \gg 1$ , in agreement with our theoretical calculations. Therefore, there is a characteristic scale for the linkage density, i.e., food webs do *not* have a scale-free structure, in contrast to reports in recent studies of food web fragility [17].

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 [4] (which is

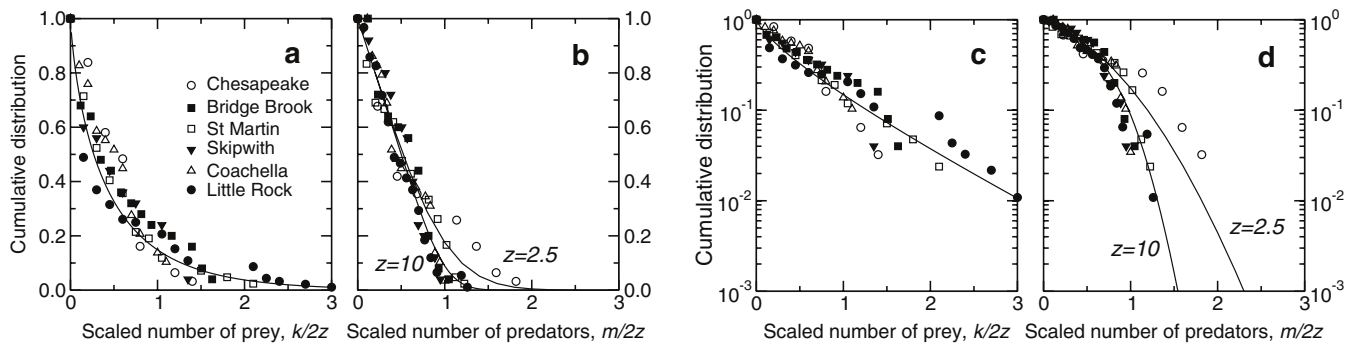


FIG. 2. We test the “scaling hypothesis” that the distributions of the number of prey (predators) have the same functional form for different food webs. (a) Cumulative distribution  $P_{\text{prey}}$  of the scaled number of prey  $k/2z$  for all the webs except Ythan [14,15]. The solid line is the prediction of Eq. (1). The data “collapse” onto a single curve that agrees well with the analytical results. (b) Cumulative distribution  $P_{\text{pred}}$  of the scaled number of predators  $m/2z$  for all the webs but Ythan [14,15]. The solid lines are the analytical predictions of Eq. (2) for the extremal values of  $z$  in the empirical data. Semilogarithmic plot of the scaled distributions of (c) number of prey and (d) number of predators.

