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A stochastic theory of community food webs
III. Predicted and observed lengths of food chains

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This paper offers a quantitative theory of the length of food chains. The theory derives from a mathematical model of community food webs called the cascade model. The paper tests the predictions against data from real webs.

An exact formula for the expected number of chains of each length in a model web with any given finite number, S, of species is, to our knowledge, the first exactly derived theory of the length of food chains. Since the numbers of chains of different lengths are dependent in the cascade model, we evaluate the goodness of fit between the observed and predicted numbers of chains by a Monte Carlo method.

Without fitting any free parameters, and using no direct information about chain lengths other than that implied by the total number of species and the total number of links in a web, we find that the cascade model describes acceptably the observed numbers of chains of each length in all but 16 or 17 of 113 webs. Of 62 webs previously used to test the cascade model, the cascade model describes acceptably the chain lengths in all but 11 or 12. With a fresh batch of 51 webs, we establish first that (apart from two outlying webs) the numbers of links are very nearly proportional to the numbers of species and that the constant of proportionality is consistent with that in the original 62 webs. This finding verifies the so-called species–link scaling law with new data. The cascade model describes acceptably the chain lengths of all but 5 of the 51 new webs.

Most of the 16 or 17 webs with chain lengths described poorly by the cascade model have unusually large average chain lengths (greater than 4 links) or unusually small average chain lengths (fewer than 2 links).

1. Introduction

The purpose of this paper is to derive a quantitative theory of the length of food chains from a mathematical model of community food webs called the cascade model and to test this theory quantitatively against data from real food webs. The cascade model was developed and tested by Cohen & Newman (1985, hereafter

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referred to as paper I) and by Cohen *et al.* (1985, hereafter referred to as paper II). The predictions of the cascade model describe, to a first approximation, several major characteristics of a collection of 62 real webs: the proportions of all species that are top, basal and intermediate, and the proportions of all links from basal to intermediate species, from basal to top species, from intermediate to intermediate species, and from intermediate to top species.

This paper determines what the cascade model implies for the frequency distribution of the length of food chains in webs with a finite number of species and compares the predictions with observations. The number of species in the observed webs ranges from 3 to 48. The theory of chain lengths is developed further for webs with a large number of species in the companion paper (Newman & Cohen 1986; hereafter referred to as paper IV).

Section 2 reviews present biological theories of food chain lengths; §3 presents terminology for chains and reviews the cascade model. Section 4 gives exact results about the frequency distribution of chain lengths for webs with a finite number of species and proposes a way to evaluate the goodness of fit of the cascade model's predictions to the observed frequency distribution of chain length in an individual web. A mathematical proof in §4 (the only one in this paper) is set off by *Proof* at the beginning and ■ at the end. Readers may defer or skip the proof with no loss of continuity.

In §5, we find that the cascade model describes acceptably most, but not all, of the frequency distributions of chain length observed in 62 webs, other aspects of which were previously used to develop and test the model. Does the cascade model succeed in most of these webs because the model was selected to describe other aspects of the same data, since such selection might constrain the possible frequency distributions of chain length?

No, according to the results of §6. There we examine the frequency distributions of chain lengths in a freshly assembled and edited collection of 51 webs that have not been previously related to the cascade model. The species-link scaling law (Cohen & Briand 1984; paper I), one of the central features of the cascade model, is not contradicted by these new data. The cascade model describes acceptably 46 of the 51 observed frequency distributions of chain lengths; this majority is even larger than the majority of its successes with the original 62 webs.

According to §7, the mean and variance calculated from the expected numbers of chains of each length cannot validly be compared with the mean and variance of chain lengths in an observed web. If such a comparison is made, nevertheless, the mean chain lengths are described acceptably, but not the variances.

In §8, we explain why we doubt the assumption that the 113 webs in our collection are a random sample from some statistical ensemble of webs. Under this dubious assumption, a Kolmogorov–Smirnov test rejects the null hypothesis that the cascade model's predictions describe the chain lengths in the ensemble of webs sampled by either the original 62 or the new 51 webs or all 113 combined.

Most of the 16 or 17 webs with chain lengths that the cascade model fits poorly have unusually large average chain lengths (greater than four links) or unusually small average chain lengths (fewer than two links).

Finally, in §9, we review the accomplishments of the paper, relate them to previous work, and propose several further studies. An appendix presents algorithms that were used to compute the frequency distribution of chain length and the length of the longest chain of a given web.

Two important descriptive tasks that will be undertaken elsewhere are, first, to relate chain lengths to characteristics of webs such as dimensionality, productivity, and variability of the environment, and the presence of man (F. Briand and J. E. Cohen, in preparation) and, second, to present in detail the sources and full data on all 113 (62+51) webs (F. Briand, in preparation).

2. THE LENGTH OF FOOD CHAINS: PRESENT ECOLOGICAL THEORY

Elton (1927 [1935], p. 56) justifies attention to food webs and food chains: 'The primary driving force of all animals is the necessity of finding the right kind of food and enough of it. Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supply'.

To our knowledge, Elton (1927 [1935], p. 56) is the first to introduce the terminology 'food chains': 'There are, in fact, chains of animals linked together by food, and all dependent in the long run upon plants. We refer to these as "food chains", and to all the food-chains in a community as the "food-cycle".' Elton's 'food-cycle' has been generally replaced by 'food-web'.

In notes added to the second impression, Elton (1927 [1935], p. xxvii) remarks that 'the first food-cycle diagram was published by V. E. Shelford' in 1913. Elton does not remark that the community described by Shelford's diagram is hypothetical, but observes elsewhere (p. 57): 'Extremely little work has been done so far on food-cycles, and the number of examples which have been worked out in even the roughest way can be counted on the fingers of one hand'.

Systematic quantitative data about food chains have been assembled only in the last decade. To our knowledge, the first numerical data on the frequency distribution of chain lengths in real food webs are presented by Cohen (1978, pp. 56–59), who emphasizes the need for, but does not provide, a quantitative theory (see also Cohen 1983).

The most comprehensive, quantitative and empirically based modern presentation of theories about the length of food chains that we know of is Pimm's (1982, ch. 6, pp. 99–130). He evaluates four hypotheses to explain why food chains rarely contain more than, roughly, five animal species (Hutchinson 1959, p. 147). Some recent perspectives on these hypotheses and their cousins are given by May (1983) and DeAngelis *et al.* (1983).

First, the *energetic* hypothesis suggested by Hutchinson (1959, p. 147) proposes that the length of food chains is limited by the inefficiency with which energy is transmitted along a chain and by the minimal energy requirements of predators at the top of a chain. This hypothesis could be interpreted to predict that food chains in ecosystems with higher primary productivity should be longer. Pimm's data do not confirm this prediction, though the ecosystems in Pimm's collection with extremely low primary productivity do have short chains. However, the energetic hypothesis could also be interpreted to predict that food chains in ecosystems with higher primary productivity can support energetically less efficient intermediate and top species without any change in chain length. Data on chain length alone, without detailed information on the energetic efficiency of the species in the chains, can neither establish nor disprove the energetic hypothesis. In a pioneering experimental study, Pimm & Kitching (1986) compared the chain lengths of artificial ecosystems with varying levels of energy input. They found no evidence of increasing chain lengths with increasing energy inputs.

Secondly, the *size* or *design* hypothesis predicts that chains should be limited in length by the requirement that a predator be larger than its prey. Pimm points out that parasites need not obey this requirement, and suggests that size or design requirements have no simple or easily testable effects on chain length.

Thirdly, the *optimal foraging* or *evolutionary shortening* hypothesis cites advantages in energetic efficiency that result from feeding low (near the primary producers) in food chains, and other energetic advantages that result from feeding high (near top predators), and suggests that the observed distributions of chain lengths result from an equilibrium of these opposing selective advantages. Although examples appear to illustrate one or another aspect of this hypothesis, precise quantitative predictions do not seem to follow from it.

Fourthly, the *dynamical stability* hypothesis argues first that, in several specific mathematical models of interacting populations, the longer the chains, the more severe the restrictions that must be imposed on the coefficients in the models for an equilibrium to be feasible or stable, and second that in certain models, those with longer food chains take longer to return to equilibrium once perturbed, so that systems with longer chains are less likely to persist in nature. The models (generally based on Lotka–Volterra equations) that support the dynamical stability hypothesis have not been independently verified. When these models are tested against data including data on chain length, it will be possible to decide what weight this hypothesis deserves as an explanation.

In addition to these four hypotheses, Kitching & Pimm (1986) describe seven environmental factors that may influence webs in phytotelmata. Phytotelmata are plant-held waters, such as occur in the axils of trees, bamboo internodal spaces, bromeliads, tree holes, and pitcher plants. The factors affecting webs include the size (surface area and volume) of the body of water, the latitude (hence climate), the size of the pool of species available to colonize the phytotelma, the evolutionary history of the host plants (see Beaver 1985), the particular host plant species, the successional stage, and altitude. Most of these factors influence webs in general. Kitching & Pimm give no quantitative predictions of the effects on chain length of changes in these factors.

Pimm (1982, appendix 6A) also presents a so-called 'null hypothesis' about chain lengths. To our knowledge, his is the first simple quantitative model of web structure that is used to derive quantitative predictions about the frequency distribution of chain length. To describe Pimm's model, we repeat some definitions from papers I and II. A *proper basal* species is a species that preys on no other species but is preyed on by at least one other. An *intermediate* species is a species that preys on at least one other species and is preyed on by at least one other species. A *proper top* species is a species that preys on at least one other species and is preyed on by no other species. If B_P, I and T_P are the numbers of proper basal, intermediate and proper top species in a community with L (trophic) links, Pimm constructs a predation matrix with (B_P+I) rows and (T_P+I) columns. All but L elements of the matrix are zero. The L elements that are equal to 1 are randomly assigned subject to three constraints: each proper top or intermediate species has at least one prey (at least one 1 in its column), each proper basal or intermediate species has at least one predator (at least one 1 in its row) and, to assure that the web is acyclic, the submatrix where intermediates prey on intermediates is strictly lower triangular. (The species are numbered from the top of the web to the bottom, contrary to the convention we adopt for the cascade model.)

For each of 13 real webs, Pimm computes the modal trophic level of each real top species (which, except for some minor details, is one greater than the modal length, defined below, of chains leading up to that species) and the modal trophic level of each (proper) top species, in simulated webs generated as just described. He then adopts a conservative procedure for deciding when the vector of simulated trophic levels of (proper) top species is smaller than the vector of real trophic levels of top species. He concludes that the simulated trophic levels of top species are smaller than the real levels in a proportion P of simulations whose mean (over different real webs) is 'significantly less' (Pimm 1982, p. 104) than 0.5, though he gives no significance level, and therefore that real chains are shorter than would be expected 'at random' according to the null hypothesis.

This conclusion seems liable to two criticisms. First, assuming with Pimm that the observed webs are independent observations (we shall return to this assumption), we believe that Pimm's null hypothesis that the expected $P = 0.5$ should be replaced by the null hypothesis that P is approximately uniformly distributed between 0 and 1. P will not be exactly uniformly distributed under the null hypothesis because the number of trophic levels is a discrete, not a continuous, random variable. When we perform a one-sample Kolmogorov–Smirnov test of the null hypothesis that Pimm's 13 P values are drawn from a uniform distribution, we obtain a D_{13}-statistic of 0.389. The probability that a value that large or larger would occur by chance alone is between 0.02 and 0.05. We conclude that the data do not overwhelmingly reject Pimm's null hypothesis.

Secondly, Pimm's test of the hypothesis that the expected $P = 0.5$ is based on adding χ^2 values for each of the 13 webs; this is equivalent to treating the webs as independent. The webs are chosen from ten papers; Paine is the author or a co-author of two of these. We doubt that different webs reported by the same observer are independent in structure because the observer brings the same, usually unstated, biases to all his observations (Briand & Cohen 1984; Cohen & Briand 1984; papers I and II). Under the worst dependence, Pimm's χ^2 value could be based on as few as nine independent observations. The probability that a D_9-statistic of 0.389 or larger would occur by chance alone is between 0.05 and 0.1 according to the Kolmogorov–Smirnov test.

We are less persuaded than Pimm that his null hypothesis is a bad idea. Pimm's model is in the same family, though perhaps not in the same genus, as the cascade model of paper I that we now review.

3. TERMINOLOGY; THE CASCADE MODEL

This section reviews and introduces terminology, then describes the cascade model (as in sections I. 2 [i.e. §2 of paper I] and II. 1).

A *food web* is a set of kinds of organisms and a relation that shows which, if any, kinds of organisms each kind of organism in the set eats. A *community food web* is a food web whose vertices are obtained by picking, within a habitat or set of habitats, a set of kinds of organisms (hereafter called *species*) on the basis of taxonomy, size, location, or other criteria, without prior regard to the eating relations (specified by trophic *links*) among the organisms (Cohen 1978, pp. 20–21). Hereafter 'web' means 'community food web'. A *basal* species is a species that eats no other species, and a *top* species is a species that is eaten by no other species.

