

A stochastic theory of community food webs IV. Theory of food chain lengths in large webs

BY C. M. NEWMAN¹ AND J. E. COHEN²

¹ *Department of Mathematics, University of Arizona, Tucson, AZ 85721, U.S.A.*

² *Rockefeller University, 1230 York Avenue, New York, NY 10021-6399, U.S.A.*

(Communicated by J. H. Steele, F.R.S. – Received 21 August 1985 – Revised 14 March 1986)

This paper develops a theory of the length of food chains in community food webs. The theory derives from a mathematical model of webs called the cascade model. Our analysis concerns the behaviour of chain lengths for webs in which the number, S , of species is large.

From an exact formula for the expected number of chains of each length, we derive a theoretical mean and variance of the length of chains in webs with a given S . For webs in which S becomes large, we compute the asymptotic distribution of the length of a randomly chosen chain, giving explicit closed-form formulas for the asymptotic mean and variance. The cascade model implies a simple rule of thumb for large webs: the mean length of chains approximately equals the mean number of predators plus prey of any species in the web. Such a quantitative relation between mean chain length and the number of links per species appears to be new.

The *height* of a web is defined as the length (number of links) in its longest chain. We show that, according to the cascade model, the median height increases very slowly with the number of species in a web. Indeed, the median height is below 17 for S up to one million. This analysis provides the first quantitative explanation, we believe, of why the longest chains are very short relative to the number of species in a web, even when the number of species is very large.

As a theoretical curiosity, we show, for webs in which S becomes unrealistically large, that the height equals one of two adjacent integers with a probability that slowly approaches 1. With increasing S , these two integers approximate $\ln S / \ln(\ln S)$, and thus grow extremely slowly.

1. INTRODUCTION

The purpose of this paper is to develop a theory of the length of food chains that is derived from a mathematical model of community food webs called the cascade model. Cohen & Newman (1985, hereafter referred to as paper I) and Cohen *et al.* (1985, hereafter referred to as paper II) showed that 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. Cohen *et al.* (1986, hereafter referred to as paper III) showed that the cascade model describes the frequency distribution of the length of food chains observed in a large majority of 113 real webs. In the light of this empirical support for the cascade model, it is desirable to analyse the properties of the model further. This paper determines what the cascade model implies for the frequency distributions of the length of a typical food chain and of the length of the longest chain, primarily in the limit as the number of species in the web becomes arbitrarily large.

Section 2 presents terminology for chains and reviews the cascade model. Section 3 derives a generating function for the expected number of chains of each length and moments of the chain length distribution for webs with a finite number of species. Section 4 describes the frequency distribution of chain lengths in the limit as the number of species in a web gets large. Section 5 describes the length of the longest chain in a web with a finite number of species. Section 6 describes the length of the longest chain as the number of species in a web gets (very) large. Section 7 analyses the sensitivity of the asymptotic behaviour of the longest chain derived in §6 to the assumptions of the cascade model. The results in §§3–7 are obtained by mathematical analysis. Numerical simulations of the cascade model in §8 confirm and amplify the prior analytical results concerning the length of the longest chain. Section 9 reviews what has been achieved in this paper, and the concluding §10 identifies some tasks that remain.

We shall accept the mathematical convention of setting off every proof with *Proof* at the beginning and ■ at the end. Readers may defer or skip proofs with no loss of continuity.

2. TERMINOLOGY; THE CASCADE MODEL

This section reviews and introduces terminology, then describes the cascade model (as in sections I. 2 (i.e. section 2 of paper I), II. 1 and III. 3).

A *food web* is a set of kinds of organism and a relation that shows which, if any, kinds of organism 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 (always 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. An n -chain is a chain of length n , i.e. a chain with n links or

equivalently $n + 1$ species. The *height* of a web is the length of the longest chain in it.

Let S be the number of species in a web, and let C_n be the number of n -chains in an acyclic web, $n = 1, 2, \dots, S - 1$. The *frequency distribution of chain length* is the vector $(C_1, \dots, C_{S-1}) \equiv C$. The total number of chains in the web will be denoted

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

As usual, $E(\cdot)$ and $\text{var}(\cdot)$ denote the expectation (or mean) and variance, respectively, of the random variable enclosed in parentheses. For any function f of any real or integer variable t , we write $f(t) = O(t)$ if $f(t)/t$ stays less than some fixed finite positive constant as $t \rightarrow \infty$, and $f(t) = o(t)$ if $\lim_{t \rightarrow \infty} f(t)/t = 0$.

The *cascade model* assumes that the $S \geq 2$ 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). The probability that species j feeds on species i is 0 if $j \leq i$. 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 $1 \leq i < j \leq S$. Unless a contrary assumption is explicitly given, it will be assumed that, for some finite positive real number $c < S$, $p = c/S$, where c is a constant independent of S . (Some results below require only the weaker assumption that $Sp(S) \rightarrow \gamma$, for some constant γ , as $S \rightarrow \infty$.)

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 (paper III):

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

3. MOMENTS OF THE FREQUENCY DISTRIBUTION OF CHAIN LENGTH IN FINITE WEBS

To find an average chain length predicted by the cascade model, we need to compute $\sum_n n f_n$, where f_n is the probability density of n -chains according to the cascade model. There are two, not one, natural candidates for f_n . The first corresponds to 'expected relative frequency', and the second corresponds to 'relative expected frequency'. To compute the first, which we denote u_n , find, for each random web, the fraction of all chains that are n -chains, and then average over all webs. The expected relative frequency of chain length n is

$$u_n = E(C_n/C), \quad n = 1, \dots, S-1.$$

To make this well defined, C_n/C may be set to zero whenever $C = 0$. For typical S and p , the probability that $C = 0$ is very small. To compute the second candidate for f_n , find the expected number of n -chains, averaged over all webs, and then express that average as a proportion of the sum of the averages of all lengths. The relative expected frequency of chain length n is

$$v_n = E(C_n)/E(C), \quad n = 1, \dots, S-1.$$

Both u_n and v_n depend on S . A random variable, H_S , with probability density $\{u_n\}$ can be obtained by taking a random web and measuring the length of a single chain chosen at random, with all of the web's chains equally likely. A random variable L_S with probability density $\{v_n\}$ can be obtained by taking (in the limit) a very large collection of webs and picking a single chain randomly from the pooled chains of all the webs, each chain again being equally likely.

We shall compute $E(L_S) = \sum_n n v_n$ and higher moments of L_S by means of a generating function, defined as

$$f_S(t) = \sum_{n=1}^{S-1} E(C_n/S) t^n, \quad 0 < t < \infty.$$

According to the cascade model,

$$f_S(t) = tSpq^{S-2}\{[1 + (p/q)(1+t)]^S - 1 - (Sp/q)(1+t)\}/\{(Sp/q)(1+t)\}^2.$$

