

## Analytical solution of a model for complex food webs

Juan Camacho,<sup>1,2,\*</sup> Roger Guimerà,<sup>1,3,†</sup> and Luís A. Nunes Amaral<sup>1,‡</sup>

<sup>1</sup>Center for Polymer Studies and Department of Physics, Boston University, Boston, Massachusetts 02215

<sup>2</sup>Departament de Física (Física Estadística), Universitat Autònoma de Barcelona, E-08193 Bellaterra, Spain

<sup>3</sup>Department d'Enginyeria Química, Universitat Rovira i Virgili, 43006 Tarragona, Spain

(Received 2 January 2001; revised manuscript received 1 November 2001; published 8 February 2002)

We investigate numerically and analytically a recently proposed model for food webs [Nature **404**, 180 (2000)] in the limit of large web sizes and sparse interaction matrices. We obtain analytical expressions for several quantities with ecological interest, in particular, the probability distributions for the number of prey and the number of predators. We find that these distributions have fast-decaying exponential and Gaussian tails, respectively. We also find that our analytical expressions are robust to changes in the details of the model.

DOI: 10.1103/PhysRevE.65.030901

PACS number(s): 87.23.Cc, 05.40.-a, 64.60.Cn, 89.75.Hc

In ecosystems, species are connected through intricate trophic relationships [1,2] defining complex networks [3–5], the so-called food webs. Understanding the structure and mechanisms underlying the formation of these complex webs is of great importance in ecology [6–9]. In particular, the food web structure provides insights into the behavior of ecosystems under perturbations such as the introduction of new species or the extinction of existing species. The non-linear response of the elements composing the network leads to possibly catastrophic effects for even small perturbations [10].

Recently, Williams and Martinez have proposed an elegant model of food webs—the “niche” model—that just with a few ingredients successfully predicts key structural properties of the most comprehensive food webs in the literature [1]. Numerical simulations of the niche model predict values for many quantities typically used to characterize empirical food webs that are in agreement with measured values for seven webs in a variety of environments, including freshwater habitats, marine-freshwater interfaces, and terrestrial environments.

Here, we investigate the niche model from a theoretical perspective. We study analytically and numerically the behavior of key quantities for sparse food webs, i.e., webs with  $L \ll S^2$ , where  $L$  is the number of trophic interactions between species and  $S$  is the number of species in the web. This is the limit of interest in ecology because (i) for most food webs reported in the literature the directed connectance, defined as  $C = L/S^2$ , takes small values and (ii) it corresponds to the limit of large web sizes  $S$  [8,9]. We calculate the probability distributions of the number of prey and predators and find that for  $C \ll 1$  they depend only on one parameter of the model—the average number  $z$  of trophic links in the network. These distributions give valuable information about the structure of the network and enable us to calculate other important quantities such as the fraction of “top,” “intermediate,” and “basal” species, and the standard deviation of the “vulnerability” and “generality” of the species in the food

web [1]. Our results provide compact patterns that describe the structure of the food webs generated by the niche model. These patterns could not have been predicted from the numerical simulations reported in Ref. [1] and may be of practical and fundamental importance for the study of empirical food webs. Moreover, we test our analytical predictions with empirical food webs and find agreement.

We first define the niche model. Consider an ecosystem with  $S$  species and  $L$  trophic interactions between these species. These species and interactions define a network with  $S$  nodes and  $L$  directed links. Initially, one randomly assigns  $S$  species to “trophic niches”  $n_i$  mapped with uniform probability into the interval  $[0,1]$ . For convenience, we will assume that the species are ordered according to their niche number, i.e.,  $n_1 < n_2 < \dots < n_S$ .

A species  $i$  is characterized by its niche parameter  $n_i$  and by its list of prey. Prey are chosen for all species according to the following rule: a species  $i$  preys on all species  $j$  with niche parameters  $n_j$  inside a segment of length  $r_i$  centered in a position chosen randomly inside the interval  $[r_i/2, n_i]$  with  $r_i = xn_i$  and  $0 \leq x \leq 1$ , a random variable with probability density function

$$p_x(x) = b(1-x)^{(b-1)}. \quad (1)$$

The values of parameters  $b$  and  $S$  determine the average connectivity  $z \equiv 2L/S$  of the food web and the directed connectance  $C = L/S^2$  [1,11]. One can also express the average number of prey per species as  $S\bar{r}$ , where the bar indicates an average over an ensemble of food webs. It then follows that the connectivity is  $z = 2S\bar{r}$ , the number of directed links is  $L = S^2\bar{r}$ , and the connectance is  $C = \bar{r}$ . One can also obtain these expressions in terms of  $b$  using the equality  $\bar{r} = \bar{x}/2 = 1/[2(1+b)]$ .