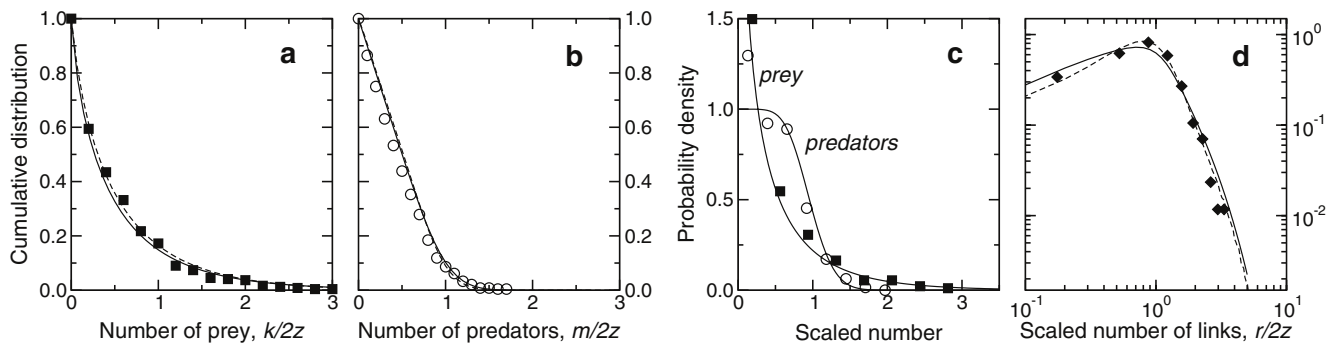


FIG. 3. Cumulative distributions (a)  $P_{\text{prey}}$  of the scaled number of prey,  $k/2z$ , and (b)  $P_{\text{pred}}$  of the scaled number of predators,  $m/2z$ , for the pooled webs (all except Ythan). The solid lines are the analytical predictions [Eqs. (1) and (2)] for the case  $z = 7.5$ , and the dashed lines are for numerical simulations 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). (c) Comparison of the probability density functions of the scaled number of prey and the 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 [Eqs. (1) and (2)] while the dashed line is obtained from numerical simulations of the niche model for  $S = 1000$  and  $z = 5$ , i.e., the limit of large web sizes and small connectances for which the analytical curves were derived [11]. The tail of the distribution decays exponentially, indicating that food webs do *not* have a scale-free structure.

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 a typical food-chain length.

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 [6], 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 paper 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

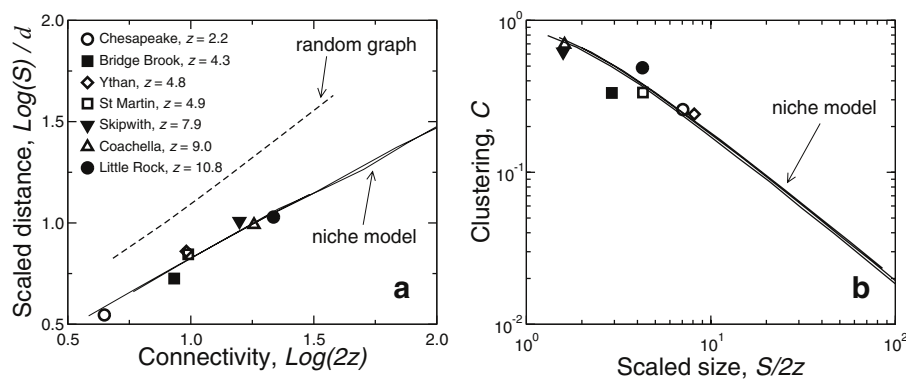


FIG. 4. (a) Scaled average trophic distance  $d$  between species versus linkage density  $z$ . We compare the data with the numerical simulations of the niche model [1] for web sizes  $S = 100, 500$ , and  $1000$  (thin solid lines). We find a logarithmic increase of the average distance with web size  $S$ , in good agreement with the model predictions. We also compare our results with the prediction for a random graph with the same linkage density as the webs studied (dashed line). The logarithmic dependence of  $d(S)$  agrees with the expectation for a random graph; however, the coefficients of the logarithmic increase differ from the predicted values, indicating that food webs have a more complex structure than that predicted by a random graph. (b) Double-logarithmic plot of the clustering coefficient  $C$  versus the scaled web size  $S/2z$ . We compare the data with numerical results for the niche model [1] for three values of the linkage density in the empirically relevant range ( $z = 2.5, 5$ , and  $10$ ). We find that the clustering coefficient of the food webs is inversely proportional to the web size  $S$ , in good agreement with the model predictions and with the asymptotic behavior predicted for a random graph [4].

of predators, and number of links of most of the best studied food webs seem to collapse onto the same curves after rescaling the number of links by its average number  $z$ . 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 the 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" type 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 and 4b support the scaling hypothesis and indicate that there is very little, if any, compartmentalization in ecosystems [18], 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 unidirectional and the in- and out-degree distributions 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 [7], and (ii) they support the possibility that fundamental concepts of modern statistical physics such as scaling and universality—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, 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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- [14] To investigate if the species in different webs have numbers of prey drawn from the same distribution we use the Kolmogorov-Smirnov test. We find that we cannot reject the null hypothesis that the species for all webs have a number of preys drawn from the same underlying distributions. The case of Little Rock is marginal with regard to the Kolmogorov-Smirnov test, but visual inspection suggests that this web follows the same patterns as the other.
- [15] The Kolmogorov-Smirnov test shows that we cannot reject the null hypothesis that the species for all webs have a number of predators drawn from the same underlying distributions, except for the case of Ythan [16]. For the Ythan Estuary web, we find results consistent with an exponential distribution of a number of predators. The finding that Ythan is different from other webs may be explained in two ways: (i) the Ythan Estuary web appears to be still quite incomplete for bottom and top species [1,10], or (ii) Ythan belongs to a different universality class.
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