Proof. Using first the formula for $E(C_n)$ and then the identity

$$\sum_{n=1}^{S-1} \sum_{k=n}^{S-1} = \sum_{k=1}^{S-1} \sum_{n=1}^k,$$

we compute

$$\begin{aligned} f_S(t) &= S^{-1} \sum_{n=1}^{S-1} (pt)^n q^{S-1} \sum_{k=n}^{S-1} (S-k) \binom{k-1}{n-1} q^{-k} \\ &= S^{-1} \sum_{k=1}^{S-1} \sum_{n=1}^k \binom{k-1}{n-1} (pt)^n q^{S-1} q^{-k} (S-k) \\ &= ptq^{S-2} \sum_{k=1}^{S-1} q^{-(k-1)} [(S-k)/S] \sum_{h=0}^{k-1} \binom{k-1}{h} (pt)^h \\ &= ptq^{S-2} \sum_{k=1}^{S-1} (1-k/S) q^{-(k-1)} (1+pt)^{k-1} \end{aligned}$$

and letting

$$r \equiv (1+pt)/q,$$

$$\begin{aligned} f_S(t) &= ptq^{S-2} \left(\sum_{k=1}^{S-1} r^{k-1} - S^{-1} \sum_{k=1}^{S-1} kr^{k-1} \right) \\ &= ptq^{S-2} [(1-r^{S-1})/(1-r) - S^{-1}(d/dr)\{(1-r^S)/(1-r)\}] \end{aligned}$$

which, upon further elementary calculation, becomes

$$= ptq^{S-2} S^{-1} [r^S - 1 - S(r-1)]/(r-1)^2,$$

which eventually simplifies, with $r = (1+pt)/q$, to the formula given. ■

It follows from the generating function $f_S(t)$ that, setting $z = 2Sp/q$,

$$E(L_S) = (z/2) [(1+z/S)^{S-1} - 1]/[(1+z/S)^S - 1 - z],$$

or

$$E(L_S) = Sp[(1+p)^{S-1} - (1-p)^{S-1}]/[(1+p)^S - (1-p)^S - 2Sp(1-p)^{S-1}]$$

and

$$\text{var}(L_S) = \frac{\frac{1}{4}\{[(S-1)/S]z^2(1+z/S)^{S-2} - 4z(1+z/S)^{S-1} + 6(1+z/S)^S - 6 - 2z\}}{(1+z/S)^S - 1 - z} - [E(L_S)]^2 + 3E(L_S) - 2.$$

Proof. $E(L_S) = f'_S(1)/f_S(1)$. The two versions of $E(L_S)$ are equivalent because $1+z/S = (1+p)/(1-p)$. The formula for $\text{var}(L_S)$ follows from a very long, but elementary, simplification of the result of substituting

$$E(t^{L_S}) = f_S(t)/f_S(1)$$

into

$$\text{var}(L_S) = \{(d/dt)^2 E(t^{L_S}) + (d/dt) E(t^{L_S}) - [(d/dt) E(t^{L_S})]^2\}_{t=1}. \quad \blacksquare$$

Figure 1 plots the mean of L_S and the mean plus or minus one standard deviation (corresponding roughly to a two-thirds confidence interval) for values of $p = c/S$ and S typical of the observed webs analysed in papers I and II. With increasing S and fixed c , the mean and confidence interval stabilize for webs with more than 30 species, but change noticeably for smaller webs.

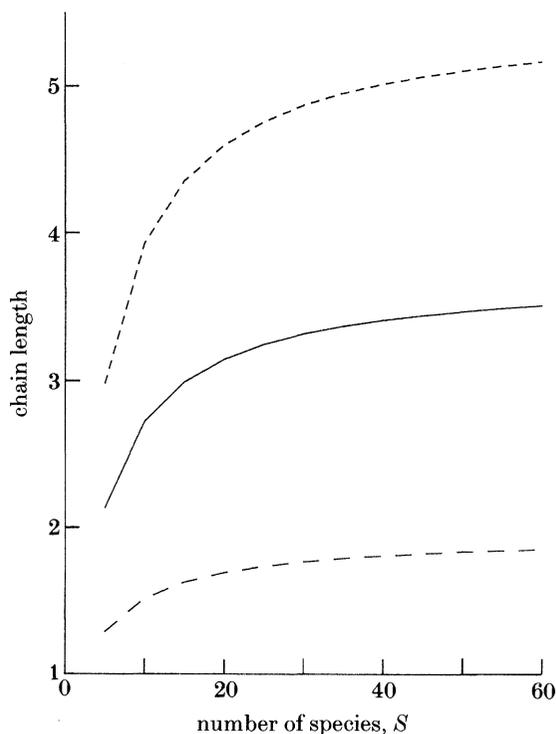


FIGURE 1. Mean (—), and mean plus (-----) or minus (---) one standard deviation, of chain length, L_S , as a function of the number of species, S , according to the cascade model with $c = 3.71$.

4. LIMITING FREQUENCY DISTRIBUTION OF CHAIN LENGTH IN LARGE WEBS

We now describe the behaviour of C_n/S , predicted according to the cascade model, as S gets large, assuming that, for large S , $p(S)$ declines like γ/S or more precisely that $\lim_{S \rightarrow \infty} Sp(S) = \gamma$. When $p(S) = c/S$, then $\gamma = c$.

Define the generating function (which does not depend on S) for $0 < \gamma < \infty$:

$$g(t) = t\gamma e^{-\gamma} \{e^{\gamma(1+t)} - 1 - \gamma(1+t)\} / \{\gamma(1+t)\}^2.$$

The coefficients K_{n-1} , $n = 1, 2, \dots$ of the (convergent) power series expansion

$$g(t) = K_0 t + K_1 t^2 + \dots$$

have the meaning

$$\lim_{S \rightarrow \infty} E(C_n)/S = K_{n-1}, \quad n = 1, 2, \dots,$$

provided $0 < \gamma < \infty$. K_{n-1} may be computed explicitly from

$$K_{n-1} = (d/dt)^n g(t)|_{t=0}/n!$$

or from

$$K_{n-1} = [\gamma^n e^{-\gamma}/(n-1)!] (d/d\gamma)^{n-1} [(e^\gamma - 1 - \gamma)\gamma^{-2}].$$

The limit of the mean total number, $E(C)$, of chains satisfies

$$\lim_{S \rightarrow \infty} E(C)/S = g(1) = \sum_{n=1}^{\infty} K_{n-1}.$$

Hence

$$\begin{aligned} \lim_{S \rightarrow \infty} v_n &\equiv \lim_{S \rightarrow \infty} E(C_n)/E(C) \\ &= K_{n-1} / \sum_{h=1}^{\infty} K_{h-1} \\ &= \{\gamma^{n-1} (d/d\gamma)^{n-1} [(e^\gamma - 1 - \gamma)\gamma^{-2}]\} / [(n-1)! (e^{2\gamma} - 1 - 2\gamma)(2\gamma)^{-2}]. \end{aligned}$$

The moments and factorial moments of the length of chains, according to the random variable L_S with probability density $\{v_n\}_1^{S-1}$, approach the limits

$$\lim_{S \rightarrow \infty} E(L_S(L_S-1) \dots (L_S-(k-1))) = g^{(k)}(1)/g(1), \quad k = 1, 2, \dots$$

$$\lim_{S \rightarrow \infty} E(L_S^k) = (d/du)^k [g(e^u)]|_{u=0}/g(1), \quad k = 1, 2, \dots$$

In particular,

$$\lim_{S \rightarrow \infty} E(L_S) = \gamma(e^{2\gamma} - 1)/(e^{2\gamma} - 1 - 2\gamma)$$

and, letting

$$h(t) = (e^t - 1 - t)/t^2,$$

$$\lim_{S \rightarrow \infty} \text{var}(L_S) = \gamma - \frac{1}{2} + [4h(2\gamma)]^{-1} [3 - 2\gamma - 1/h(2\gamma)].$$

It follows that

$$\lim_{\gamma \rightarrow \infty} [\lim_{S \rightarrow \infty} E(L_S) - \gamma] = 0$$

$$\lim_{\gamma \rightarrow \infty} [\lim_{S \rightarrow \infty} \text{var}(L_S) - (\gamma - \frac{1}{2})] = 0.$$