In the niche model, isolated species—that is, species with no prey or predators—are eliminated and species with the same list of prey and predators—that is, trophically identical species—are “merged” [12].

Next, we address the statistics of the number of prey. For large  $S$ , the number of prey of a species  $i$  is  $k_i = Sr_i$ , so that the probability distribution  $p_{\text{prey}}$  is given directly by the distribution of  $r$ . Specifically,  $p_{\text{prey}}(k) = p(r)/S$ .

\*Email address: juan.camacho@uab.es

†Email address: rguimera@etseq.urv.es

‡Email address: amaral@buphy.bu.edu

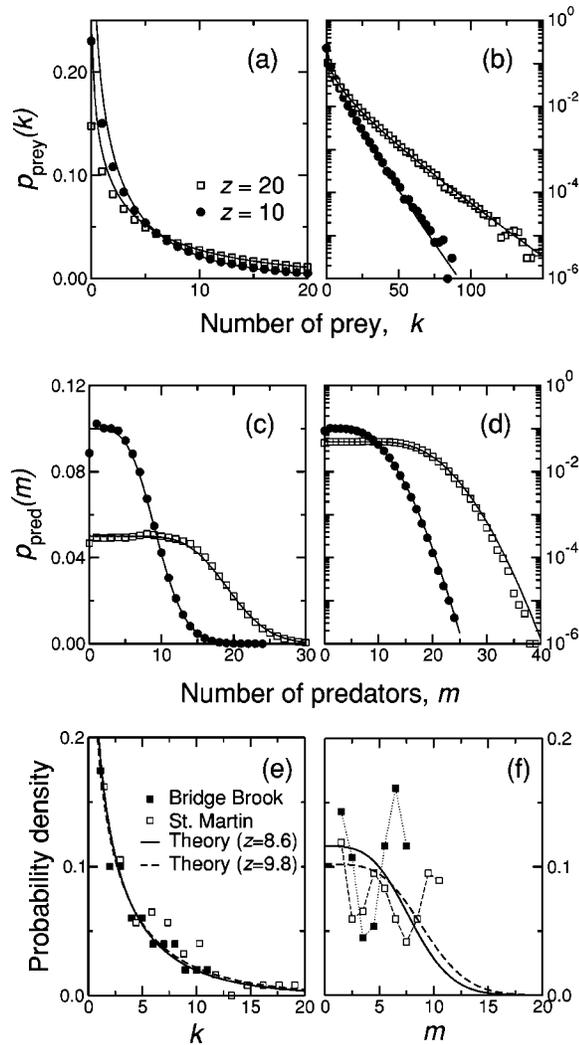


FIG. 1. (a) Linear and (b) log-linear plots of the distribution of the number of prey for 1000 simulations of food webs with  $S = 1000$ . We show results for  $z = 10, 20$  and the corresponding theoretical predictions. As expected, we find an exponential decay of the distributions. (c) Linear and (d) log-linear plots of the distribution of the number of predators for the same food webs as in (a) and (b). As predicted, we find a regime where the distribution is uniform followed by a Gaussian decay. We test our analytical predictions with empirical data [1] for (e)  $p_{\text{prey}}(k)$  and (f)  $p_{\text{pred}}(m)$  for Bridge Brook (solid line) and St. Martin (broken line).