In the representation of a web by a directed graph or digraph (see section I. 2), each vertex corresponds to a (lumped trophic) species. An edge (alway directed) (a, b) from vertex a to vertex b corresponds to a link from species a to species b, meaning that species b eats species a. An example of a walk in a digraph is the sequence a, (a, b), b, (b, c), c of alternating vertices and edges. The *length* of a walk is the number of edges in it. An n-walk is a walk of length n. The digraph of any web generated by the cascade model is acyclic, so no vertex (or species) can figure more than once in a walk in such a web. A *chain* is a walk from a basal species to a top species. A chain in this sense is identical to a 'maximal food chain' as defined by Cohen (1978, p. 56). An n-chain is a chain of length n, i.e. a chain with n links. The length of a chain is one less than the number of species involved in that chain.

Let S be the number of species in a web, and let C_n be the number of n-chains in an acyclic web, $n = 1, 2, \ldots, S-1$. Algorithms for computing C_n for a given web are presented in the appendix. Chains of length greater than $S-1$ are impossible. The *frequency distribution of chain length* is the vector $(C_1, \ldots, C_{S-1}) \equiv \mathbf{C}$. The total number of chains in the web will be denoted

$$C \equiv \sum_{n=1}^{S-1} C_n.$$

The *cascade model* assumes that species in a community are arranged in a hierarchy, pecking order or cascade of potential feeding relations. Whether a potential feeding relation becomes an actual feeding relation is determined randomly, independently of all other potential feeding relations. The probability that a potential feeding relation becomes actual is the same for every potential feeding relation within a community, and varies inversely as the number of species in the community.

More formally, the cascade model assumes that the $S \geqslant 2$ species of a web may be labelled from 1 (at the bottom, subject to predation by all other species) to S (at the top, subject to predation by no other species). (In graph theory, this labelling is called a *topological sorting* (Gibbons 1985, p. 122) because for every edge (i, j), we have $i < j$.) The probability that species j feeds on species i is 0 if $j \leqslant i$. If $i < j$, then j feeds on i with probability $p = p(S)$, i.e. with a probability between 0 and 1 that depends on S, and does not feed on i with probability $q = 1-p$, independently for all $1 \leqslant i < j \leqslant S$. Unless a contrary assumption is explicitly given, it will be assumed that for some finite positive real number $c \leqslant S$, $p = c/S$, where c is a constant independent of S.

All numerical predictions of the cascade model depend on the values of the model's two parameters c and S. These two parameters, in turn, may be estimated from only two observations: the observed number, L', of links and the observed number, S', of species.

4. FREQUENCY DISTRIBUTION OF CHAIN LENGTH IN FINITE WEBS; TESTING FIT

As usual, $E(.)$ denotes the expectation (or mean) of the random variable enclosed in parentheses. According to the cascade model, with probability p of a random link, the expected number of n-chains in a web with S species is

$$E(C_n) = p^n q^{S-1} \sum_{k=n}^{S-1} (S-k) \binom{k-1}{n-1} q^{-k}, \quad n = 1, 2, \ldots, S-1.$$

Proof. There is an n-chain going upward from vertex (species) i to vertex j if and only if: (a), $1 \leqslant i \leqslant S-n$; ($b$), $i+n \leqslant j \leqslant S$; ($c$), all n links on one of the $\binom{j-i-1}{n-1}$ possible walks of length n from i to j are present; (d), i is basal, i.e. no link is present from one of the $i-1$ vertices below i to i; and (e), j is top, i.e. no link is present from j to one of the $S-j$ vertices above j. Therefore

$$E(C_n) = \sum_{i=1}^{S-n} \sum_{j=i+n}^{S} \binom{j-i-1}{n-1} p^n q^{i-1} q^{S-j}.$$

Now

$$\sum_{i=1}^{S-n} \sum_{j=i+n}^{S} = \sum_{k=n}^{S-1} \sum_{i=1}^{S-k} \quad \text{if} \quad k = j-i;$$

therefore

$$E(C_n) = p^n q^{S-1} \sum_{k=n}^{S-1} \sum_{i=1}^{S-k} \binom{k-1}{n-1} q^{-k}$$

$$= p^n q^{S-1} \sum_{k=n}^{S-1} (S-k) \binom{k-1}{n-1} q^{-k}. \qquad \blacksquare$$

Figure 1, which we discuss in more detail below, plots $E(C_n)$ as a function of n for parameter values that are typical of the webs in the sample of 62 webs analysed in papers I and II.

This analysis leaves open a question concerning dependence, which we will answer roughly by numerical simulations of the cascade model. For typical webs, is there enough dependence between the number of chains of one length and the number of chains of another length to affect what statistical test we use to evaluate the goodness of fit between the observed and the predicted frequency distributions of chain length? In the cascade model of a web with S species, for any two different positive integers m and n, $1 \leqslant m \neq n \leqslant S-1$, if C_m and C_n, the (random) numbers

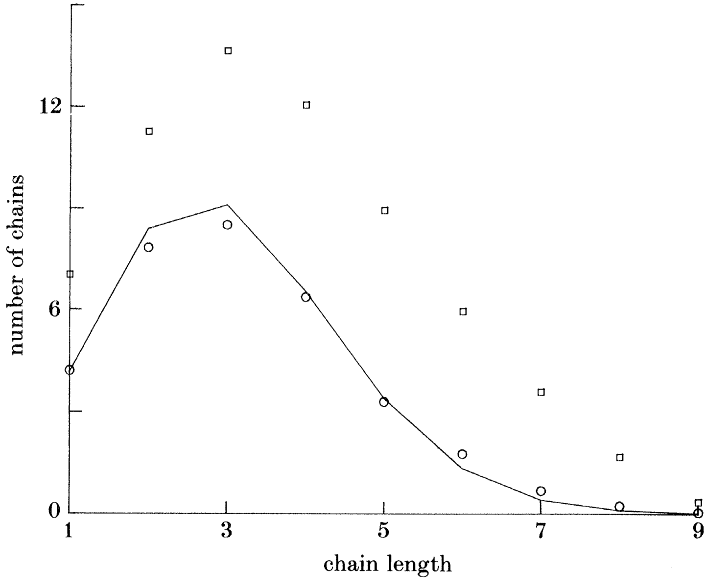

FIGURE 1. Theoretically expected number (——) of chains of length 1 to 9 in a web of $S = 17$ species, according to the cascade model with $c = 3.75$, sample mean number (○) of chains of each length in 100 simulations of the cascade model, and sample mean plus one sample standard deviation (□) in the number of chains of each length. No chains with more than nine links occurred in the simulations; the expected total number of such chains per simulation is 0.003.

of chains of length m and n, were independent, then we might measure the goodness of fit of the observed to the expected frequency distributions of chain lengths by Pearson's χ^2 statistic. However, if C_m and C_n, $m \neq n$, were not independent, then the tabulated probability distribution of χ^2 would bear no relation to the actual probability distribution of the computed χ^2 statistic. In the case of dependence, it would be necessary to compute the correct probability distribution or find another way to measure goodness of fit.

To answer this question, we chose $S = 17$ as a typical number of species, because the mean number of species per web in the 62 webs analysed in papers I and II is 16.7. We chose $c = 3.75$, near the observed estimate of 3.71, so that the expected number of links per web would be 30, near the observed mean in the 62 webs of 30.95 links per web. Given these two parameters, we generated 100 random webs according to the cascade model and recorded various statistics.

The mean number, averaged over the 100 simulated webs, of chains of each length is plotted in figure 1 along with the theoretically expected number derived above. The excellent agreement serves as a check both on the simulation and on the theoretical derivation. Also plotted in figure 1 is the mean number plus one sample standard deviation in the number of chains of each length.

To investigate dependence among the numbers of chains of each length, we computed the dispersion matrix or variance-covariance matrix of the simulated random variables $\{C_n, n = 1, 2, \ldots, 9\}$. (No chains of length greater than nine

Table 1. DISPERSION OR VARIANCE–COVARIANCE MATRIX OF THE NUMBERS OF CHAINS OF EACH LENGTH 1, 2, ..., 9 IN 100 SIMULATIONS OF THE CASCADE MODEL WITH $S = 17$ AND $c = 3.75$

(For example, the sample covariance of C_3 and C_4 was 19.85. No chains of length greater than 9 occurred.)

	chain length								
chain length	1	2	3	4	5	6	7	8	9
1	8.08	2.42	−5.74	−8.08	−5.83	−3.85	−1.61	−0.58	−0.10
2	2.42	11.87	1.87	−1.90	−3.07	−3.39	−2.42	−1.14	−0.28
3	−5.74	1.87	26.82	19.85	16.19	7.96	1.28	−0.26	−0.14
4	−8.08	−1.90	19.85	32.64	28.02	16.16	5.29	1.12	0.06
5	−5.83	−3.07	16.19	28.02	32.13	20.00	8.31	2.49	0.37
6	−3.85	−3.39	7.96	16.16	20.00	17.70	10.26	4.14	0.72
7	−1.61	−2.42	1.28	5.29	8.31	10.26	8.52	3.98	0.80
8	−0.58	−1.14	−0.26	1.12	2.49	4.14	3.98	2.12	0.44
9	−0.10	−0.28	−0.14	0.06	0.37	0.72	0.80	0.44	0.10

occurred.) Table 1 gives the dispersion matrix. In general, the numbers of chains of similar length appear to be positively correlated, while the numbers of very short chains are negatively correlated with the numbers of very long chains.

To test whether $\{C_n,\ n = 1, 2, \ldots, 9\}$ could be treated as independent, we applied a test for independence given by Kendall & Stuart (1968, p. 271). If the $p \times p$ dispersion matrix D (for p random variables) has diagonal elements d_{ii} and determinant $\det D$ and is based on a sample of N observations, then the test statistic

$$-2(1-[2p+11]/[6n])\ln\left(\det D/\prod_{i=1}^{p} d_{ii}\right)^{\frac{1}{2}N}$$

has approximately the distribution of χ^2 with $p(p-1)/2$ degrees of freedom. For the dispersion matrix in table 1, $p = 9$, and $N = 100$, we obtain a test statistic of nearly 1050 with 36 degrees of freedom. The test statistic is so large that it decisively rejects the null hypothesis that $\{C_n,\ n = 1, 2, \ldots, 9\}$ are independent.

We therefore measure the goodness of fit of the predicted frequencies $E(C_n)$ to the observed frequencies, for each web separately, by a Monte Carlo procedure. For brevity, let $E_n = E(C_n)$ be the expected number of chains of length n according to the cascade model and D_n the observed number in a given web. (We reserve C_n for the random variable that denotes the number of n-chains in the cascade model.) If M (for maximum) is the length of the longest chain observed in the given web, we take as data the vector

$$\boldsymbol{D} = (D_1, \ldots, D_M, 0),$$

where the final 0 is the total observed frequency of chains of all lengths greater than M (namely, none). We take as our theoretical predictions the vector of expectations computed using the values of S and c estimated by the iterative procedure in the appendix of paper II:

$$\boldsymbol{E} = \left(E_1, \ldots, E_M, \sum_{h=M+1}^{S-1} E_h\right).$$

Table 2 gives $\boldsymbol{D}$ and $\boldsymbol{E}$ for all 113 webs analysed here; and shows that the sum of the expected number of chains of each length, i.e. the expected total number of chains, does not, in general, equal the sum of the observed number of chains of each length, i.e. the observed total number of chains. The values of the parameters c and S used to compute $\boldsymbol{E}$ match the expected with the observed numbers of links, but these links can be arranged to yield widely varying numbers of chains.