Proof. To establish all the above limits, it suffices to prove that $f_S(t)$ and its derivatives converge to $g(t)$ and its corresponding derivatives for $t \in [0, 1]$. Because $Sp \rightarrow \gamma$, $q^S \rightarrow e^{-\gamma}$ and so on, f_S converges to g on $(-\infty, +\infty)$. To show that the derivatives of f_S converge to those of g , it suffices, by standard arguments in the theory of analytic functions, to show that $f_S(w)$ is uniformly bounded in some neighbourhood of $[0, 1]$ in the complex plane, as $S \rightarrow \infty$. But that follows because, for complex w ,

$$|[(1 + w/S)^S - 1 - w]/w^2| \leq (e^{|w|} - 1 - |w|)/|w|^2.$$

This last inequality may be established by comparing the power series expansions of both sides term by term. Given convergence of the generating function and its derivatives, $\lim E(L_S) = g'(1)/g(1)$ and $\lim \text{var}(L_S) = g''(1)/g(1) + g'(1)/g(1) - [g'(1)/g(1)]^2$. The formulae given then follow by long but elementary calculations. ■

Figure 2 plots $\lim_{S \rightarrow \infty} v_n$, the limiting relative expected frequency of chains of length n , as a function of n , for $\gamma = 3.71$, a value suggested by the data of papers I and II, and for $\gamma = 10$. The graph for $\gamma = 3.71$ is very similar in shape to the theoretical and simulated graphs for $\gamma = c = 3.75$ and finite $S = 17$ given in figure III. 1. In effect, for this value of γ , $S = 17$ is ‘large’. The graph in figure 2 for

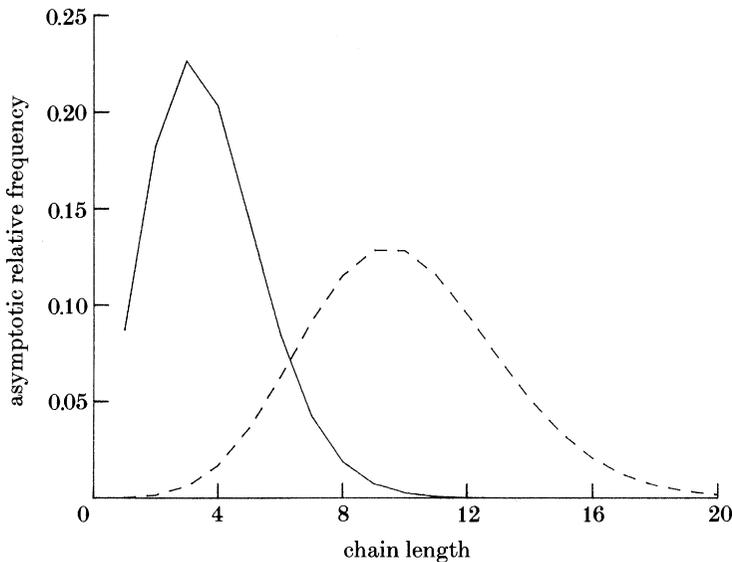


FIGURE 2. Asymptotic relative expected frequency of chains of each length, in webs with an arbitrarily large number of species, according to the cascade model with $\gamma = 3.71$ (—) and with $\gamma = 10$ (---). When $p(S) = c/S$, then $\gamma = c$.

$\gamma = 10$ illustrates the general numerical observation that, for large values of γ , $\lim_{S \rightarrow \infty} v_n$ increases monotonically up to a value of n very near γ and then decreases very nearly symmetrically, in a shape closely resembling a normal distribution. We conjecture that $\lim_{S \rightarrow \infty} v_n$ is maximal for n equal to the largest integer less than γ or one less than the largest integer less than γ . We have numerical examples in which either of these two values of n makes $\lim_{S \rightarrow \infty} v_n$ maximal. The approximate normality, for large γ , of this limiting distribution (with mean approximately γ and variance approximately $\gamma - \frac{1}{2}$) can be proved mathematically. We do not present the proof, since typical values of γ (e.g. 3.71 or 4) are too small for the approximate normality to hold, and we have no significant application of the result for larger values of γ .

Figure 3 plots $\lim_{S \rightarrow \infty} E(L_S)$ and $\lim_{S \rightarrow \infty} E(L_S)$ plus or minus $[\lim_{S \rightarrow \infty} \text{var}(L_S)]^{\frac{1}{2}}$ (corresponding roughly to a two-thirds confidence interval) as a function of γ , for a range of γ likely to include that suggested by the largest observed webs in papers I and II. Figure 3 shows that $\lim_{S \rightarrow \infty} E(L_S)$ approaches the asymptotic (for large γ) limit γ quite rapidly, even within the range estimated from the data in papers I and II. The cascade model thus implies a simple rule of thumb: in webs with a large number of species, the mean length of a chain roughly equals the mean of

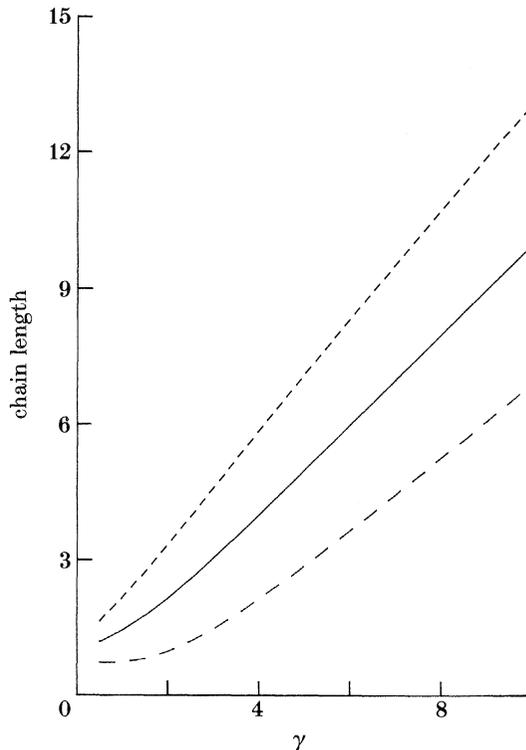


FIGURE 3. Asymptotic mean (—), and asymptotic mean plus (-----) or minus (---) one asymptotic standard deviation, of chain length, L_S , as a function of γ , according to the cascade model. When $p(S) = c/S$, then $\gamma = c$.

the numbers of predators and prey of any species in the web (i.e. the mean total number of links that enter and leave any vertex or, in graph theoretic jargon, the mean in-degree plus the mean out-degree).

For any fixed length n , the standard deviation of the number C_n of n -chains vanishes relative to S as S gets large. Equivalently, for fixed length n in large webs the variance of C_n/S vanishes as S gets large. That is, for fixed $n \geq 1$,

$$\lim_{S \rightarrow \infty} \text{var}(C_n/S) = 0 \quad \text{if} \quad \lim_{S \rightarrow \infty} Sp(S) = \gamma < \infty.$$

Proof. For $1 \leq i_0 < i_1 < \dots < i_n \leq S$, let W_i denote the indicator random variable of the event that $\mathbf{i} \equiv (i_0, i_1, \dots, i_{n-1}, i_n)$ is a chain. Thus $W_i = 1$ if \mathbf{i} is a chain, and $W_i = 0$ if not. Then $C_n = \sum_i W_i$, where the summation covers all possible n -chains. Then

$$\begin{aligned} \text{var}(C_n) &= \text{var}\left(\sum_i W_i\right) \\ &= \sum_i \sum_j \text{cov}(W_i, W_j), \end{aligned}$$

where the covariances are summed over all n -chains \mathbf{i} and \mathbf{j} . If the chains \mathbf{i} and \mathbf{j} share exactly m links, $0 \leq m \leq n$, then

$$\text{cov}(W_i, W_j) \leq P(W_i = 1, W_j = 1) \leq p^m p^{2(n-m)} = p^{2n-m}.$$