The cumulative probability  $P(r' > r) = \int_r^1 dr' p(r')$  is the area of the region  $R$  of the  $n-x$  diagram bounded by lines  $x = 1$ ,  $n = 1$  and the hyperbole  $r = nx$ ,

$$P(r' > r) = \int_r^1 dx \int_{r/x}^1 dn p_n(n) p_x(x), \quad (2)$$

where  $p_n(n) = 1$  is the probability density function of  $n$ . The integration of Eq. (2) gives rise to a function involving hypergeometric functions [13]. To obtain a more “physical” solution, one can differentiate Eq. (2) twice to obtain

$$\frac{dp(r)}{dr} = -\frac{p_x(r)}{r}. \quad (3)$$

In the limit  $C \ll 1$ , one has  $b \gg 1$  (see [12]), so that  $p_x(x) \approx be^{-bx}$ , and the term in the right-hand side vanishes exponentially, indicating that  $p(r)$  and  $P(r' > r)$  have exponentially decaying tails [14].

To obtain a simpler analytical solution for  $p(r)$  than given by the hypergeometric functions, we approximate  $p_x$  in the entire  $x$  range by an exponential. We expect the results to be the same for  $\bar{x} \ll 1$  [12] because  $p_x$  takes nonvanishing values only for small  $x$ . Under this approximation, the integration of Eq. (3) yields

$$p(r) = bE_1(br), \quad (4)$$

where  $E_1(x) = \int_x^\infty dt t^{-1} \exp(-t)$  is the exponential-integral function [13]. The probability distribution  $p_{\text{prey}}(k)$  is obtained from Eq. (4) making the substitutions  $r = k/S$  and  $b = S/z$ , yielding

$$p_{\text{prey}}(k) = (1/z)E_1(k/z). \quad (5)$$

We compare in Figs. 1(a) and 1(b) the predictions of Eq. (4) with numerical simulations. We find close agreement between our analytical expression and the numerical results. In particular, they show an exponential decay for large  $k$ . The deviations observed for small values of  $k$  are due to the fact that  $k_j = Sr_j$  is an average value implying that it is a good approximation only when the fluctuations of  $k_j$  are small, which is no longer true for small  $k$ .

Next, we address the statistics of the number of predators. Note that for  $\bar{r} \ll 1$  [12], the predators of species  $i$  have, to first approximation, niche values  $n_j > n_i$  and that the segment  $r_j$  is placed with equal probability in the interval  $[0, n_j]$ . Therefore, the probability for a species  $j$  to prey on  $i$  is  $r_j/n_j = x_j n_j/n_j = x_j$ , implying that the average probability for the species with  $n_j > n_i$  to prey on species  $i$  is  $\bar{x}$ .

If we assume that  $S \gg 1$ , the number of predators of  $i$  is the result of  $S - i$  independent “coin throws” with probability  $\bar{x}$  of being a predator and probability  $1 - \bar{x}$  of not being a predator, implying that the probability of species  $i$  having  $m$  predators is given by the binomial distribution. It then follows that the distribution of the number of predators for a general species is the average over the different binomials

$$p_{\text{pred}}(m) = \frac{1}{S} \sum_{i=1}^{S-m} \binom{S-i}{m} \bar{x}^m (1 - \bar{x})^{S-m-i}. \quad (6)$$

In the limit of interest,  $S \gg 1$ ,  $\bar{x} \ll 1$ , and  $S\bar{x} = z$ , one can approximate the binomial distribution as Poisson, and the sum by an integral

$$p_{\text{pred}}(m) = \frac{1}{z} \int_0^z dt \frac{t^m e^{-t}}{m!} = \frac{1}{z} \gamma(m+1, z), \quad (7)$$

where  $\gamma$  is the “incomplete gamma function” [13,15]. For  $m < z/2$ , the function  $\gamma$  is approximately constant, while it decays with a Gaussian tail for  $m \approx z$ . In Figs. 1(c) and 1(d),