TABLE 2. SPECIES, LINKS, AND NUMBERS OF CHAINS OF EACH LENGTH OBSERVED IN 11 WEBS, AND THE CASCADE MODEL'S ESTIMATED PARAMETERS S, c, AND EXPECTE NUMBERS OF CHAINS OF EACH LENGTH

(Under 'S', the upper number for each web is the observed number of species, the lower number the estimated valu of the parameter S. Under 'L', the upper number is the observed number of links, the lower number the estimate value of the parameter c. Under the number of chains of each length, the upper number is the observed number, whil the lower number is the predicted number. The last positive predicted number is the number predicted for all chair of that length and longer.)

web number	S	L	number of chains of length										
			1	2	3	4	5	6	7	8	9	10	> 10
1	8	14	0	2	3	3	0	0	0	0	0	0	0
1	8.1	4.0	1.9	4.0	3.8	2.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
2	14	22	0	4	10	0	0	0	0	0	0	0	0
2	14.5	3.3	3.7	6.1	5.3	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	24	34	1	19	10	0	0	0	0	0	0	0	0
3	25.5	2.8	7.1	9.4	7.4	6.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	13	26	0	7	10	2	0	0	0	0	0	0	0
4	13.1	4.3	2.9	7.1	8.7	6.7	5.5	0.0	0.0	0.0	0.0	0.0	0.0
5	6	5	0	3	0	0	0	0	0	0	0	0	0
5	8.1	1.4	2.4	1.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6	25	43	1	12	8	18	18	3	0	0	0	0	0
6	25.7	3.5	6.3	11.7	12.1	8.7	4.7	2.0	0.9	0.0	0.0	0.0	0.0
7	18	30	1	5	16	2	0	0	0	0	0	0	0
7	18.5	3.4	4.6	8.2	8.0	5.3	3.8	0.0	0.0	0.0	0.0	0.0	0.0
8	15	25	5	6	12	2	0	0	0	0	0	0	0
8	15.4	3.5	3.9	6.9	6.7	4.2	2.7	0.0	0.0	0.0	0.0	0.0	0.0
9	9	13	0	1	6	0	0	0	0	0	0	0	0
9	9.3	3.1	2.5	3.7	2.7	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	3	2	0	1	0	0	0	0	0	0	0	0	0
10	3.0	2.0	1.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11	5	4	0	2	0	0	0	0	0	0	0	0	0
11	6.9	1.4	1.8	0.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	9	13	0	6	2	0	0	0	0	0	0	0	0
12	9.3	3.1	2.5	3.7	2.7	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0
13	9	14	0	4	4	0	0	0	0	0	0	0	0
13	9.2	3.4	2.4	4.0	3.3	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	8	10	1	1	3	0	0	0	0	0	0	0	0
14	8.5	2.7	2.4	2.7	1.5	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	7	7	0	2	1	0	0	0	0	0	0	0	
15	8.1	2.0	2.5	1.8	0.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16	14	20	1	10	3	0	0	0	0	0	0	0	0
16	14.7	2.9	3.9	5.4	4.1	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17	14	23	0	2	9	9	3	0	0	0	0	0	0
17	14.4	3.4	3.6	6.4	6.0	3.7	1.6	0.6	0.0	0.0	0.0	0.0	0.0
18	23	35	13	10	5	4	0	0	0	0	0	0	0
18	24.1	3.0	6.5	9.9	8.6	5.2	3.6	0.0	0.0	0.0	0.0	0.0	0.0

TABLE 2 (*cont.*)

			number of chains of length										
web number	S	L	1	2	3	4	5	6	7	8	9	10	> 10
19	17	32	0	4	17	4	0	0	0	0	0	0	0
19	17.3	3.9	4.0	8.7	10.1	7.7	6.7	0.0	0.0	0.0	0.0	0.0	0.0
20	19	30	0	5	9	7	2	0	0	0	0	0	0
20	19.7	3.2	5.1	8.2	7.4	4.6	2.1	1.0	0.0	0.0	0.0	0.0	0.0
21	9	20	0	2	8	15	16	10	3	0	0	0	0
21	9.0	5.0	1.8	5.4	7.4	5.7	2.7	0.8	0.1	0.0	0.0	0.0	0.0
22	28	58	4	13	34	36	19	6	2	0	0	0	0
22	28.3	4.2	6.2	15.3	20.6	18.9	13.0	7.0	3.1	1.6	0.0	0.0	0.0
23	15	27	1	11	7	1	0	0	0	0	0	0	0
23	15.3	3.8	3.7	7.4	8.0	5.6	4.2	0.0	0.0	0.0	0.0	0.0	0.0
24	12	18	3	5	12	4	0	0	0	0	0	0	0
24	12.4	3.1	3.3	5.0	4.0	2.1	1.0	0.0	0.0	0.0	0.0	0.0	0.0
25	24	37	3	16	5	1	0	0	0	0	0	0	0
25	25.1	3.1	6.8	10.4	9.3	5.8	4.1	0.0	0.0	0.0	0.0	0.0	0.0
26	32	56	7	16	16	10	5	2	0	0	0	0	0
26	32.9	3.5	8.0	15.1	16.2	12.2	6.9	3.2	1.7	0.0	0.0	0.0	0.0
27	22	39	0	12	28	7	0	0	0	0	0	0	0
27	22.5	3.6	5.5	10.6	11.4	8.4	7.4	0.0	0.0	0.0	0.0	0.0	0.0
28	32	35	6	15	5	0	0	0	0	0	0	0	0
28	37.5	1.9	11.2	9.2	4.9	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
29	16	22	1	5	8	6	2	0	0	0	0	0	0
29	17.0	2.7	4.9	6.3	4.6	2.3	0.8	0.3	0.0	0.0	0.0	0.0	0.0
30	14	32	0	0	5	21	39	25	4	0	0	0	0
30	14.1	4.9	2.8	8.4	12.4	11.6	7.5	3.5	1.2	0.4	0.0	0.0	0.0
31	14	51	0	9	39	51	29	7	0	0	0	0	0
31	14.0	7.8	1.8	10.4	28.4	47.2	53.5	43.4	41.8	0.0	0.0	0.0	0.0
32	14	52	0	11	40	51	29	7	0	0	0	0	0
32	14.0	8.0	1.7	10.5	29.2	49.9	57.8	48.0	47.8	0.0	0.0	0.0	0.0
33	29	48	14	20	7	2	0	0	0	0	0	0	0
33	30.0	3.3	7.8	13.4	13.3	9.3	7.9	0.0	0.0	0.0	0.0	0.0	0.0
34	12	27	1	22	18	4	0	0	0	0	0	0	0
34	12.0	4.9	2.4	7.1	10.2	9.0	8.3	0.0	0.0	0.0	0.0	0.0	0.0
35	13	36	1	33	36	12	0	0	0	0	0	0	0
35	13.0	6.0	2.2	8.7	16.5	19.2	28.5	0.0	0.0	0.0	0.0	0.0	0.0
36	19	35	14	13	11	3	0	0	0	0	0	0	0
36	19.3	3.8	4.6	9.5	10.7	8.1	7.2	0.0	0.0	0.0	0.0	0.0	0.0
37	23	38	0	21	23	8	0	0	0	0	0	0	0
37	23.8	3.3	6.0	10.3	10.1	6.8	5.3	0.0	0.0	0.0	0.0	0.0	0.0
38	31	95	20	55	34	0	0	0	0	0	0	0	0
38	31.0	6.3	4.9	21.2	47.6	314.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
39	33	70	19	34	7	0	0	0	0	0	0	0	0
39	33.4	4.3	7.2	18.3	25.5	59.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
40	11	15	4	10	2	0	0	0	0	0	0	0	0
40	11.6	2.8	3.2	4.1	2.8	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
41	18	49	0	0	5	18	55	86	59	14	0	0	0
41	18.0	5.8	3.1	11.8	22.3	27.1	23.5	15.4	7.8	3.1	1.3	0.0	0.0
42	15	36	2	3	17	37	56	43	15	2	0	0	0
42	15.0	5.1	2.9	9.2	14.6	14.7	10.4	5.4	2.1	0.6	0.2	0.0	0.0
43	20	38	0	16	27	16	4	0	0	0	0	0	0
43	20.3	3.9	4.7	10.3	12.1	9.6	5.6	3.7	0.0	0.0	0.0	0.0	0.0
44	12	29	0	3	19	19	7	0	0	0	0	0	0
44	12.0	5.3	2.3	7.5	11.8	11.3	7.3	4.6	0.0	0.0	0.0	0.0	0.0

TABLE 2 (*cont.*)

web number	S	L	number of chains of length										
			1	2	3	4	5	6	7	8	9	10	> 10
45	11	20	1	10	3	0	0	0	0	0	0	0	0
45	11.1	3.9	2.6	5.6	5.9	6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
46	19	68	3	12	59	85	84	45	13	2	0	0	0
46	19.0	7.6	2.5	14.0	37.5	64.2	77.8	70.9	50.1	28.0	18.8	0.0	0.0
47	27	50	0	1	10	22	25	0	0	0	0	0	0
47	27.6	3.8	6.5	13.5	15.5	12.3	7.4	5.4	0.0	0.0	0.0	0.0	0.0
48	13	20	0	2	7	8	2	0	0	0	0	0	0
48	13.4	3.2	3.5	5.5	4.7	2.6	1.0	0.3	0.0	0.0	0.0	0.0	0.0
49	12	20	0	8	7	1	0	0	0	0	0	0	0
49	12.3	3.6	3.1	5.6	5.3	3.1	1.7	0.0	0.0	0.0	0.0	0.0	0.0
50	14	23	0	10	8	0	0	0	0	0	0	0	0
50	14.4	3.4	3.6	6.4	6.0	5.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
51	25	46	0	4	17	9	2	0	0	0	0	0	0
51	25.5	3.8	6.0	12.4	14.2	11.1	6.5	4.5	0.0	0.0	0.0	0.0	0.0
52	20	32	2	19	4	0	0	0	0	0	0	0	0
52	20.7	3.2	5.3	8.7	8.1	8.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
53	22	31	1	19	0	0	0	0	0	0	0	0	0
53	23.4	2.8	6.5	8.6	12.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
54	14	20	1	4	6	1	0	0	0	0	0	0	0
54	14.7	2.9	3.9	5.4	4.1	2.1	1.0	0.0	0.0	0.0	0.0	0.0	0.0
55	12	18	0	7	6	0	0	0	0	0	0	0	0
55	12.4	3.1	3.3	5.0	4.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
56	10	14	0	7	2	0	0	0	0	0	0	0	0
56	10.4	3.0	2.9	3.9	2.7	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
57	9	19	0	5	14	10	2	0	0	0	0	0	0
57	9.0	4.7	1.9	5.2	6.6	4.8	2.1	0.7	0.0	0.0	0.0	0.0	0.0
58	17	21	1	3	3	2	3	4	2	0	0	0	0
58	18.7	2.4	5.4	5.7	3.5	1.5	0.5	0.1	0.0	0.0	0.0	0.0	0.0
59	29	61	0	34	17	1	0	0	0	0	0	0	0
59	29.3	4.3	6.3	16.0	22.0	20.6	28.2	0.0	0.0	0.0	0.0	0.0	0.0
60	33	69	1	54	33	0	0	0	0	0	0	0	0
60	33.4	4.3	7.3	18.1	24.7	56.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
61	8	10	2	3	2	0	0	0	0	0	0	0	0
61	8.5	2.7	2.4	2.7	1.5	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
62	11	12	1	0	3	2	0	0	0	0	0	0	0
62	12.6	2.1	3.7	3.1	1.5	0.5	0.1	0.0	0.0	0.0	0.0	0.0	0.0
63	18	75	2	50	131	100	0	0	0	0	0	0	0
63	18.0	8.8	2.0	13.9	45.1	91.9	516.8	0.0	0.0	0.0	0.0	0.0	0.0
64	19	28	7	14	0	0	0	0	0	0	0	0	0
64	20.0	3.0	5.3	7.6	11.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
65	13	25	3	17	0	0	0	0	0	0	0	0	0
65	13.1	4.1	3.0	6.9	18.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
66	10	18	0	4	8	3	0	0	0	0	0	0	0
66	10.1	4.0	2.4	5.1	5.2	3.2	1.7	0.0	0.0	0.0	0.0	0.0	0.0
67	21	62	1	8	30	48	30	6	0	0	0	0	0
67	21.0	6.2	3.4	14.2	30.1	41.3	40.9	30.9	32.2	0.0	0.0	0.0	0.0
68	22	32	4	8	20	3	0	0	0	0	0	0	0
68	23.2	2.9	6.4	9.0	7.3	4.1	2.6	0.0	0.0	0.0	0.0	0.0	0.0
69	29	73	6	4	37	36	19	2	0	0	0	0	0
69	29.1	5.2	5.5	18.0	31.3	36.6	31.9	21.8	20.8	0.0	0.0	0.0	0.0
70	14	28	0	19	18	0	0	0	0	0	0	0	0
70	14.1	4.3	3.1	7.6	9.4	13.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0