If $m = 0$, i.e. \mathbf{i} and \mathbf{j} share no links, and if in addition none of i_0, \dots, i_n coincides with any of j_0, \dots, j_n , then W_i and W_j are independent so $\text{cov}(W_i, W_j) = 0$. Let Q_m be the number of ordered pairs (\mathbf{i}, \mathbf{j}) such that \mathbf{i} and \mathbf{j} share exactly m links. Let Q be the number of pairs (\mathbf{i}, \mathbf{j}) such that at least one species (vertex) of the chain \mathbf{i} is a vertex of the chain \mathbf{j} . Then

$$\text{var}(C_n) \leq \sum_{m=1}^n Q_m p^{2n-m} + Q p^{2n}.$$

Now Q_n is just the number of n -chains, so

$$Q_n = \binom{S}{n+1} \leq S^{n+1}.$$

For $m < n$, if \mathbf{i} and \mathbf{j} share m links, they will share at least $m+1$ species; but \mathbf{i} and \mathbf{j} could share $m+1$ species without necessarily sharing $m+1$ links; so Q_m does not exceed the number of pairs (\mathbf{i}, \mathbf{j}) in which \mathbf{i} and \mathbf{j} have $m+1$ species in common. Therefore $Q_m \leq S^{m+1} S^{2(n+1-(m+1))} = S^{2n+1-m}$. Similarly $Q \leq S^{2n+1}$. Therefore

$$\begin{aligned} \text{var}(C_n) &\leq \sum_{m=0}^n S^{2n+1-m} p^{2n-m} \\ &= \sum_{m=0}^n O(S^{2n+1-m} S^{-(2n-m)}) = O(S) \end{aligned}$$

and thus $\text{var}(C_n/S) = O(1/S)$, which tends to zero as S tends to ∞ . ■

It follows that, for any fixed $n = 1, 2, \dots$,

$$C_n/C \rightarrow K_{n-1} \Big/ \sum_{h=1}^{\infty} K_{h-1} = g^{(n)}(0)/[n!g(1)] \quad \text{in probability as } S \rightarrow \infty,$$

$$\lim_{S \rightarrow \infty} E(C_n/C) \rightarrow K_{n-1} / \sum_{h=1}^{\infty} K_{h-1}.$$

As in §3, C_n/C is set to zero when $C = 0$.

Proof. We have already proved that $E(C_n/S) \rightarrow K_{n-1}$ and $\text{var}(C_n/S) \rightarrow 0$. It follows that, for each fixed n , $C_n/S \rightarrow K_{n-1}$ in mean square (i.e. in L^2) and hence in probability, and therefore that, for any fixed positive integer M ,

$$\sum_{n=1}^M C_n/S \rightarrow \sum_{n=1}^M K_{n-1} \quad \text{in probability.}$$

Our next goal is to prove that this implies

$$C/S \rightarrow \sum_{n=1}^{\infty} K_{n-1} \quad \text{in probability.}$$

Since

$$\begin{aligned} P\left(\left|\sum_{n=1}^M C_n/S - C/S\right| \geq \epsilon\right) &= P\left(\sum_{n=M+1}^{S-1} C_n/S \geq \epsilon\right) \\ &\leq \epsilon^{-1} \sum_{n=M+1}^{S-1} E(C_n)/S \\ &= \epsilon^{-1} \left(E(C)/S - \sum_{n=1}^M E(C_n)/S\right) \\ &\rightarrow \epsilon^{-1} \sum_{n=M+1}^{\infty} K_{n-1} \quad \text{as } S \rightarrow \infty, \end{aligned}$$

we have

$$\begin{aligned} P\left(\left|C/S - \sum_{n=1}^{\infty} K_{n-1}\right| \geq 3\epsilon\right) &\leq P\left(\left|C/S - \sum_{n=1}^M C_n/S\right| \geq \epsilon\right) \\ &\quad + P\left(\left|\sum_{n=1}^M C_n/S - \sum_{n=1}^M K_{n-1}\right| \geq \epsilon\right) \\ &\quad + P\left(\left|\sum_{n=1}^M K_{n-1} - \sum_{n=1}^{\infty} K_{n-1}\right| \geq \epsilon\right). \end{aligned}$$

Taking $\limsup_{S \rightarrow \infty}$ of this last inequality and choosing M large enough, we have

$$\limsup_{S \rightarrow \infty} P\left(\left|C/S - \sum_{n=1}^{\infty} K_{n-1}\right| \geq 3\epsilon\right) \leq \epsilon^{-1} \sum_{n=M+1}^{\infty} K_{n-1} + 0 + 0.$$

Letting $M \rightarrow \infty$ establishes that

$$C/S \rightarrow \sum_{n=1}^{\infty} K_{n-1} \quad \text{in probability.}$$

Hence

$$C_n/C = (C_n/S)/(C/S) \rightarrow K_{n-1} \Big/ \sum_{h=1}^{\infty} K_{h-1} \quad \text{in probability.}$$

Since $|C_n/C| \leq 1$, all moments of C_n/C converge. In particular,

$$E(C_n/C) \rightarrow K_{n-1} / \sum_{h=1}^{\infty} K_{h-1}.$$

Since u_n and v_n converge to the same limit for large S , it makes no difference, for large enough S , which probability density is used to describe typical chain lengths. Of course, for finite S (and all observed webs have finite S), the two probability densities $\{u_n\}$ and $\{v_n\}$ are different; we have obtained exact formulae only for the latter.

5. THE LONGEST CHAIN IN FINITE WEBS

We now show that the cascade model explains remarkably well the qualitative observation, frequently made (see, for example, Hutchinson 1959), that the length of the longest chain, and hence the height, of a web is small compared to the number of species in the web.

In a web with S species, define M_S to be the height. For random webs generated by the cascade model, M_S is a random variable. For brevity, we henceforth drop the subscript S , bearing in mind that the distribution of M does depend on S .

To investigate the distribution of M , given S and $p = c/S$, we find, for a positive integer m , upper bounds for $P(M \geq m)$ and $P(M < m)$.

First, for any positive integer $m \leq S-1$ with $p = c/S$,

$$\begin{aligned} P(M \geq m) &\leq L_1(S, m) \equiv 1 - (1 - p^m)^{\binom{S}{m+1}} \\ &\leq L_2(S, m) \equiv \binom{S}{m+1} p^m \\ &\leq L_3(S, m) \equiv c^m S / (m+1)!. \end{aligned}$$

Proof. Let B_n be the number of n -walks, $n = 1, 2, \dots, S-1$. Such walks may or may not be chains, which are walks from basal to top species. For $1 \leq i_0 < i_1 < \dots < i_n \leq S$, let V_i denote the indicator random variable of the event that there is a walk $i \equiv i_0, (i_0, i_1), i_1, \dots, (i_{n-1}, i_n), i_n$. Then $B_n = \sum_i V_i$, where the summation covers all possible n -walks. The V_i 's are non-decreasing functions of the independent random variables that determine whether individual links are present and hence are associated random variables (Harris 1960; Esary *et al.* 1967). This justifies the inequality in the computation (where we set $n = m$)

$$\begin{aligned} P(M \geq m) &= P(B_m > 0) = 1 - P(B_m = 0) \\ &= 1 - P(\text{for every } i \text{ of length } m, V_i = 0) \\ &\leq 1 - \prod_i P(V_i = 0) \end{aligned}$$

[the product taken over all m -walks i]

$$\begin{aligned} &= 1 - \prod_i (1 - p^m) \\ &= 1 - (1 - p^m)^{\binom{S}{m+1}}. \end{aligned}$$

The last step holds because there are exactly $\binom{S}{m+1}$ possible m -walks in the cascade model.