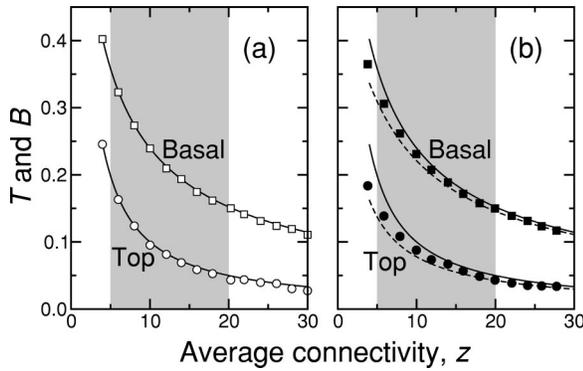


FIG. 2. Fraction of top and basal species as a function of the average connectivity  $z$ . The shaded region corresponds to the interval of  $z$  typically observed in empirical food webs. (a) Comparison of the results of 100 simulations of food webs with  $S=1000$ —for which isolated species were *not* removed—with our theoretical predictions, Eqs. (8) and (9). Note the good agreement between the analytical expressions and the numerical results. (b) Comparison of the results of 100 simulations of food webs with  $S=1000$ —for which isolated species were removed—with our theoretical predictions, Eqs. (8)–(10). Note that the theoretical predictions provide narrow bounds for the numerical results.

we compare the predictions of Eq. (7) with numerical solutions and find good agreement.

In Figs. 1(e) and 1(f), we compare our analytical predictions, Eqs. (5)–(7), with data from two food webs: Bridge Brook ( $S=25, z=8.6$ ) and St. Martin Island ( $S=42, z=9.8$ ). We find that the distributions of the number of preys is well approximated by the data and that the distributions of the number of predators are “noisy” but still show the expected cutoff for  $m \approx z$  and it is approximately constant for  $m < z$  as predicted by Eq. (7). This agreement is remarkable since the webs analyzed are quite small, so one might not expect the theoretical expressions to hold.

Next, we evaluate the fraction of top  $T$ , intermediate  $I$ , and basal  $B$  species. As the names indicate, top species have no predators and basal species have no prey, while intermediate species are those with both prey and predators. The fraction of intermediate species is just  $I = 1 - (T + B)$ . The fraction  $T$  of top species is, by definition,

$$T \equiv p_{\text{pred}}(0) = \frac{1 - \exp(-z)}{z}. \quad (8)$$

Note that a similar result is obtained if one calculates the sum (6) for  $m=0$ . Since typically  $5 < z < 20$ , Eq. (8) can be approximated simply as  $T = 1/z$ .

To calculate the fraction  $B$  of basal species, we note that a species has no prey only if its range  $r$  falls in a region with no species [16]. In the limit of large  $S$ , the probability density for finding an empty interval of length  $\delta$  is  $S e^{-S\delta}$ , as predicted by the canonical distribution [17]. Thus, the probability of finding a species-free segment of length larger than  $r$  is  $e^{-Sr}$ , which gives the probability for a species of range  $r$  not to prey on other species. Using Eq. (4), it follows that the average probability is

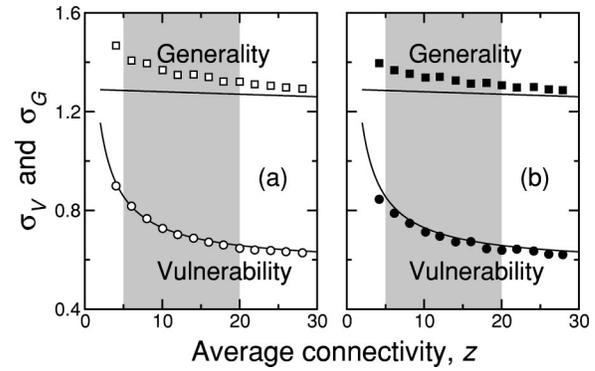


FIG. 3. Normalized standard deviations of generality and vulnerability as a function of the average connectivity  $z$ . The shaded region corresponds to the interval of  $z$  typically observed in empirical food webs. (a) Comparison of the results of 100 simulations of food webs with  $S=1000$ —for which isolated species were *not* removed—with our theoretical predictions, Eqs. (11) and (12). (b) Comparison of the results of 100 simulations of food webs with  $S=1000$ —for which isolated species were removed—with our theoretical predictions, Eqs. (11) and (12). Note that as for Fig. 2, removing isolated species leads to slightly less good agreement with the simulation results for  $\sigma_V$ . However, the removal of isolated species does not appear to be a factor in the deviations found for  $\sigma_G$ . The reason why  $\sigma_G$  underestimates the simulation results at small  $z$  values relates to the fact that  $k_j = Sr_j$  is a good approximation only when the fluctuations of  $k_j$  are small, which is no longer true for small  $k$ .