TABLE 2 (*cont.*)

web			number of chains of length										
umber	*S*	*L*	1	2	3	4	5	6	7	8	9	10	> 10
71	16	32	0	1	7	17	28	25	11	0	0	0	0
71	16.2	4.2	3.6	8.6	10.8	8.8	5.1	2.2	0.7	0.2	0.0	0.0	0.0
72	17	32	0	3	6	19	10	0	0	0	0	0	0
72	17.3	3.9	4.0	8.7	10.1	7.7	4.2	2.5	0.0	0.0	0.0	0.0	0.0
73	10	15	2	6	8	0	0	0	0	0	0	0	0
73	10.3	3.2	2.7	4.2	3.3	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
74	21	36	2	14	8	2	0	0	0	0	0	0	0
74	21.6	3.5	5.3	9.8	10.1	7.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0
75	9	14	1	3	6	2	0	0	0	0	0	0	0
75	9.2	3.4	2.4	4.0	3.3	1.6	0.6	0.0	0.0	0.0	0.0	0.0	0.0
76	14	17	1	4	5	2	0	0	0	0	0	0	0
76	15.4	2.4	4.5	4.6	2.8	1.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0
77	13	24	1	3	9	13	6	0	0	0	0	0	0
77	13.2	3.9	3.1	6.6	7.3	5.1	2.5	1.1	0.0	0.0	0.0	0.0	0.0
78	16	27	0	5	8	6	1	0	0	0	0	0	0
78	16.4	3.5	4.1	7.4	7.3	4.8	2.2	1.1	0.0	0.0	0.0	0.0	0.0
79	21	29	0	4	8	7	3	0	0	0	0	0	0
79	22.4	2.7	6.3	8.0	6.1	3.2	1.2	0.5	0.0	0.0	0.0	0.0	0.0
80	27	70	3	16	18	33	8	0	0	0	0	0	0
80	27.1	5.4	4.9	17.0	30.7	37.0	33.0	45.3	0.0	0.0	0.0	0.0	0.0
81	12	19	0	6	7	2	0	0	0	0	0	0	0
81	12.3	3.4	3.2	5.3	4.6	2.6	1.3	0.0	0.0	0.0	0.0	0.0	0.0
82	10	14	0	0	3	3	1	0	0	0	0	0	0
82	10.4	3.0	2.9	3.9	2.7	1.2	0.3	0.1	0.0	0.0	0.0	0.0	0.0
83	25	67	2	31	25	2	0	0	0	0	0	0	0
83	25.1	5.6	4.4	16.1	30.2	37.6	82.9	0.0	0.0	0.0	0.0	0.0	0.0
84	12	23	0	4	10	11	6	0	0	0	0	0	0
84	12.1	4.1	2.8	6.4	7.3	5.2	2.5	1.1	0.0	0.0	0.0	0.0	0.0
85	27	49	2	6	27	35	13	0	0	0	0	0	0
85	27.6	3.7	6.6	13.2	14.9	11.5	6.7	4.7	0.0	0.0	0.0	0.0	0.0
86	16	37	0	0	13	43	16	2	0	0	0	0	0
86	16.1	4.9	3.2	9.6	14.5	14.2	9.8	5.0	2.7	0.0	0.0	0.0	0.0
87	11	17	1	5	11	5	0	0	0	0	0	0	0
87	11.3	3.3	3.0	4.8	4.0	2.1	0.9	0.0	0.0	0.0	0.0	0.0	0.0
88	16	42	3	59	0	0	0	0	0	0	0	0	0
88	16.0	5.6	2.8	10.3	73.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
89	18	32	0	6	18	3	0	0	0	0	0	0	0
89	18.4	3.7	4.4	8.8	9.4	6.7	5.4	0.0	0.0	0.0	0.0	0.0	0.0
90	22	39	6	32	0	0	0	0	0	0	0	0	0
90	22.5	3.6	5.5	10.6	27.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
91	10	13	0	2	4	2	0	0	0	0	0	0	0
91	10.6	2.7	3.0	3.5	2.2	0.9	0.3	0.0	0.0	0.0	0.0	0.0	0.0
92	18	18	3	5	3	0	0	0	0	0	0	0	0
92	22.0	1.7	6.7	4.6	2.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
93	26	70	1	51	8	0	0	0	0	0	0	0	0
93	26.1	5.6	4.6	16.8	31.7	130.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
94	12	19	1	4	8	6	4	0	0	0	0	0	0
94	12.3	3.4	3.2	5.3	4.6	2.6	1.0	0.3	0.0	0.0	0.0	0.0	0.0
95	10	12	1	3	3	1	0	0	0	0	0	0	0
95	10.9	2.4	3.0	3.1	1.7	0.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0
96	9	16	1	11	0	0	0	0	0	0	0	0	0
96	9.1	4.0	2.2	4.6	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 2 (*cont.*)

web			number of chains of length										
number	S	L	1	2	3	4	5	6	7	8	9	10	> 1
97	11	17	1	14	1	0	0	0	0	0	0	0	0
97	11.3	3.3	3.0	4.8	4.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.
98	17	39	1	11	21	35	10	0	0	0	0	0	0
98	17.1	4.9	3.4	10.1	15.2	14.9	10.4	8.5	0.0	0.0	0.0	0.0	0.
99	48	138	14	115	98	21	0	0	0	0	0	0	0
99	48.1	5.9	8.1	31.8	66.1	93.7	315.8	0.0	0.0	0.0	0.0	0.0	0.
100	22	59	3	27	28	28	16	3	0	0	0	0	0
100	22.0	5.6	3.9	14.2	26.6	32.7	29.2	20.0	18.2	0.0	0.0	0.0	0.
101	6	5	1	2	0	0	0	0	0	0	0	0	0
101	8.1	1.4	2.4	1.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.
102	9	27	0	7	19	24	16	6	1	0	0	0	0
102	9.0	6.7	1.3	6.3	13.0	14.9	10.3	4.3	1.0	0.1	0.0	0.0	0.
103	23	133	1	46	260	602	769	856	621	285	88	12	0
103	23.0	12.1	1.9	19.2	92.7	284.8	624.1	1036.8	1355.1	1427.1	1230.6	877.9	937.
104	27	62	2	21	17	22	7	0	0	0	0	0	0
104	27.2	4.7	5.5	15.8	24.4	25.4	19.6	21.2	0.0	0.0	0.0	0.0	0.
105	10	22	0	3	6	11	4	0	0	0	0	0	0
105	10.0	4.9	2.0	5.9	8.1	6.5	3.3	1.4	0.0	0.0	0.0	0.0	0.
106	35	73	7	44	22	6	2	0	0	0	0	0	0
106	35.4	4.2	7.7	19.1	26.1	24.7	17.6	17.4	0.0	0.0	0.0	0.0	0.
107	10	14	1	2	5	0	0	0	0	0	0	0	0
107	10.4	3.0	2.9	3.9	2.7	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.
108	14	20	0	11	4	0	0	0	0	0	0	0	0
108	14.7	2.9	3.9	5.4	4.1	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.
109	21	57	0	18	40	10	0	0	0	0	0	0	0
109	21.0	5.7	3.6	13.7	25.9	32.1	66.4	0.0	0.0	0.0	0.0	0.0	0.
110	13	23	3	7	5	0	0	0	0	0	0	0	0
110	13.2	3.8	3.2	6.4	6.6	7.2	0.0	0.0	0.0	0.0	0.0	0.0	0.
111	19	36	2	15	17	0	0	0	0	0	0	0	0
111	19.3	3.9	4.5	9.8	11.4	17.3	0.0	0.0	0.0	0.0	0.0	0.0	0.
112	14	17	3	8	1	0	0	0	0	0	0	0	0
112	15.4	2.4	4.5	4.6	2.8	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.
113	11	12	1	6	2	0	0	0	0	0	0	0	0
113	12.6	2.1	3.7	3.1	1.5	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.

We compute the difference between data and predictions by one of two measures: the sum of squared differences,

$$d_1(\boldsymbol{D},\boldsymbol{E}) = \sum_{h=1}^{M+1} (D_h - E_h)^2,$$

or a Pearson χ^2 measure,

$$d_2(\boldsymbol{D},\boldsymbol{E}) = \sum_{h=1}^{M+1} (D_h - E_h)^2/E_h.$$

Large values of these measures of difference confound two distinct kinds of discrepancies between $\boldsymbol{D}$ and $\boldsymbol{E}$: differences in the expected and observed total numbers of chains, and differences in the expected and observed proportions of all chains that are of given lengths. However, both measures are useful in that low values of either measure signify good agreement between observation and expectation in both total numbers of chains and proportions of each length.

To measure how likely the difference d_m, $m = 1, 2$, is to arise by chance alone according to the cascade model, we generate random strictly upper triangular adjacency matrices according to the cascade model. For S, the size of the matrix, we use the integer part of the value of S obtained by the iterative procedure in the appendix of paper II. In most but not all cases, the size of the matrix is identical to the observed number of species in the web. For c, we use exactly the value of c obtained by the iterative procedure in the appendix of paper II. Rounded values of S and c for each web are also given in table 2. For each randomly generated adjacency matrix, we compute the frequency distribution of chain lengths (see the appendix of this paper). We then combine the frequencies of all chains longer than M and compute the difference between the resulting $(M+1)$-vector of simulated frequencies and $\boldsymbol{E}$. Call this difference $d_m^{(i)}$ for the ith simulated web.

We take our null hypothesis to be that the difference, d_m, between the observed and expected frequency distributions is greater than 95% of randomly chosen values of $d_m^{(i)}$, i.e. that the cascade model provides a description of observed chain lengths that is poor enough to reject at the 5% level of significance. If our simulations show that a sufficiently small proportion of the simulated differences satisfy $d_m^{(i)} < d_m$, then we can reject the null hypothesis and conclude that the cascade model could not be rejected at the 5% level, and hence describes the data on chain lengths.

For each observed web, we test the goodness of fit between $\boldsymbol{E}$ and $\boldsymbol{D}$ as follows. We generate 20 random webs according to the cascade model and find the number, X_{20}, of those simulated webs for which $d_m^{(i)} < d_m$. We then consult a table (previously calculated and stored) of the binomial cumulative distribution function with parameters $N = 20$ and $p' = 0.95$ to find the probability, P, of X_{20} or fewer successes. If this probability P is less than or equal to 0.01, we reject the null hypothesis that the difference d_m between the observed and expected frequency distributions is greater than or equal to 95% of randomly chosen values of $d_m^{(i)}$ and accept $\boldsymbol{E}$ as describing $\boldsymbol{D}$. In this case, we then go on to the next observed web. However, if $P > 0.01$, we generate another 20 random webs according to the cascade model and find the cumulative number, X_{40}, of the 40 simulated webs for which $d_m^{(i)} < d_m$. We then consult the table of the cumulative binomial distribution with parameters $N = 40$ and $p' = 0.95$ to find the probability P of X_{40} or fewer successes. Once again, if $P \leqslant 0.01$, we stop and accept the cascade model. If $P > 0.01$, we continue to generate additional batches of 20 random webs, up to a total of 100 random webs, until either we find a $P < 0.01$ and accept the cascade model or we are left with $X_{100}/100$ as the estimated fraction of random webs that satisfy $d_m^{(i)} < d_m$.

For every web, we record the number, N, of simulated webs generated, the number, X_N, of 'successes' among the simulated webs, and either the probability P (provided $P \leqslant 0.01$) of X_N or fewer successes from a binomial distribution with parameters N and $p' = 0.95$ or, if $P > 0.01$, the fraction X_N/N. We carry out this analysis for all observed webs once with d_1 and again, generating new random webs for each observed web, with d_2, to see whether the choice of difference measure affects our conclusions.

This procedure tests the goodness of fit of $\boldsymbol{E}$ to $\boldsymbol{D}$ for an observed individual web without making any assumption that $\boldsymbol{D}$ for one observed web is independent of $\boldsymbol{D}$ for another observed web.

5. THE ORIGINAL BATCH OF 62 WEBS

By using the sum-of-squares measure, d_1, of difference between observed and predicted frequency distributions, we find that 40 of 62 observed webs (65%) reject at the 0.01 significance level the null hypothesis that the cascade model's expectations fit the data worse than 95% of random webs generated by the cascade model. For brevity, we say that the cascade model describes the observed frequency distribution of chain lengths well in 40 of 62 webs. In 11 of 62 webs (18%), more than 95% of the generated random webs had chain length distributions that were closer to expectation than is the observed chain length distribution. For brevity, we say that the cascade model describes badly the observed frequency distribution of chain lengths in 11 of 62 webs (serial numbers 10, 21, 30, 37, 41, 42, 47, 53, 58, 59, 60). For the remaining 11 ($=62-40-11$) webs, we say that the cascade model describes chain lengths moderately well (serial numbers 3, 5, 6, 9, 34, 35, 38, 39, 43, 52, 62). Figure 2 plots the frequency histogram of X_N/N for the

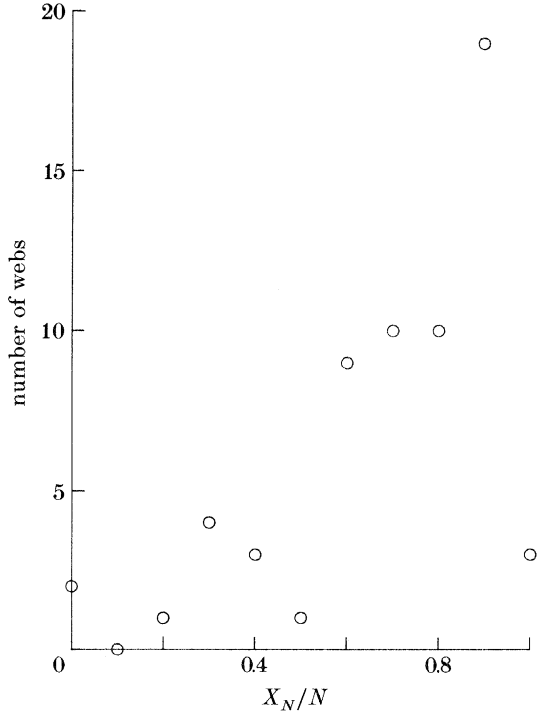

FIGURE 2. Frequency histogram of X_N/N for 62 webs previously studied: the number of webs with X_N/N in the interval $[0.1i, 0.1(i+1))$, for $i = 0, 1, 2, .., 10$. Here N is the number of random webs generated for each real web and X_N is the number of those random webs with chain length distributions closer (using d_1) to that expected from the cascade model than is that of the real web.