For any positive integer n and any $x \in (0, 1)$, $1 - (1 - x)^n \leq nx$, as is easy to show by comparing derivatives with respect to x . Setting $x = p^m$ and $n = \binom{S}{m+1}$ gives $L_1 \leq L_2$. Finally,

$$\binom{S}{m+1} (c/S)^m = [c^m S / (m+1)!] [(S-1)! / \{(S-1-m)! S^m\}] \leq c^m S / (m+1)! \blacksquare$$

On the other side of M ,

$$\begin{aligned} P(M < m) &\leq U_1(S, m) \equiv \binom{S}{m+1}^{-1} \left[\sum_{k=1}^m (m-k+1) \binom{S-k-1}{m-k} (p^{-k} - 1) \right. \\ &\quad \left. + \sum_{k=1}^{m-2} \binom{m}{k} \binom{S-k-2}{m-k-1} (p^{-k} - 1) \right] \\ &\leq U_2(S, m) \equiv \left[\binom{S}{m+1} p^m \right]^{-1} \left[\sum_{k=0}^m (m-k+1) (Sp)^{m-k} / (m-k)! \right. \\ &\quad \left. + \sum_{k=0}^m \binom{m}{k} S^{m-k-1} p^{m-k} \right] \\ &\leq U_3(S, m) \equiv [c^m S(1-1/S) \dots (1-m/S) / (m+1)!]^{-1} \\ &\quad \times \left[\sum_{j=0}^{\infty} (j+1) (Sp)^j / j! + S^{-1} \sum_{j=0}^m \binom{m}{j} (Sp)^j \right], \end{aligned}$$

and if $\frac{1}{2}m(m+1) < S$,

$$\begin{aligned} &\leq U_4(S, m) \equiv [c^m S(1 - m(m+1)/(2S)) / (m+1)!]^{-1} \\ &\quad \times [e^{Sp} + Sp e^{Sp} + S^{-1}(1 + Sp)^m] \\ &= 2(m+1)! [(1+c)e^c + (1+c)^m / S] / [c^m (2S - m(m+1))] \end{aligned}$$

Proof. In the notation used in the previous proof,

$$P(M < m) = P(B_m = 0) \leq P[|B_m - E(B_m)| \geq E(B_m)],$$

and now, from Chebychev's inequality,

$$\leq \text{var}(B_m) / [E(B_m)]^2.$$

We now seek an upper bound for $\text{var}(B_m) = \sum_i \sum_j \text{cov}(V_i, V_j)$, where the summations cover all m -walks. If i and j have exactly k links in common, then

$$\begin{aligned} \text{cov}(V_i, V_j) &= P(V_i = 1 \text{ and } V_j = 1) - P(V_i = 1)P(V_j = 1) \\ &= p^{2m-k} - p^{2m}. \end{aligned}$$

Let Q_k be the number of ordered pairs (i, j) of m -walks (not chains now) i, j such that i and j have exactly k links in common. Then

$$\begin{aligned} \text{var}(B_m) &= \sum_{k=0}^m Q_k (p^{2m-k} - p^{2m}) \\ &= \sum_{k=1}^m Q_k (p^{2m-k} - p^{2m}). \end{aligned}$$

Define Q_k^α to be the number of ordered pairs (i, j) of m -walks with exactly k links in common in which the k common links form a k -walk. Define Q_k^β to be the number of ordered pairs (i, j) of m -walks with exactly k links in common in which the k common links do not form a single k -walk. Clearly, $Q_m^\beta = Q_{m-1}^\beta = 0$ and

$$Q_k = Q_k^\alpha + Q_k^\beta.$$

Moreover,

$$Q_k^\alpha \leq \binom{S}{m+1} (m-k+1) \binom{S-k-1}{m-k}, \quad k = 1, \dots, m$$

because there are $\binom{S}{m+1}$ ways to choose the m -walk i , there are $(m-k+1)$ ways to choose a subwalk of i of length k , the links of which will be the links in common with j , and since each common subwalk of length k determines $k+1$ vertices of j , there are not more than $\binom{S-(k+1)}{(m+1)-(k+1)} = \binom{S-k-1}{m-k}$ ways to choose the remaining $(m+1)-(k+1)$ vertices of j . Also,

$$Q_k^\beta \leq \binom{S}{m+1} \binom{m}{k} \binom{S-k-2}{m-k-1}, \quad k = 1, \dots, m-2,$$

because (again) there are $\binom{S}{m+1}$ ways to choose i , there are at most $\binom{m}{k}$ ways to choose the k links of i that will be the links in common with j , and since these links form at least two subwalks which determine not less than $k+2$ vertices of j , leaving at most $(m+1)-(k-2) = m-k-1$ vertices to be determined, there are at most $\binom{S-k-2}{m-k-1}$ ways to choose the remaining vertices of j . This last step depends on the observation that $\binom{S-h}{m+1-h}$ is a non-increasing function of $h = 0, \dots, m+1$.

Since $E(B_m) = \binom{S}{m+1} p^m$, collecting all the inequalities gives

$$\begin{aligned} P(M < m) &\leq \sum_{k=1}^m (Q_k^\alpha + Q_k^\beta) (p^{2m-k} - p^{2m}) \left/ \left[\binom{S}{m+1} p^m \right]^2 \right. \\ &\leq \binom{S}{m+1}^{-1} \left[\sum_{k=1}^m (m-k+1) \binom{S-k-1}{m-k} (p^{-k} - 1) \right. \\ &\quad \left. + \sum_{k=1}^{m-2} \binom{m}{k} \binom{S-k-2}{m-k-1} (p^{-k} - 1) \right]. \end{aligned}$$

This establishes $P(M < m) \leq U_1(S, m)$. The remaining approximations follow by elementary calculations. ■

These inequalities imply bounds on any quantile of the distribution of the height M . For example, to bound the median of M , we determine numerically m_1 , the smallest integer m such that $L_2(S, m) < \frac{1}{2}$, and m_2 , the largest integer m such that $U_1(S, m) < \frac{1}{2}$. Then

$$m_2 \leq \text{median of } M \leq m_1 - 1.$$

(Why do we use $L_2(S, m)$ to determine m_1 rather than $L_1(S, m)$, which is a sharper bound? For moderately large values of S and m , when p^m becomes very small, e.g.

less than 10^{-15} , a computer approximates $1-p^m$ by 1 and the results become nonsense. $L_2(S, m)$ and $L_3(S, m)$ avoid the problem of subtracting numbers of very different orders of magnitude.)

For a fixed value of c typical of observed webs and a broad range of values of S , table 1 gives the lower and upper bounds on the median height. In other examples, in a web of 20 species with $c = 3.71$, the median height is between 2 and 7 links. In a web with 250 times as many, or 5000, species, the median height is between 8 and 13 links. The upper bound on the median has increased by less than a factor of two.