$$B = \int_0^1 dr e^{-Sr} p(r) = \frac{\ln(1+z)}{z}. \quad (9)$$

In the model [1], isolated species are eliminated, so they are not counted towards top or basal species. To correct the estimates (8) and (9) for this effect, we remove the isolated species. We estimate the number of isolated species to first order by assuming that having no prey is statistically independent of having no predators, implying that the fraction of isolated species is just the product of the fractions of top and basal species. This assumption does not take into account the possibility that a species with no prey is likely to have a low niche value  $n$  and hence it has a high probability to have predators. Nonetheless, this simple approximation provides an upper bound for the number of isolated species, which leads to a lower bound on  $T$  and  $B$ ,

$$T' = \frac{T - TB}{1 - TB}, \quad B' = \frac{B - TB}{1 - TB}. \quad (10)$$

In Fig. 2, we compare our analytical predictions for the fraction of top and basal species with numerical simulations of the model. As expected, Eqs. (8)–(10) provide bounds for the numerical results.

Finally, we calculate the standard deviations of the vulnerability and generality of the species in food webs generated according to the model. The vulnerability of a prey is defined as its number  $m$  of predators, and the generality of a predator as its number  $k$  of preys. Following Ref. [1], we define the normalized standard deviations of the vulnerability

as  $\sigma_V^2 = \overline{m^2}/\bar{m}^2 - 1$  and of the generality as  $\sigma_G^2 = \overline{k^2}/\bar{k}^2 - 1$ . By definition, one has  $\bar{m} = \bar{k} = z/2$  for both cases.

To evaluate  $\sigma_V$ , we first calculate  $\overline{m^2}$ . Equation (7) yields  $\overline{m^2} = z^2/3 + z/2$ , so that

$$\sigma_V = \sqrt{\frac{1}{3} + \frac{2}{z}}. \quad (11)$$

We next calculate  $\sigma_G$ , for any value of  $C$ , by direct evaluation of  $\overline{k^2}$ . If  $S \gg 1$ , the number of preys of a species having a range  $r$  is  $k = Sr$ , and we find that  $\overline{k^2}/\bar{k}^2 = \overline{r^2}/\bar{r}^2 = 8(b+1)/[3(b+2)]$ , implying that

$$\sigma_G = \sqrt{\frac{8}{3} \frac{1}{1+2C} - 1}. \quad (12)$$

For  $C \ll 1$ ,  $\sigma_G$  becomes a constant with value  $\sqrt{5/3}$ , a result that can also be obtained from Eq. (5). We show in Fig. 3 the results for our analytical expressions (11) and (12) and compare them with results from numerical simulations of the niche model.

We have also studied the robustness of our predictions to changes in the particular formulation of the *details* of the model. The nature of approximations used in the derivations of the expressions for the distributions of the number of preys and predators, Eqs. (5)–(7), allow us to conclude the following.

(i) The distribution of the number of predators does not depend on the specific form of  $p(x)$ . The only requirement is

that the connectance  $C = \bar{x}/2$  tends to zero under some limit, so that  $z = SC$  remains finite when  $S$  tends to infinity

(ii) The distribution of the number of preys depends on the functional form of  $p(x)$ , but Eq. (7) will still be obtained for all  $p(x)$  decaying exponentially as  $C$  tends to zero.

Thus, it appears that our findings are robust under quite general conditions, a result that is not possible to obtain without an analytic treatment of the problem.

Our results are also of interest for a number of other reasons. First, we demonstrate for the first time that the distributions of the number of preys and predators have different functional forms. Second, we show that both distributions have characteristic scales, i.e., both distributions have well-defined means and standard deviations as  $S$  increases to infinity. Third, we find that the functional forms of the distributions of the number of preys and predators depend only on the average connectivity  $z$  and agree with empirical data. This result is rather surprising in the face of the complexity of the empirical and model food webs. Finally, we show that other quantities of biological interest also depend exclusively on  $z$ .