62 webs, where (as above) N is the number of random webs generated for a given web and X_N is the number of these random webs with a chain length distribution closer to the theoretical expectations than is the observed chain length distribution. Evidently a majority of webs have X_N/N greater than or equal to 0.6.

According to the χ^2 measure, d_2, of difference between observed and predicted frequency distributions, 43 of 62 observed webs (69 %) have frequency distributions of chain length that are described well by the cascade model, and 7 have frequency distributions that are described moderately well (serial numbers 3, 6, 9, 27, 47, 52, 59). The cascade model describes badly the observed frequency distribution of chain lengths in 12 of 62 webs (serial numbers 10, 21, 30, 35, 37, 38, 39, 41, 42, 53, 58, 60). In this batch of webs, the measure of difference chosen makes very little difference to the overall performance of the cascade model.

The frequency distributions of chain lengths that are described badly by the cascade model are of at least three kinds. First, in some webs, the number of chains is so small that it is not clear whether to take seriously any measure of fit (e.g. web 10 has only one chain of length 2). Second, in some webs, most of the observed chains are shorter than most of the predicted chains (e.g. webs 53, 60). Third, in some webs, most of the observed chains are longer than most of the predicted chains (e.g. webs 21, 30, 41, 42, 58).

We conclude that, when webs are considered one at a time, the cascade model predicts the observed frequency distributions of chain length well or moderately well in 50 or 51 of the 62 webs in our original batch, although no information about chain length was used in developing the cascade model or in estimating its parameters.

6. A FRESH BATCH OF 51 WEBS

The finding that 11 or 12 of the 62 webs in the first batch have frequency distributions of chain length that the cascade model describes badly shows that there is no logical necessity for the cascade model to describe well, or moderately well, the chain lengths of an individual web. However, such bad fits do not exclude the possibility that the cascade model describes chain lengths, at least in part, because the cascade model also describes, for most webs, the other major features of web structure considered in papers I and II. One of us therefore assembled and edited a fresh batch of 51 community webs (to be described in detail elsewhere: F. Briand, in preparation) and extracted, for each web, the observed number, S', of species, the observed number, L', of links, and the observed frequencies D_n, $n = 1, \ldots, M$, of chain length. These webs provide a strong test of the ability of the cascade model to describe new observations.

6.1. *Checking the assumptions of the cascade model*

One central structural assumption of the cascade model is that species are arranged in a hierarchy so that (ignoring cannibalism, as in paper I), cycles should be absent. The 51 new webs contain only one cycle of length 2 (in the web numbered 100 in the serial numbering of Briand) and no longer cycles. Cycles are rare enough that the assumption of a hierarchy is a reasonable assumption.

A second structural assumption of the cascade model is that the probability of a link from one species to another above it in the hierarchy varies inversely as the number of species in the web. This assumption implies that the total number of links in a web should be directly proportional to the total number of species: this is the species–link scaling law. Figure 3 plots the number, L', of observed links as a function of the number, S', of observed species for the 51 webs in the new batch. Apart from two clear outliers with 75 and 133 links (webs numbered 63 and 103), the points appear to fall along a straight line through the origin. Web 63 is an extended version of the River Rheidol subweb depicted by Jones (1950). High connectance aside, nothing special appears to distinguish this web from the others. Web 103, one of three webs in the collection of 113 provided by Petipa (1979), describes a tropical plankton community in the Pacific Ocean. This web contains the longest chain, with ten links, in the entire collection of 113 webs.

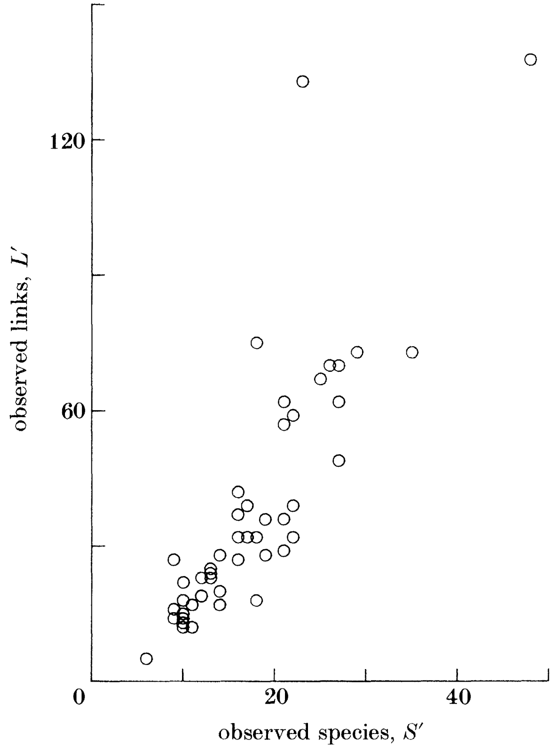

FIGURE 3. Observed number, L', of links as a function of the observed number, S', of species in 51 webs not previously studied.

The cascade model implies that the variance of the number, L, of links is asymptotically (for S considerably greater than c) proportional to S, and figure 3 makes it plausible that the variance of the number, L', of observed links is proportional to the number, S', of observed species. When this is true (see, for example, Snedecor & Cochran 1967, p. 168), the least squares estimate of the slope of the line through the origin is the ratio of the total number of links to the total number of species. The standard error of the slope may be estimated by a formula, also given by Snedecor & Cochran.

In the 51 webs of this batch, there are 1878 links and 874 species, giving an estimated slope of 2.1487 with an estimated standard error of 0.1220. If webs 63 and 103 are omitted, there remain 1670 links and 833 species, giving an estimated slope of 2.0048 with an estimated standard error of 0.0801. For comparison, Cohen & Briand (1984, p. 4105) report, in the first batch of 62 webs, that L' is approximately proportional to S' with slope 1.8559 and estimated standard error 0.0740. Figure 4 plots links, L', versus species, S', for all 113 ($= 62+51$) webs. The lack of marked difference between the slopes 1.86 ± 0.07 for the old batch of 62 webs and 2.00 ± 0.08 for the new batch of 49 webs (51 minus the two outliers), and the lack of clear separation between the old and the new sets of data points in figure 4, suggest that underlying both batches of webs is a common direct proportionality between numbers of species and numbers of links, with a constant of proportionality near 2. Combining all 113 webs gives 1908 species, 3797 links and an estimated slope of 1.9900 ± 0.0697. Without webs 63 and 103, the slope is 1.9223 ± 0.0546.

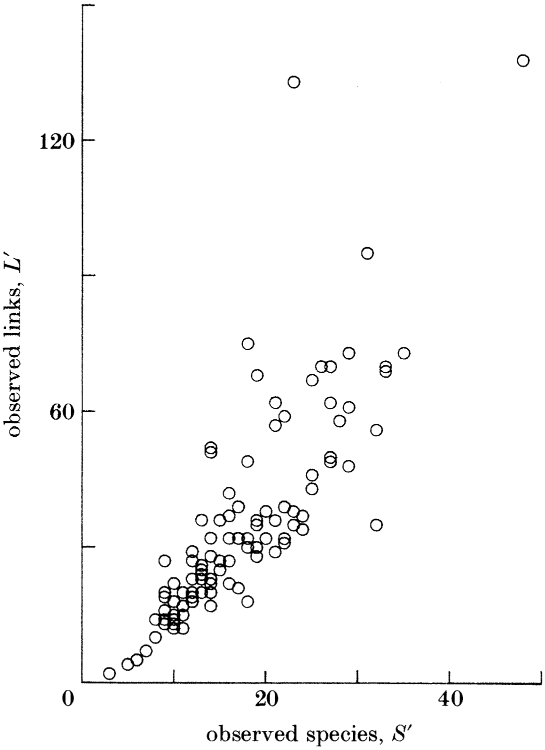

FIGURE 4. Observed number, L', of links as a function of the observed number, S', of species in all 113 webs.

Cohen & Briand (1984) remark that the 62 webs available to them do not exclude a slightly nonlinear relation, as noted by Briand (1983), between species and links, i.e. a relation of the form $E(L) = aS^b$ with b slightly different from 1. They find that a graph of $L'^{\frac{3}{4}}$ against S' looks very nearly linear through the origin. The same caveat and observation hold here. The use of the ordinary linear least squares method to regress log L' on log S' for all 113 webs gives the allometric model $L = 0.6713\ S^{1.3559+\epsilon}$, where ϵ is the error term, or (taking $1/1.3559 \approx \frac{3}{4}$) $L^{\frac{3}{4}}$ proportional to S. The parameters obtained by this procedure are not the least squares estimates for the nonlinear allometric model in the original scales of L and S. Scatter plots (not shown) of the residuals (observed links L' minus predicted) as a function of S' show very little difference between the fitted allometric model and the linear model $L = 1.9900\ S + \epsilon$. The sum (rounded to three significant figures) of the absolute residuals of the allometric model, namely 897, is smaller than the corresponding sum for the linear model, namely 999. The sum of the squared residuals of the allometric model (20000) is also smaller than the sum of the squared residuals of the linear model (21400). The data thus suggest that a relation between $E(L)$ and S that is mildly nonlinear for the observed range of species may be more precise than a simple proportionality. The exact relation between $E(L)$ and S deserves further empirical and theoretical investigation.

However, taking $E(L)$ as proportional to S does not do serious violence to the data. Moreover, in this paper, we estimate c independently for each web rather than assuming c to be constant for all webs. Hence this empirical test of the cascade model is less sensitive to how many links there are than to how the links that do occur are connected into chains.

6.2 *Testing the predictions of chain length*

On the basis of the rarity of cycles and the near-proportionality shown in figure 3, we conclude that the underlying assumptions of the cascade model are approximately satisfied by (nearly all of) the new batch of webs. As with the old batch, for each web in the new batch, we estimate the parameters S and c (given in table 2 after rounding), compute the expected frequency of chains of each length, and measure the goodness of fit between observed and predicted frequencies by the procedure described in §4.

From the sum-of-squares measure, d_1, of difference between observed and predicted frequency distributions, we find that the cascade model describes well 36 of 51 observed webs (71 %) and moderately well 10 webs (serial numbers 63, 68, 70, 72, 77, 85, 86, 93, 96, 103). In 5 of 51 webs (18 %), the cascade model describes the observed frequency distribution of chain lengths badly (serial numbers 65, 71, 88, 90, 97). The outlying webs 63 and 103 are *not* among these badly described five webs. Figure 5 plots the frequency histogram of X_N/N for the 51 webs, where (as above) N is the number of random webs generated for a given web and X_N is the number of these random webs with a chain length distribution closer to the theoretical expectations than is the observed chain length distribution. As in figure 2, a majority of the webs have X_N/N greater than or equal to 0.6.

According to the χ^2 measure, d_2, of difference between observed and predicted frequency distributions, 34 of 51 observed webs (67 %) have frequency distributions of chain length that the cascade model describes well. Twelve webs have frequency distributions that the cascade model describes moderately well (serial numbers 63, 65, 68, 70, 72, 77, 86, 87, 96, 97, 99, 106). The cascade model describes the observed frequency distribution of chain lengths badly in 5 of 51 webs (serial numbers 71,

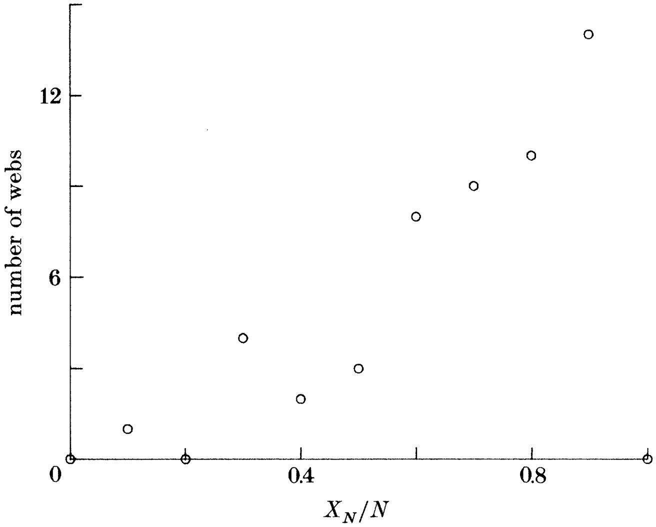

FIGURE 5. Frequency histogram of X_N/N for 51 webs not previously studied: the number of webs with X_N/N in the interval $[0.1i, 0.1(i+1))$, for $i = 0, 1, 2, \ldots, 10$. Here N is the number of random webs generated for each real web and X_N is the number of those random webs with chain length distributions closer (using d_1) to that expected from the cascade model than that of the real web.

85, 88, 90, 93). In this batch of webs, as in the first, which measure of difference we choose makes very little difference to the overall performance of the cascade model.