TABLE 1. THE LENGTH OF THE LONGEST CHAIN IN LARGE WEBS ACCORDING TO THE CASCADE MODEL

($c = 3.71$.)

number of species	bounds on the median		limiting value, m^*	asymptotic value $\ln S / \ln (\ln S)$
	lower	upper		
10^2	4	10	11	3.0
10^4	8	14	14	4.1
10^6	12	17	17	5.3
10^8	15	19	20	6.3
10^{10}	18	22	22	7.3
10^{12}	21	24	25	8.3

6. ASYMPTOTIC BEHAVIOUR OF THE LENGTH OF THE LONGEST CHAIN IN LARGE WEBS

In the cascade model with a fixed $c > 0$, as the number of species, S , gets very large (as we shall see, far larger than the number of species on Earth), the limiting behaviour of the height, the length of the longest chain, is simple. For each S , there is a positive integer m^* (which depends on S , but we drop the subscript S for brevity), such that the probability that the height is m^* or $m^* - 1$ approaches one as S gets large. Thus in a web generated by the cascade model the height is either m^* or $m^* - 1$, with probability approaching one for large S .

A qualitatively similar phenomenon has been observed elsewhere in the theory of random graphs. Bollobás & Erdős (1976) and, according to them, D. W. Matula independently proved that the size of the maximal complete subgraph (clique) in a random graph takes one of at most two values (that depend on the size of the random graph) with a probability that approaches 1 as the random graph gets large, when the edge probability is held fixed, independent of the number of vertices.

For very, very large numbers, S , of species, m^* grows at a rate that is essentially independent of c or $p = c/S$ (provided $c > 0$) and depends only on S . For extremely large S , m^* is approximately $\ln S / \ln (\ln S)$ in the sense that their ratio approaches 1. By contrast, according to Bollobás & Erdős (1976), the asymptotic behaviour of the (at most two) possible values for the size of the largest clique does depend on the fixed probability that there is an edge between any two given vertices.

We now describe more precisely the height M in very large webs according to the cascade model. Define m^* to be the smallest positive integer m such that

$$c^{m+1}S/(m+2)! \leq (m+2)^{-\frac{1}{2}}.$$

Then, for large enough S , m^* is a non-decreasing sequence such that

$$\lim_{S \rightarrow \infty} m^*/[\ln S/\ln(\ln S)] = 1$$

and

$$\lim_{S \rightarrow \infty} P(M = m^* \text{ or } M = m^* - 1) = 1.$$

However, the estimated rate of convergence of $P(M = m^* \text{ or } M = m^* - 1)$ to 1 is very slow, namely,

$$1 - P(M = m^* \text{ or } M = m^* - 1) = O(m^{*-\frac{1}{2}}).$$

Proof. We begin by establishing that, for every positive integer S and every $c > 0$, there is a positive integer m such that $c^{m+1}S(m+2)! < (m+2)^{-\frac{1}{2}}$ or equivalently $(m+2)^{\frac{1}{2}}c^{m+1}S/(m+2)! \leq 1$. (If m exists, then m^* exists.) Sterling's approximation may be written

$$n! = (2\pi)^{\frac{1}{2}}n^{n+\frac{1}{2}}e^{-n}(1+O(n^{-1})).$$

Substituting into $(m+2)^{\frac{1}{2}}c^{m+1}S/(m+2)!$ shows that this quantity approaches 0 as $m \rightarrow \infty$, so the desired m exists. The least such m , namely m^* , satisfies $S \leq (m^*+2)!/[c^{m^*+1}(m^*+2)^{\frac{1}{2}}]$ and must not decrease as S increases. The next question is: how fast does m^* increase?

Pick any $\epsilon > 0$. If

$$m(S) \sim (1+\epsilon) \ln S/\ln(\ln S),$$

then

$$\begin{aligned} \ln m(S) &= \ln(\ln S) - \ln(\ln(\ln S)) + O(1) \\ &\sim \ln(\ln S) \end{aligned}$$

so

$$-m(S) \ln m(S) \sim -(1+\epsilon) \ln S.$$

Now, by using Sterling's formula and dropping ineffectual constants,

$$\begin{aligned} \ln [m(S)^{\frac{1}{2}}c^{m(S)}S/m(S)!] &\sim m(S) \ln c + \ln S - \ln [m(S)!] + \frac{1}{2} \ln m(S) \\ &\sim \ln S - m(S) \ln m(S) \\ &\sim \ln S - (1+\epsilon) \ln S \\ &\sim -\epsilon \ln S \rightarrow -\infty \quad \text{as } S \rightarrow \infty. \end{aligned}$$

Consequently

$$m(S)^{\frac{1}{2}}c^{m(S)}S/m(S)! \rightarrow 0 \quad \text{as } S \rightarrow \infty,$$

so $m^* < (1+\epsilon) \ln S/\ln(\ln S)$ for large enough S . On the other hand, if

$$m(S) \sim (1-\epsilon) \ln S/\ln(\ln S),$$

then the same argument shows that

$$m(S)^{\frac{1}{2}} c^{m(S)} S / m(S)! \rightarrow \infty \quad \text{as } S \rightarrow \infty,$$

so $m^* > (1 - \epsilon) \ln S / \ln(\ln S)$ for large S . This establishes that

$$m^* \sim \ln S / \ln(\ln S).$$

So m^* increases without bound (but very slowly) as $S \rightarrow \infty$.

We can now prove $\lim_{S \rightarrow \infty} P(M = m^* \text{ or } m^* - 1) = 1$. By the inequalities established for $P(M \geq m)$ and $P(M < m)$ for finite S , with S large enough that $m^*(m^* + 1)/2 < S$,

$$\begin{aligned} P(M \geq m^* + 1) &\leq c^{m^*+1} S / (m^* + 2)! \leq (m^* + 2)^{-\frac{1}{2}} \rightarrow 0 \quad \text{as } S \rightarrow \infty, \\ P(M < m^* - 1) &\leq 2m^*! [(1 + c) e^c + (1 + c)^{m^*-1} / S] / [c^{m^*-1} (2S - m^*(m^* - 1))] \\ &\sim (1 + c) e^c m^*! / [Sc^{m^*-1}] = (1 + c) e^c [c^{m^*} S / (m^* + 1)!]^{-1} c / (m^* + 1). \end{aligned}$$

But m^* is the smallest m such that $c^{m+1} S / (m + 2)! < (m + 2)^{-\frac{1}{2}}$. Therefore $c^{m^*} S / (m^* + 1)! > (m^* + 1)^{-\frac{1}{2}}$, and hence $[c^{m^*} S / (m^* + 1)!]^{-1} < (m^* + 1)^{\frac{1}{2}}$. As $S \rightarrow \infty$, $P(M < m^* - 1)$ is therefore of order of magnitude not greater than $(1 + c) c e^c (m^* + 1)^{-\frac{1}{2}}$, which approaches 0 as $O(m^{*-\frac{1}{2}})$. ■

For each value, m , of m^* , there is a range of values of S such that m^* for that S is m . When S is large and at the upper end of this range of values, then the height equals m^* with a probability that approaches 1. When S is large and at the lower end of this range of values, the height equals $m^* - 1$ with a probability that approaches 1. When S is in the middle of this range, it can happen that both the event that the height equals m^* and the event that the height equals $m^* - 1$ occur with non-negligible probabilities.