We thank A. Arenas, J. Bafaluy, M. Barthélémy, A. Díaz-Guilera, G. Franzese, F. Giralt, E. LaNave, S. Mossa, A. Scala, H. E. Stanley, and especially N. D. Martinez and R. J. Williams for stimulating discussions and helpful suggestions. J.C. and R.G. thank the Generalitat de Catalunya and the Spanish CICYT (Grant Nos. PPQ2000-1339, BFM2000-0620, and BFM2000-0351-C03-01) for support. L.A.N.A. thanks NIH/NCRR (Grant No. P41 RR13622) and NSF for support.

- 
- [1] R. J. Williams and N. D. Martinez, *Nature (London)* **404**, 180 (2000).
- [2] K. S. McKann, A. Hastings, and G. R. Huxel, *Nature (London)* **395**, 794 (1998); R. T. Paine, *ibid.* **355**, 73 (1992).
- [3] D. J. Watts and S. H. Strogatz, *Nature (London)* **393**, 440 (1998); M. Barthélémy and L. A. N. Amaral, *Phys. Rev. Lett.* **82**, 3180 (1999).
- [4] L. A. N. Amaral, A. Scala, M. Barthélémy, and H. E. Stanley, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 11 149 (2000); F. Liljeros, C. Edling, L. A. N. Amaral, H. E. Stanley, and Y. Åberg, *Nature (London)* **411**, 907 (2001).
- [5] S. H. Strogatz, *Nature (London)* **410**, 268 (2001); R. Albert and A.-L. Barabási, *Rev. Mod. Phys.* (to be published).
- [6] J. E. Cohen, F. Briand, and C. M. Newman, *Community Food Webs: Data and Theory*, *Biomathematics Vol. 20* (Springer, Berlin, 1990); S. L. Pimm, J. H. Lawton, and J. E. Cohen, *Nature (London)* **350**, 669 (1991).
- [7] G. A. Polis, *Am. Nat.* **138**, 123 (1991); N. D. Martinez, *Science* **260**, 242 (1993); S. J. Hall and D. Raffaelli, *J. Anim. Ecol.* **60**, 823 (1991).
- [8] M. Rejmanek and P. Stary, *Nature (London)* **280**, 311 (1979).
- [9] F. Briand and J. E. Cohen, *Nature (London)* **307**, 264 (1984); F. Briand and J. E. Cohen, *Science* **238**, 956 (1987).
- [10] E. L. Berlow, *Nature (London)* **398**, 330 (1999); F. S. Chapin *et al.*, *ibid.* **405**, 234 (2000); K. S. McKann, *ibid.* **405**, 228 (2000).
- [11] The “highest-quality” food webs reported in the literature have 50–100 species with  $10 < z < 20$  and connectance of 0.1–0.3 [1]. Empirical studies suggest that  $z$  is either a constant [8] or grows as  $S^{0.4}$  [9], implying that  $C$  tends to zero for large food webs.
- [12] Note that the limit  $C \ll 1$  is equivalent to  $\bar{x}$  and  $\bar{r} \ll 1$  and  $b \gg 1$ . For  $\bar{r} \ll 1$  the probability that two species are trophically identical is very small. This suggests that taxonomic and trophic classifications of species lead to similar results [1].
- [13] I. S. Gradshteyn *et al.*, *Table of Integrals, Series and Products*, 6th ed. (Academic Press, New York, 2000); S. Wolfram, *The Mathematica Book*, 3rd ed. (Cambridge University Press, Cambridge, 1996).
- [14] The exponential decay is found when  $\bar{r} \ll r \ll 1$ . When  $r$  approaches 1, the decay is much faster and  $p(r)$  becomes identically zero.
- [15] There are two incomplete  $\gamma$  functions defined in the literature,  $\gamma(\alpha, x) = \int_0^x e^{-t} t^{\alpha-1} / \Gamma(\alpha)$  and  $\Gamma(\alpha, x) = \int_x^\infty e^{-t} t^{\alpha-1} / \Gamma(\alpha)$ . In some cases they are defined without the  $\Gamma(\alpha)$  in the denominator.
- [16] The definition of the fraction  $B$  of basal species,  $p_{\text{prey}}(0)$ , leads, in the continuous analysis, to a wrong approximation because the exponential-integral function  $E_1(x)$  diverges as  $x$  approaches zero.
- [17] R. K. Pathria, *Statistical Mechanics* (Pergamon Press, New York, 1972).