As in the original batch of 62 webs, in this new batch sometimes more short chains are observed than expected (e.g. webs 65, 88, 90) and sometimes more long chains are observed than expected (e.g. webs 71, 85).

Table 3 lists, for all 113 webs, the number of random webs generated and the number of those random webs with chain length distributions closer to the expected than that of the real web. For the sum-of-squares measure of difference, d_1, all 74 real webs for which fewer than 100 random webs were generated fitted the cascade model's predictions well. In addition, webs 48 and 87, for each of which 100 random webs were generated, also fitted the cascade model's predictions well.

We conclude that, considering webs one at a time, the cascade model predicts the observed frequency distributions of chain length well, or moderately well, in 46 of the 51 webs in a new batch of webs not previously used to calibrate the model. This success rate is slightly higher than that of the cascade model with the original batch of 62 webs.

TABLE 3. CHARACTERISTICS OF 113 WEBS

(Serial numbers are the same as in table 2, in Briand (1983), and in all previous joint publications of Briand & Cohen. d_1 measures the difference between observed and predicted frequency distributions of chain length by the sum of squared differences; d_2, by a Pearson χ^2 function; see text. N is the number of random webs generated. X is the number of random webs with frequency distributions of chain length closer to that predicted theoretically than is the observed distribution. Variability: 0, unclassified; 1, fluctuating; 2, constant. Dimension: 0, unclassified; 2, two-dimensional; 3, three-dimensional. Productivity: 0, unclassified; 1, low productivity; 2, high productivity. Man: 0, absent from web; 1, present in web.)

web	d_1		d_2					
number	N	X	N	X	variability	dimension	productivity	man
1	20	6	20	10	0	0	0	1
2	40	33	40	33	1	0	0	0
3	100	94	100	92	1	2	0	0
4	20	5	20	11	1	0	0	0
5	100	92	60	51	0	0	2	0
6	100	94	100	93	1	0	0	1
7	60	50	20	14	0	0	0	1
8	20	6	20	13	1	0	2	1
9	100	92	100	93	0	0	0	0
10	100	100	100	100	1	2	0	0
11	40	33	60	49	1	2	0	0
12	20	12	20	12	1	2	0	0
13	20	8	20	12	1	2	0	0
14	20	13	20	11	0	0	0	0
15	20	14	20	10	1	0	0	0
16	40	30	20	14	1	0	2	0
17	20	14	20	14	0	3	0	0
18	20	7	40	30	0	0	0	1
19	40	31	40	32	1	3	1	0
20	20	13	20	15	0	3	1	0
21	100	99	100	100	0	3	0	0
22	20	11	20	14	1	0	0	0
23	20	14	40	32	1	2	0	0
24	20	14	40	31	1	3	0	0
25	40	29	20	15	1	3	0	0
26	20	0	20	0	1	0	0	0
27	60	51	100	94	1	3	2	0
28	40	30	40	33	1	0	0	0
29	40	31	60	51	0	3	1	0
30	100	96	100	99	0	3	1	1
31	20	12	40	28	0	3	0	0
32	20	13	20	13	2	3	0	0
33	60	52	40	32	2	0	0	0
34	100	92	40	33	2	2	0	0
35	100	92	100	97	0	2	0	0
36	20	13	80	69	0	0	0	0
37	100	98	100	96	2	0	0	0
38	100	94	100	96	2	0	0	0
39	100	94	100	96	2	0	0	0
40	60	51	40	33	2	3	0	0
41	100	100	100	100	2	3	1	0
42	100	100	100	100	2	3	2	0
43	100	94	80	67	2	3	0	0
44	40	27	20	13	2	0	2	0
45	60	49	20	15	2	2	0	0
46	20	6	20	9	0	3	1	0
47	100	96	100	92	2	0	0	0
48	100	88	60	52	1	0	0	1
49	20	8	20	13	1	0	0	1
50	20	13	20	15	1	2	0	0
51	20	14	20	13	0	0	0	0
52	100	92	100	91	1	2	0	0
53	100	99	100	96	1	2	0	0

TABLE 3 (*cont.*)

web number	d_1		d_2		variability	dimension	productivity	man
	N	X	N	X				
54	20	8	20	6	0	0	0	0
55	20	13	40	30	1	2	2	0
56	60	50	40	31	1	2	0	0
57	60	52	20	15	0	0	2	0
58	100	96	100	100	1	0	0	0
59	100	98	100	95	1	3	0	0
60	100	97	100	99	1	3	0	0
61	20	0	20	1	1	2	1	0
62	100	93	100	84	1	2	1	0
63	100	91	100	93	0	2	0	0
64	60	52	60	52	0	2	0	0
65	100	97	100	93	0	2	0	0
66	20	7	20	6	0	2	0	0
67	40	25	20	11	0	0	0	0
68	100	91	100	91	1	3	0	1
69	20	14	20	8	1	0	0	0
70	100	92	100	92	1	0	0	0
71	100	99	100	99	1	3	0	1
72	100	90	100	95	1	3	0	0
73	20	13	20	15	1	3	0	0
74	20	9	20	9	1	2	0	0
75	20	7	20	6	1	3	0	0
76	20	11	20	10	1	0	1	0
77	100	90	100	89	2	0	0	1
78	20	3	20	8	2	0	2	1
79	40	33	60	48	1	0	0	0
80	20	15	20	12	1	0	0	0
81	20	11	20	9	0	0	1	0
82	20	15	60	51	1	0	0	0
83	60	50	60	51	1	0	1	0
84	20	14	60	50	1	0	0	0
85	100	95	100	97	1	0	2	0
86	100	93	100	94	1	3	0	1
87	100	87	100	93	0	0	1	0
88	100	96	100	98	0	2	0	0
89	60	51	40	30	0	3	0	0
90	100	97	100	97	1	2	0	0
91	20	13	40	28	1	3	0	0
92	20	12	20	7	0	2	1	0
93	100	93	100	96	1	2	1	0
94	20	15	60	51	1	2	1	0
95	20	7	20	7	1	2	1	0
96	100	94	100	93	1	2	1	0
97	100	96	100	93	1	2	1	0
98	60	51	20	14	0	2	1	0
99	60	52	100	93	0	2	1	0
100	20	8	20	12	0	2	1	0
101	20	7	20	9	1	0	0	0
102	20	12	20	12	2	3	1	0
103	20	12	40	33	2	3	1	0
104	20	15	20	12	0	2	0	0
105	20	12	20	7	1	2	0	0
106	100	89	100	93	1	2	0	0
107	20	15	20	10	1	2	0	0
108	60	49	60	52	1	2	0	0
109	20	15	40	32	1	2	0	0
110	20	11	20	11	1	2	0	0
111	20	14	40	32	1	2	0	0
112	20	13	20	12	1	0	0	0
113	40	32	20	11	1	0	0	0

7. DOES THE CASCADE MODEL PREDICT THE MOMENTS OF CHAIN LENGTH?

After examining table 2 in a previous draft of this paper, S. L. Pimm (personal communication, 3 September 1985) suggested that the cascade model does not predict adequately the variance and kurtosis of the distribution of chain lengths. He allowed that the cascade model may predict roughly the mean chain length, according to table 2.

Direct comparisons of the mean and variance of the observed chain lengths with the corresponding quantities calculated from the expected numbers of chains of each length shown in table 2 confirm Pimm's observations regarding the first two moments. However, we claim that to evaluate the cascade model's ability to predict the moments of chain length the expected numbers in table 2 may not be the right numbers to compare with the observed. We will explain what calculations are required, although they remain to be done.

In computing numerically the mean and variance from the observed and expected numbers of chains of each length, separately for each web in table 2, we truncate (i.e. ignore) all predicted frequencies for chains of length 9 or greater. This truncation lowers the predicted mean and variance of chain length. The effect is small for all webs other than the exceptional web 103 because, for the remaining 112 webs, the expected number of chains of each length greater than or equal to 9 is less than 0.05. (We do not cumulate all predicted frequencies of chains longer than the largest observed, as we did in testing goodness of fit between observed and predicted frequencies.)

Temporarily, we shall call the mean calculated from the theoretically expected numbers of chains of each length the 'predicted mean', and the variance calculated from the theoretically expected numbers of chains of each length the 'predicted variance'. The terminology is misleading, for reasons we shall explain.

The scatter plot (figure 6) of 'predicted means' against the observed means clusters around a line of slope one through the origin. The observed mean chain lengths exceed the 'predicted means' in 50 of 113 webs. The 'predicted means' of the cascade model do reasonably well in predicting the observed mean chain length, as Pimm conceded.

In contrast to the acceptable performance of the 'predicted mean', the observed variance of chain length exceeds the 'predicted variance' in only two of 113 webs. Most points in the scatter plot (figure 7) of 'predicted variance' against observed variance lie well above a line of slope one through the origin. This finding confirms Pimm's suggestion that chain lengths observed for a single web generally have a smaller variance than the 'predicted variance'.

However, this finding does not imply that the cascade model predicts the variance of chain lengths badly. Also, unfortunately, the acceptable performance of the 'predicted mean' does not imply that the cascade model predicts the mean of chain lengths well. It is not possible to infer the mean or variance of chain length in one realization of the cascade model with a finite number of species from the expected numbers of chains of each length, averaged over all realizations, which are given in table 2.

The 'predicted mean' and 'predicted variance' are (except for the truncation

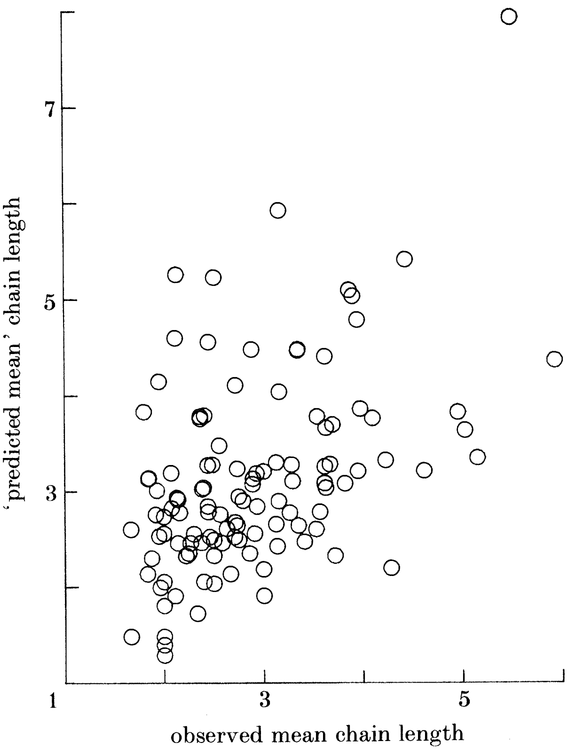

FIGURE 6. 'Predicted mean' chain length, i.e. mean calculated from the expected numbers of chains of each length according to the cascade model, as a function of the observed mean chain length in 113 webs. The points fall about a line of slope one through the origin. See text for an explanation of why the 'predicted mean' is not the mean chain length predicted by the cascade model.

of chains of length 9 or greater) the mean and variance of a distribution in which the relative frequency of chains of length n is

$$E(C_n)/E(C),$$

where, as before, C_n is the number of chains of length n and C is the total number of chains. As explained in § IV. 3, for finite S this distribution does not describe the chain length distribution of a single web randomly generated by the cascade model, but rather describes the distribution of the pooled chains from many webs generated by the cascade model with a fixed c and S.

The proper theoretical mean to compare with the observed mean chain length is (again ignoring truncation and conditional on $C > 0$)

$$E[\sum_k kC_k/C].$$

The proper theoretical variance to compare with the observed variance is (ignoring truncation and assuming $C > 0$)

$$E[\sum_k k^2C_k/(C-1)-(\sum_k kC_k)^2/[C(C-1)]].$$

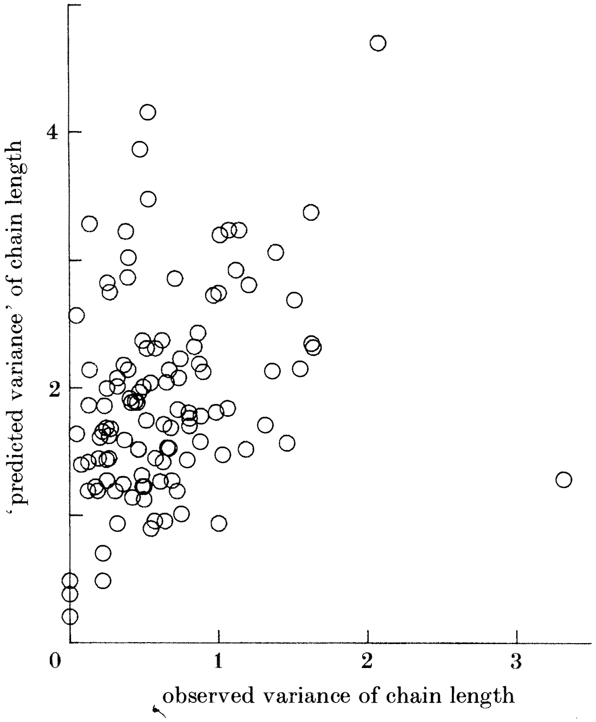

FIGURE 7. 'Predicted variance' of chain length, i.e. variance calculated from the expected numbers of chains of each length, as a function of the observed variance of chain length in 113 webs. All but two of the points fall above a line of slope one through the origin. See text for an explanation of why the 'predicted variance' is not the variance of chain lengths predicted by the cascade model.