Proof. For any positive integer m , let S_m^+ be the greatest integer less than or equal to $(m + 2)! / [c^{m+1}(m + 2)^{\frac{1}{2}}]$ and let $S_m^- = S_{m-1}^+ + 1$ (with $S_0^+ = 0$). Then $S_m^+ \sim m^{\frac{1}{2}}(m + 1)! / c^{m+1}$, $S_m^- / S_m^+ \sim c / m$ and the range of values of S such that $m^* = m$ is precisely $\{S_m^-, S_m^- + 1, \dots, S_m^+\}$. Suppose S_m is a sequence satisfying $S_m \leq S_m^+$ and $m^{\frac{1}{2}} S_m / S_m^+ \rightarrow \infty$; then with $S = S_m$, we find by using $U_4(S, m)$ that

$$\begin{aligned} P(M = m - 1) &\leq P(M < m) = O[(m + 1)! / (c^m S_m)] \\ &= O[S_m^+ / (m^{\frac{1}{2}} S_m)] \rightarrow 0 \quad \text{as } m \rightarrow \infty, \end{aligned}$$

so that $P(M = m^*) \rightarrow 1$ for such a sequence S_m . Similarly if S_m satisfies $S_m \geq S_m^-$ and $S_m / (m^{\frac{1}{2}} S_m^-) \rightarrow 0$, or equivalently $m^{\frac{1}{2}} S_m / S_m^+ \rightarrow 0$, then with $S = S_m$, we find, by using $L_3(S, m)$, that

$$\begin{aligned} P(M = m) &\leq P(M \geq m) = O[c^m S_m / (m + 1)!] \\ &= O[S_m / (m^{\frac{1}{2}} S_m^-)] \rightarrow 0 \quad \text{as } m \rightarrow \infty, \end{aligned}$$

so that $P(M = m^* - 1) \rightarrow 1$ for such a sequence S_m .

We now consider S_m^0 in the middle of the range from S_m^- to S_m^+ . Define S_m^0 to

be the greatest integer less than or equal to $2(1+c)e^c(m+1)!/c^m$. Then for large m , $S_m^- < S_m^0 < S_m^+$ and for $S = S_m^0$, we have $m^* = m$. In this case,

$$\begin{aligned} P(M = m-1) &\leq P(M < m) \\ &\leq [c^m S(1+o(1))/(m+1)!]^{-1} [(1+c)e^c + o(1)] \\ &\rightarrow [2(1+c)e^c]^{-1} (1+c)e^c = \frac{1}{2} \quad \text{as } m \rightarrow \infty, \end{aligned}$$

and $L_1(S, m)$ gives

$$\begin{aligned} P(M = m) &\leq P(M \geq m) \leq 1 - (1 - (c/S)^m)^{\binom{S}{m+1}} \\ &\rightarrow 1 - \exp[-2(1+c)e^c] < 1 \quad \text{as } m \rightarrow \infty. \end{aligned}$$

Since $P(M = m \text{ or } m-1) \rightarrow 1$ as m and $S = S_m^0$ increase without bound, we conclude that

$$\liminf_{m \rightarrow \infty} P(M = m-1) > 0,$$

$$\liminf_{m \rightarrow \infty} P(M = m) > 0$$

for $S = S_m^0$. ■

To find m^* numerically for various numbers, S , of species, we find the smallest integer m such that

$$S \leq (m+2)!/[c^{m+1}(m+2)^{\frac{1}{2}}].$$

For a range of values of S , table 1 gives the calculated values of m^* as well as the values of the asymptotic expression for m^* , $\ln S/\ln(\ln S)$. For three values of S (10^2 , 10^8 , 10^{12}), the calculated value of m^* exceeds the upper bound given for the median height. This is consistent with the understanding that the height will be concentrated on m^* or $m^* - 1$ only in the limit as S becomes extremely large. In table 1, for finite S as large as 10^{12} , evidently m^* is larger than the range of possible values for the median height. Simulations described below for (for example) $S = 1000$ give an estimated median height of 9 links; this height falls between the lower and upper bounds of 6 and 12, respectively, although the calculated value of m^* is 13 (see table 2).

The values of $\ln S/\ln(\ln S)$, which fall far below m^* , emphasize further that m^* is dependent on c and converges (in ratio) to the c -independent quantity $\ln S/\ln(\ln S)$ only for *very* large S . For values of S in the range considered in table 1, second and higher order terms in the asymptotic expansion for m^* are evidently influential in addition to the leading term $\ln S/\ln(\ln S)$. Calculations similar to those used above to prove that

$$m^* = [\ln S/\ln(\ln S)](1+o(1))$$

establish that, to second order,

$$m^* = [\ln S/\ln(\ln S)]\{1 + [\ln(\ln(\ln S))/\ln(\ln S)](1+o(1))\}.$$

For $S = 10^{12}$, $\ln(\ln(\ln S))/\ln(\ln S) = 0.36$, a non-negligible correction. It is interesting that even the second-order term in the expansion of m^* , like the first, depends only on S and is independent of c .

7. SENSITIVITY ANALYSIS: ANISOTROPIC CASCADE MODELS

If the assumptions of the cascade model are relaxed, what happens? This question arises first from the scepticism that Cohen *et al.* (1985) express about the exact truth of these assumptions. For example, would the ability of the cascade model to explain, qualitatively, the slow growth of the height be destroyed by a small change in the parameter c ? No, because for very large webs the height grows very slowly regardless of the value of the parameter c .

If one retained the assumption that the probability p_{ij} of a random link from species i to species j were 0 for $j \leq i$ (this is the ‘cascade’ assumption) but permitted values for p_{ij} to depend on i and j when $i < j$ (we propose to call all such models anisotropic cascade models), the webs can be qualitatively different from those generated by the (isotropic) cascade model (with $p_{ij} = p > 0$, for all $i < j$). Consider three examples.

First, suppose that the web were partitioned into what some ecologists call ‘compartments’, meaning that the adjacency matrix of the web is block diagonal (see Pimm [1982, ch. 8] for a review). Suppose that each compartment or block contained at most S^* species, where S^* is some fixed finite positive integer. As the total number, S , of species in the web increased, suppose that more and more blocks of size at most S^* were added. Obviously the height will not exceed $S^* - 1$, regardless of S .

Second, consider an anisotropic cascade model with block diagonal (strictly upper) triangular matrix $\{p_{ij}\}$ of edge probabilities and blocks (or compartments) of size S_1, \dots, S_n , where $S_1 + \dots + S_n = S$. Suppose in block h , of size S_h , that $p_{ij} = c_h/S_h > 0$ for $i < j$. Then the height, M , satisfies

$$P(M \geq m) \leq 1 - \prod_{h=1}^n (1 - (c_h/S_h)^m)^{\binom{S_h}{m+1}}$$

$$\leq \left(\sup_{1 \leq h \leq n} c_h \right)^m S / (m+1)!$$

Proof. Let $M(h)$ be the maximum chain length in the h th block. Then, since different blocks are independent and $M = \sup_h M(h)$, it follows, by using $L_1(S_h, m)$ for each block, that

$$P(M \geq m) = 1 - P(M < m)$$

$$= 1 - \prod_{h=1}^n P(M(h) < m)$$

$$\leq 1 - \prod_{h=1}^n (1 - (c_h/S_h)^m)^{\binom{S_h}{m+1}}$$

$$\leq \sum_{h=1}^n \binom{S_h}{m+1} (c_h/S_h)^m \leq \sum_{h=1}^n (c_h)^m S_h / (m+1)!$$

where the next to last inequality follows from $\prod_i (1 - x_i) \leq 1 - \sum_i x_i$. ■

Now if $S_1 = \dots = S_n \sim \ln S$ so that the number, n , of blocks grows as $S/\ln S$ while $c_h = c$ independent of S for $h = 1, \dots, n$, then, within each block, $p_{ij} \sim c/\ln S$. The expected number of links to and from each species, i.e. the expected number of predators plus the expected number of prey, is asymptotically $c = S_h p_{ij} \sim \ln S(c/\ln S)$. Since here $P(M \geq m) \leq c^m S/(m+1)!$, exactly as in the isotropic cascade model, M cannot grow asymptotically faster than $\ln S/\ln(\ln S)$.