In addition to the difference between $E(C_n/C)$ and $E(C_n)/E(C)$, there are correlations between C_m and C_n, $m \neq n$, illustrated by table 1, which influence the theoretical variance of chain length but not the 'predicted variance'. This additional discrepancy may explain why the 'predicted variance' (figure 7) does worse in describing the variance of observed chain lengths than the 'predicted mean' (figure 6) does in describing the mean of observed chain lengths.

It follows from the results of section IV. 4 that the corresponding theoretical and 'predicted' moments have the same limit for large S. However, for any finite S, the corresponding theoretical and the 'predicted' moments need not agree. We are not able analytically to compute the theoretical mean or variance, or higher moments, of chain length according to the cascade model for finite S. It may be impossible to do so. Simulation, observed web by observed web, would make it possible to compare the observed mean and variance of chain lengths with the mean and variance in each of, say, 100 simulations. We have yet to carry out this computation.

Because of the success of the cascade model according to the measures of goodness of fit that we have used so far, we expect that the observed moments should not fall far in the tail of the distributions of the simulated moments. The theoretical moments could not be systematically and grossly different from the observed if the simulated distributions of chain lengths are usually near the observed distributions of chain lengths. However, we have not conclusively demonstrated that the moments of chain lengths according to the cascade model correspond well to the moments of observed chain lengths in real webs.

8. TRYING TO EXPLAIN THE CASCADE MODEL'S FAILURES

In this section, we seek characteristics of webs that explain why the cascade model's predictions sometimes fit badly the observed frequency distributions of chain length. We find that bad fits occur far more often than expected among webs in which the mean length of chains is either unusually large (more than four links) or unusually small (less than two links). Twenty-one other characteristics do not appear to be associated with bad fits.

First, we explain why we do not use the conventional statistical tools of hypothesis testing; we then present our descriptive analyses.

Throughout, we have been sceptical of the assumption that our observed webs are a random sample from some statistical ensemble of webs. One reason for scepticism is that webs reported by the same author sometimes share idiosyncrasies that differentiate them from webs reported by others. Sixty-one of our 113 webs were described by distinct observers or teams (two sets of observers are considered distinct here if they have no member in common). The remaining 52 webs were reported by 20 distinct observers or teams, each contributing between two and five webs; there is therefore likely to be dependence among the webs.

A second reason for scepticism is that field ecologists with special training in some taxon (birds or insects or fishes) or in some habitat (lacustrine or marine intertidal or tropical montane) pick communities in which their special training can be used, rather than at random. Until it is shown that the properties of webs are invariant with respect to major taxa, habitats and other characteristics that may bias ecologists' choices of webs to study, it seems implausible a priori to regard any given batch of webs as a random sample of webs from the world.

If the webs *were* a random sample from a cascade model ensemble, then the frequency histograms in figures 2 and 5 should approximate histograms sampled from the uniform distribution, which is a horizontal straight line. Under the assumption of random sampling of webs, it would be valid to use the Kolmogorov–Smirnov test (Kendall & Stuart 1973, p. 469) to assign a probability value to the deviation between the sample and uniform cumulative distribution functions. Denoting the test statistic by D (not to be confused with our notation above for the observed total number of chains), with a subscript that gives the sample size, we compute for the first batch of webs $D_{62} = 0.4403$, for the second batch $D_{51} = 0.4127$ and for all webs combined $D_{113} = 0.4142$. These values are all far beyond the 0.01 critical values for the corresponding sample sizes. Because we regard the assumption of random sampling with scepticism, we also regard with scepticism the 'significance' of this rejection of the fit of predicted to observed chain length distributions in the collection of webs as a whole.

Nevertheless, 16 or 17 of 113 webs (11 or 12 in the first batch, 5 in the second) individually have chain lengths that the cascade model describes badly. We now seek a simple explanation for these bad fits in terms of the characteristics of webs.

S. L. Pimm (personal communication, 3 September 1985) suggested that the cascade model describes worse the chain length distributions of webs with large numbers of species. To examine this suggestion, we identified the 45 webs with more than 17 species as 'above average' in size. (The average number of species per web in 113 webs is 16.9.) We also identified the 19 webs with more than 24 species as 'large' in size.

As figure 6 shows, most webs have mean chain lengths of two to four links. We defined the 12 webs with mean chain length less than two links (webs numbered 28, 33, 39, 40, 53, 64, 65, 88, 90, 96, 101, and 112) and the 10 webs with mean chain length greater than four links (webs numbered 21, 30, 41, 42, 46, 47, 58, 71, 86, and 103) to be webs with 'extreme mean chain length'.

As figure 7 shows, most webs have a variance of chain length that is less than 1. We defined the 22 webs with variance greater than or equal to 1 to be webs with 'high variance of chain length'. We also defined the 17 webs with variance less than 0.25 to be webs with 'low variance of chain length'.

For all 113 webs, we determined four characteristics in addition to trophic structure: dimension, variability, and productivity of the environment, and the presence of man in the web (table 3).

A web is classified as having dimension 2 if it occurs in an environment that is essentially flat, such as grassland, a sea or lake bottom, a stream bed or the rocky intertidal zone. A web is classified as having dimension 3 if it occurs in a solid environment, such as the pelagic water column or forest canopy. Webs that could not clearly be assigned dimension 2 or 3 are shown in table 3 as having dimension 0.

As in paper II, the variability of a web's environment is classified as 'fluctuating' or 'constant'. The environment is 'fluctuating' if the original report indicates temporal variations of substantial magnitude in temperature, salinity, water availability or any other major physical parameter. The magnitude, and not the predictability, of the variations is the criterion of classification. In this paper we apply stricter criteria than previously for deciding whether an environment is fluctuating or constant. Whereas previously webs 1 to 28 and 48 to 62 were classified as from fluctuating environments, while webs 29 to 47 were considered to be from constant environments, we now regard a number of webs from each former category as unclassifed. These are shown by 0 in table 3.

In several instances, the original observers measured and reported the net primary productivity of the ecosystems they studied. For such cases, we classify the productivity of a web as *low* if it falls below 100 g C m^{-2} a^{-1}, and as *high* if it exceeds 1000 g C m^{-2} a^{-1}. When productivity is unknown or has an intermediate value, we treat it as unclassified (shown by 0).

Man is present in a web if explicitly recorded as one of the species, and is absent otherwise.

We then cross-classified the webs by 22 pairs of dichotomous criteria. One member of each pair was bad fit between predicted and observed frequency distributions of chain length ($X_N/N > 0.95$, with the sum-of-squares measure of difference, d_1) against not a bad fit. Another member of the pair was selected from this list of dichotomies: above-average number of species (more than 17 observed species) versus average or below number of species (17 or fewer observed species); large number of species (more than 24 observed species) against not large number of species (24 or fewer observed species); high value (greater than 3.6) of the parameter c against low value ($c \leqslant 3.6$); extreme mean chain length against not extreme; high variance of chain length against not high; low variance of chain length against not low; man absent against man present; dimension unclassified against dimension known; dimension 2 against dimension not 2; dimension 3 against dimension not 3; dimension 2 against dimension 3; environment not classified against environment fluctuating or constant; environment fluctuating against environment not fluctuating; environment constant against environment not constant; environment fluctuating against environment constant; productivity unclassified against productivity low or high; productivity low against productivity not low; productivity high against productivity not high; productivity low against productivity high; dimension 2 and fluctuating against dimension 3 and constant; no basal–top links against one or more basal–top links; one or fewer basal–top links against more than one basal–top link. (The last two dichotomies explore the possibility that the webs with anomalously few basal–top links, apparent in figures 2 and 3 of Cohen & Briand (1984), might also be those badly described here by the cascade model.) Some of these cross-classifications involve all 113 webs; others involve fewer (for example, only 34 webs are either dimension 2 and fluctuating or dimension 3 and constant).

For each cross-classification, we compute the χ^2 measure of association corrected for continuity (Snedecor & Cochran 1967, p. 217). If we could accept the doubtful assumption that the webs are a random sample, we could assign a level of statistical significance to the computed values of χ^2 with one degree of freedom. Under this assumption, the critical value for significance at the (very weak) 10% level is 2.71. Only three of the 22 values of χ^2 exceed this level: $\chi^2 = 4.55$ for the cross-classification with dimension not classified, $\chi^2 = 5.45$ for the cross-classification with low variance of chain length, and $\chi^2 = 25.33$ for the cross-classification with extreme mean chain length. The first two of these χ^2 values do not exceed the one percent significance level. The third is very large. Table 4 shows the counts of bad and not-bad fits cross-classified according to whether or not the mean chain length is extreme.

When we carry out the same 22 cross-classifications with bad fit based on d_2, which is the χ^2 measure of difference between observed and predicted chain length

TABLE 4. CROSS-CLASSIFICATION OF 113 WEBS ACCORDING TO FIT (BASED ON d_1) BETWEEN OBSERVED AND PREDICTED FREQUENCY DISTRIBUTIONS OF CHAIN LENGTH, AND EXTREME VALUES OF MEAN CHAIN LENGTH

(χ^2 with one degree of freedom (corrected for continuity) = 25.3265.)

	mean chain length	
goodness of fit	$\geqslant 2$ and $\leqslant 4$	< 2 and > 4
not bad	86	11
bad ($X_N/N > 0.95$)	5	11

distributions, only two of the 22 values of the association χ^2 exceed the 10% critical value: $\chi^2 = 4.60$ for the cross-classification with high c, and $\chi^2 = 16.92$ for cross-classification with extreme mean length of chains. The former value does not exceed the 2.5 % significance level. The latter value far exceeds the 1 % significance level.

We conclude that a single dichotomy, extreme mean lengths of chains, explains at least partly why the cascade model's predictions sometimes fit badly the observed frequency distributions of chain length. This finding does not exclude the possibility that a more elaborate stratification of webs by combinations of other characteristics could yield another, and perhaps better, explanation of the bad fits (Mantel 1982). However, we have not explored possible explanations based on more elaborate combinations of characteristics. Table 3 provides raw data for a more sophisticated analysis.

We now speculate briefly on how the deviations between the observed and predicted frequency distributions of chain lengths could arise. To explain the excess numbers of observed long chains relative to the numbers expected, suppose that, instead of describing all species and links in a community, as we assume, an observer initially samples a link at random and then follows a chain containing that link up to a top species and down to a basal species; and then samples another link at random from those not previously recorded and repeats the procedure. The longer a chain is, the more links it contains, and therefore the more likely it is to be sampled by this procedure. This sampling procedure would produce an observed excess of long chains compared to sampling in which each chain is sampled randomly.

To explain the excess numbers of observed short chains relative to the numbers expected, suppose that, as above, an observer picks a link at random and finds some of the other (if any) links in the same chain but, wary of the bias of sampling chains in proportion to their length, interrupts recording the entire chain after a small number of links. This hypothetical procedure would selectively sample long chains at first and would then selectively break the long chains into short chains, producing an observed excess of short chains compared to sampling in which each chain is sampled randomly.

A plausible model of the process of observation that would not explain an observed excess of either long or short chains is to suppose that an observer attempts to record all links, but has a probability ϵ (for 'error'), $0 < \epsilon < 1$, of failing to observe or record any given link, independently and identically for all links. The recorded web will then be identical to that of a cascade model in which the true probability $p = c/S$ of an edge is replaced by the recorded probability $p' = p(1-\epsilon)$. The mean length of chains will be reduced by these errors of omission, but conditional on the net probability, p', that a link occurs and is recorded, the distribution of the expected number of chains of each length will be as predicted by the cascade model with parameter p'.

The original reports of webs rarely describe the sampling procedures by which the links are determined. Different investigators may use different sampling procedures. It is not possible to prove, from the original reports, either of the above explanations for deviations from the predictions of the cascade model. Still, it is some comfort that simple explanations exist.

9. DISCUSSION AND CONCLUSION

Here we review the accomplishments of this paper, relate them to previous work, and indicate some useful further efforts.

9.1. *Accomplishments of this paper*

From an exact analysis of the cascade model, we derive the expected number of chains of each length in a web with any finite number, S, of species. Simulations of the cascade model demonstrate substantial dependence among the numbers of chains of different lengths. Because of the dependence, we develop a Monte Carlo method of evaluating the goodness of fit between the numbers of chains observed in an individual web and the numbers expected from the cascade model.

Without fitting any free parameters, and with the use of no direct information about chain lengths other than that implied by the total number of species and the total number of links in a web, the cascade model describes acceptably the observed numbers of chains of each length in all but 16 or 17 of 113 real webs. The cascade model describes well, in the technical sense defined in §5, the chain lengths of 40 or 43 of the 62 webs previously used to test the cascade model, and well or moderately well, again in the technical sense, the chain lengths of all but 11 or 12 of these webs. In a fresh batch of 51 webs, the numbers of links are very nearly proportional to the numbers of species (apart from two outlying webs). The constant of proportionality is consistent with that in the original 62 webs. This finding independently verifies the species–link scaling law (Cohen & Briand 1984; paper I). The cascade model describes well the chain lengths of 34 or 36 of the 51 webs, and well or moderately well all but 5 of these webs. When the collection of webs is viewed as a whole, the cascade model describes adequately the mean chain lengths.

The poor fit of the cascadsde model to 16 or 17 webs is associated with one characteristic of the webs, namely, an unusually large (more than four links) or an unusually small (fewer than two links) mean length of chains.

In papers I and II, we evaluated the cascade model's fit to the data on the proportions of each kind of species and link largely by visual inspection of graphical displays. Even measured by that very crude procedure, the fit between predictions and observations was not always good, e.g. for the proportions of basal–top links. Here, in paper III, we examine a much finer aspect of web structure than in papers I and II, namely, the frequency distribution of chain lengths, and we use far more delicate measures of goodness of fit. *A priori*, the apparent performance of the cascade model should be worse than in papers I and II. We consider it significant that the approximation between observed and predicted frequency distributions of chain length, though far from perfect, is as good as it is.

9.2. *Relation to previous work*

This paper offers three novelties in ecological theory. First, this paper presents, to our knowledge, the first exactly derived theory of the length of food chains. The only previous quantitative model to predict chain length (Pimm 1982) has been simulated but not analysed mathematically. Secondly, this paper represents, we believe, the first instance in which an ecological model that was initially developed to explain an aspect of webs different from chain length (namely the proportions of species and links of various kinds) is used to predict chain lengths quantitatively. Thirdly, this paper gives the first quantitative predictions (obtained either by simulation or by analysis) of the entire frequency distribution of chain length. Pimm (1982, ch. 6) considers only the modal trophic level of top species.

Although the cascade model is the first to be analysed exactly in the detail given here, it is one of a family of similar models that have been proposed for webs. Cohen's (1978, p. 60) model 5 proposes that webs be generated by constructing a matrix with a number of rows equal to the observed number of prey (basal plus intermediate species), a number of columns equal to the observed number of predators (intermediate plus top species), and a number of 1-elements equal to the observed number of links, all other elements of the matrix being 0. According to this model 5, the positive elements of the 'predation matrix' (a condensed adjacency matrix) are to be distributed randomly.

From comparisons of real food webs with simulations of model 5 and other similar models, Cohen (1978, p. 92) 'concluded that the high observed frequency of arrangements of niche overlap that can be represented in a one-dimensional niche space does not result from the operation, within the framework of several plausible models, of chance alone', i.e. that the species' feeding relations have a one-dimensional ordering.

The null model of Pimm (1982, appendix 6A) adds to Cohen's model 5 the constraints that each prey have a predator and each predator a prey, and that the intermediate species be in a strict hierarchy or cascade. Such a hierarchy or cascade is a natural interpretation of Cohen's finding that feeding relations have a one-dimensional ordering. Sugihara (1982, 1984, §3.1.2) also discusses the importance of a hierarchical ordering in assembly rules for food webs, but does not analyse the lengths of food chains.

When we proposed the cascade model (paper I), we had not read appendix 6A of Pimm (1982) because we were considering questions other than the length of chains. Whereas Pimm's null model takes as given the numbers of links and of basal, intermediate and top species, the cascade model takes as given the total number of species and the number of links. The cascade model *predicts* the fractions of species that are basal, intermediate and top and the numbers of links of each of four kinds. Pimm's null model could be viewed as a conditional version of the cascade model: given numbers of links and of basal, intermediate and top species produced by the chance mechanisms of the cascade model, the distribution of these links among pairs of species in the cascade model is identical to that in Pimm's null model (ignoring the negligible probabilities in the cascade model that top species are not proper top and basal species are not proper basal).

Cohen (1978) and Pimm (1982) propose the models just described as 'null' models, models that would describe how webs should look in the absence of interesting biological structure. Here we consider the cascade model as a 'theory'. We suggest that between 'null models' and 'theories' is a continuum of increasingly sophisticated and successful models. The null models at one extreme are models that do *not* describe much of nature well. 'Theories', at the other extreme, provide a unifying and quantitatively successful view of diverse phenomena. The cascade model provides explanations for some aspects of webs that Cohen's (1978) and Pimm's (1982) models take as given and describes with moderate success the observed frequency distributions of chain lengths. Whether the cascade model should continue to be dignified as theory depends on its success in describing other aspects of real webs.

9.3. *Further work required*

How well does the cascade model describe the variance and higher moments of the distribution of chain length? A key difficulty in answering this question, which was raised by S. L. Pimm, is the dependence among the numbers of chains of different lengths. Attacks via mathematical analysis and via numerical simulation are both desirable.

Why does the cascade model fail to predict 16 or 17 observed frequency distributions of chain length? One possibility is that, like a straight line tangent to a parabola, the predictions of the cascade model are systematically of the wrong shape but are locally good approximations in a certain neighbourhood. According to this possibility, a better model could explain all the observed frequency distributions of chain length, as well as explain better the other features of webs that are described approximately by the cascade model. As noted in paper II, some assumptions underlying the cascade model are unrealistic. For example, the model assumes that the species at the top of the cascade is equally likely to prey on all other species in the community, and that the prey species a predator eats are chosen statistically, once and for all, independently of the abundance of the prey species and of the existence of other links. A better model might replace these assumptions by more realistic ones. However, we cannot provide and analyse a better model at this point.

A second possibility is that the bad fits of the cascade model are associated with some combination of the characteristics of webs. According to this possibility, the cascade model is acceptable for a large class of webs, e.g. those with mean chain length between two and four links, but for another relatively small class of webs a different model is required.

A third possibility is that the original data are wrong; that links have been overlooked, or that inconsistent criteria have been used for reporting links, or that stomach contents have been misidentified and mistaken links have been reported, or that error has crept into the process of writing, publishing and transcription.

The consequences for action of these three possible explanations are different. If the cascade model is only an approximation to a better global model, then one should try to construct a better global model. If combinations of characteristics could identify exactly webs for which the cascade model fails, one should try to discriminate the webs where the cascade model succeeds from those where it fails. If the reported frequency distributions of chain length are materially wrong, one should go back into the field and do better field work and reporting. There is no shortage of opportunities for diverse skills.

The empirical successes of the cascade model are great enough to encourage the hope that efforts in all three directions may yield further successes. The present successes of the cascade model also justify attempts to exploit the model further as it stands. Can the cascade model describe or explain yet other aspects of webs, such as the frequency of omnivory, i.e. predation on different trophic levels (S. L. Pimm, personal communication, 3 September 1985), however 'trophic levels' are to be defined? Can the cascade model account for the relative importance of predation against competition (Schoener 1982), the occurrence of compartments (Pimm 1982), and the frequency of intervality (Cohen 1978)?

APPENDIX: COMPUTING ALGORITHMS

This appendix describes procedures for computing the frequency distribution of chain length and the length of the longest chain of a given acyclic web.

The frequency distribution of chain length

A digraph (directed graph) with S vertices (species) and L edges (links) may be represented by its $S \times S$ adjacency matrix, A. The elements of A are $a_{ij} = 1$ if (i, j) is an edge, $a_{ij} = 0$ if (i, j) is not an edge, $1 \leqslant i, j \leqslant S$.

An easily programmed, but inefficient, way to compute the number of n-chains, C_n, from the adjacency matrix A of an acyclic web uses the powers A^n of A. If S_B and S_T are the subsets of $\{1, 2, \ldots, S\}$ that contain the labels of, respectively, the basal and the top species, then

$$C_n = \sum_{i \in S_B} \sum_{j \in S_T} (A^n)_{ij}, \quad n = 1, 2, \ldots, S-1.$$

If each power is computed by $O(S^2)$ multiplications, then the computation of the frequency distribution of chain length $\{C_n\}$ requires $O(S^3)$ multiplications.

A much more efficient algorithm that requires $O(S^2)$ steps (additions or multiplications) was outlined in conversation (1984) by P. H. Sellers. Assume that the adjacency matrix A is strictly upper triangular, so that the vertices are numbered from 1 at the bottom of the web to S at the top of the web, i.e. edges point from vertices with lower numbers to vertices with higher numbers. The following algorithm requires as input the adjacency matrix A and returns as output an $(S-1)$-vector, C, with nth element C_n, the number of n-chains.

Step 1. Set $I = 1$ and set V to be an $S \times S-1$ matrix with all elements 0. (After completion of the loop on I below, $V(I, J)$ will hold the number of maximal J-walks that terminate at vertex I, i.e. the number of J-walks that originate at some basal species and terminate at species I.)

Step 2. Increment I by 1. If the result exceeds S, go to step 8.

Step 3. Set $H = 0$.

Step 4. Increment H by 1. If the result equals I, go to step 2. (We are going to compute for each J the contribution, to the number of maximal J-walks terminating at vertex I, of maximal $(J-1)$-walks terminating at vertex H, for every $H < I$.)

Step 5. If $A(H, I) = 0$, go to step 4. (If there is no edge from H to I, then walks terminating at H either do not pass through I at all or must pass through some other vertex on their way to I.)

Step 6. If the sum of the Hth row of V is positive, then for $J = 2, \ldots, S-1$, set $V(I, J) = V(I, J) + V(H, J-1)$. Then go to step 4. (Each maximal $(J-1)$-walk that terminates at a vertex H that is connected by an edge to vertex I determines a maximal J-walk that terminates at vertex I.)

Step 7. Otherwise, increment $V(I, 1)$ by 1. Then go to step 4. (If no walks terminate at vertex H but H is joined to I by an edge, then there is a maximal 1-walk terminating at I.)

Step 8. For $J = 1, \ldots, S-1$, set C_J equal to the sum of $V(I, J)$ over only those I such that the Ith row sum of A is 0. (The chains are the maximal walks that terminate at top vertices. Vertex I is a top vertex if and only if the Ith row sum of A is 0. After all the maximal walks terminating at all the vertices have been counted, the number of J-chains is the total number of maximal J-walks that terminate at top vertices.)

We programmed both the algorithm based on powers and Sellers' algorithm in APL, with the APL68000 interpreter running on the WICAT 150–6, a microprocessor that uses the Motorola 68000 chip. For the 14×14 adjacency matrix of Briand's (1983) web number 31, the algorithm based on powers required approximately 10 s to produce the frequency distribution of chain length, whereas Sellers' algorithm required approximately 5 s. For a 50×50 adjacency matrix generated according to the cascade model with $c = 3.71$, the powers algorithm required approximately 25.5 min and Sellers' algorithm required approximately 0.6 min.

The length of the longest chain

For a digraph with a strictly upper triangular adjacency matrix A, finding the *height*, i.e. the length M of the longest chain, is a standard problem in network theory. For example, Gibbons (1985, pp. 121–122) gives a recursive algorithm for finding the longest path from a specified vertex to every other vertex. The following algorithm for finding the longest path from any vertex to any other, which requires in general $O(S^2)$ multiplications, was outlined in conversation (1985) by F. R. K. Chung. The algorithm requires as input the adjacency matrix A and returns as output the height M.

Step 1. Set V equal to an S-vector with all elements 0, and set $I = 0$. (After completion of the loop on I below, $V(I)$ will hold the length of the longest walk terminating at vertex I.)

Step 2. Increment I by 1. If the result exceeds S, go to step 4.

Step 3. Set $V(I) = \max\{A(H, I)(V(H)+1) | 1 \leqslant H \leqslant I-1\}$.Then go to step 2. (The length of the longest walk terminating at vertex I is 1 greater than the maximum over all $H < I$ with an edge from H to I of the length of the longest walk terminating at H.)

Step 4. Set $M = \max\{V(I) | 1 \leqslant I \leqslant S\}$. (The longest chain is as long as the longest of the maximal walks.)

For a 50×50 adjacency matrix, generated according to the cascade model with $c = 3.71$, independently of the matrix used in the previous example, the computation of $M = \max\{n | C_n > 0\}$ based on Sellers' algorithm for C required 38 s and Chung's algorithm required only 6 s.

As S gets large, the number of positive elements in adjacency matrices generated by the cascade model increases only as $O(S)$ rather than as $O(S^2)$. The number of multiplications and the amount of memory required by the preceding algorithm may be reduced from $O(S^2)$ to $O(S)$ as S gets large by representing the digraph by an $L \times 2$ matrix that lists, in some order, the initial and final vertex of each of its L edges. Step 3 above is then modified to pay attention only to those vertices $H < I$ for which there is an edge from H to I. By using this modified algorithm, we simulated webs of S species where S^2 far exceeded the words of memory available in our microprocessor.

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