Third and finally, consider an anisotropic cascade model chosen, not for its realism, but to illustrate that without some special structure in the matrix $\{p_{ij}\}$ of edge probabilities the height could be asymptotically proportional to S (even when the expected number of links per species is kept fixed), contrary to observation. This example is taken from a study of one-dimensional percolation by Newman & Schulman (1985) and incidentally illustrates that there are interesting connections between percolation models and cascade models.

Suppose, for $j = 2, 3, \dots$, that $\{y_j\}$ is a fixed sequence of probabilities, independent of S , such that, for some $s < 2$,

$$\liminf_{j \rightarrow \infty} j^s y_j > 0,$$

e.g. suppose $y_j \sim K j^{-s}$ as $j \rightarrow \infty$, for some $K > 0$ and $s < 2$. For any ρ such that $0 < \rho < 1$, there is an ϵ , $0 < \epsilon < 1$, such that if

$$p_{i, i+1} \geq 1 - \epsilon \quad \text{for all } S \quad \text{and} \quad i = 1, \dots, S-1,$$

$$p_{ij} \geq y_{j-i}, \quad \text{for} \quad i+2 \leq j \leq S,$$

$$p_{ij} = 0 \quad \text{for} \quad j \leq i,$$

then

$$\lim_{S \rightarrow \infty} P(M \geq \rho S) = 1.$$

To give a concrete instance of this example, pick some $c > 2$ and define $\{p_{ij}\}$ by

$$\begin{aligned} p_{ij} &= (c-2) \left/ \left[2 \left(\sum_{k=2}^{\infty} k^{-\frac{3}{2}} \right) (j-i)^{\frac{3}{2}} \right] \right., \quad j \geq i+2, \\ &= 1 - \epsilon, \quad j = i+1 \\ &= 0, \quad j \leq i. \end{aligned}$$

Taking, say, $\rho = 0.999$, there is a small enough ϵ that

$$\lim_{S \rightarrow \infty} P(M \geq 0.999S) = 1$$

even though

$$\begin{aligned} &\sup_{1 \leq i \leq S} E(\text{number of predators and prey of species } i) \\ &= \sup_{1 \leq i \leq S} \left(\sum_{k=1}^{i-1} p_{ki} + \sum_{j=i+1}^S p_{ij} \right) \\ &\leq 2(1-\epsilon) + 2 \sum_{h=2}^{\infty} (c-2) \left/ \left[2 \left(\sum_{k=2}^{\infty} k^{-\frac{3}{2}} \right) h^{\frac{3}{2}} \right] \right. \\ &= 2(1-\epsilon) + c-2 < c, \quad \text{for all } S. \end{aligned}$$

The example demonstrates that even when the expected number of links per species is kept below a fixed c , not every anisotropic cascade model will explain the observed slow increase in the height of real webs.

8. SIMULATIONS OF THE CASCADE MODEL

The preceding analysis leaves open the question: how good are our theoretical bounds for the median height? We set $c = 3.71$ based on the sample of 62 webs, then generated webs according to the cascade model for each of $S = 50, 100, 150$ and 1000 and found the height of each simulated web (by using an algorithm described in the appendix of paper III). Table 2 presents the simulated frequency distributions of height, and beneath each simulated distribution the numerical values of our theoretical bounds on the median height. Evidently the bounds on the median do contain the sample median height. The concentration of height on at most two values established above in the limit of unrealistically large S does not occur for the values of S used in these simulations. There is however a suggestion of more concentration for $S = 1000$ than for $S = 50$.

TABLE 2. FREQUENCY DISTRIBUTIONS OF THE LENGTH OF THE LONGEST CHAINS IN WEBS OF VARIOUS SIZES, AND THEORETICAL ESTIMATES OF THE MEDIAN

(Web sizes were simulated according to the cascade model with $c = 3.71$.)

longest chain	number of species			
	50	100	150	1000
	relative frequency			
4	0.03	0.00	0.01	0.00
5	0.17	0.24	0.07	0.00
6	0.32	0.31	0.27	0.00
7	0.24	0.24	0.33	0.05
8	0.15	0.14	0.18	0.25
9	0.08	0.05	0.08	0.40
10	0.02	0.02	0.05	0.20
11	0.01	0.00	0.01	0.10
	number of simulations			
	200	100	100	20
	theoretical estimates of median longest chain			
lower bound	3	4	4	6
upper bound	9	10	10	12
m^*	10	11	11	13
$\ln S / \ln(\ln S)$	2.87	3.02	3.11	3.57

9. ACHIEVEMENTS OF THIS THEORY

This paper presents the first, to our knowledge, exactly derived theory of the length of food chains in webs with a large number of species. This theory suggests for the first time a (simple) quantitative relation between the mean length of chains and the mean number of predators plus prey per species. The analysis also

provides the first quantitative explanation, derived from an explicit model that is not invented *ad hoc* for the purpose, of why the longest chains are very short relative to the number of species in a web even when the number of species is large.

From a generating function for the expected numbers of chains of each length, we derive the mean and variance of the length of chains by using the relative expected frequency as the probability density function of chain length. For webs in which S becomes arbitrarily large, we show that the limiting relative expected frequency and the limiting expected relative frequency of chain lengths are the same, so that either may be used to describe the distribution of chain lengths. We compute the asymptotic distribution and all moments of chain length, giving explicit closed-form formulas for the asymptotic mean and variance. We show that the relative frequency of chains of any given length converges in probability to its expectation as S gets large. The cascade model implies a simple 'rule of thumb' for large webs: the mean length of chains equals the mean number of predators plus prey of any species in the web.

We also derive, from the cascade model, upper bounds on the upper and lower tails of the probability distribution of the height, or length of the longest chain, of a web. From these, we compute bounds on the median height in webs with a finite number of species. These bounds show that the median height is a very slowly increasing function of the number of species in a web, remaining below 20 up to 10^8 species. For webs in which S becomes unrealistically large, the height equals one of two adjacent integers (that depend on S) with a probability that approaches 1. For very large S , these integers approximate $\ln S / \ln(\ln S)$, a function that grows very slowly with S .

By considering variations on the assumptions of the cascade model, we show that the ability of the cascade model to explain the slow growth of the height is robust with respect to changes in the probability that one species eats another. However, if the probability that one species eats another is permitted to depend on the pair of species concerned, then the height may increase either not at all or linearly with the total number of species. Hence not every variation on the cascade model will explain the observed short height, relative to the number of species, of real webs.

Simulations of the cascade model show that the concentration of the height on just two integer values, predicted by the asymptotic theory, occurs only in webs with an unrealistically large number of species.

10. SOME REMAINING TASKS

Although the cascade model yields to mathematical analysis, the acyclic model (model 2 in paper I) resists analysis. We do not know, for example, whether the median height in the acyclic model grows slowly with S , as demonstrated here for the cascade model. A solution to this problem might reveal whether the asymptotic behaviour of the height could be used to discriminate between different models of webs.

The cascade model and its kin are static models. They describe data that are snapshots, sketches of webs at a single moment. Static models and static data

ignore the reality that the species and links of webs may change with the seasons and over longer intervals. It would be highly desirable to develop and test dynamic models of communities that are consistent with the static empirical regularities on which the cascade model is based.

The cascade model and the data it is intended to interpret ignore the numbers of individuals or biomass of each species and the quantities of flows in each link. Far fewer observed webs give quantitative measurements than give, like the webs studied here, all-or-none information about species and links. Thus the whole line of work from Cohen (1978) to this paper is only a first step towards a real understanding of webs, because it deals entirely with combinatorial structure rather than with quantities of stocks and flows in webs. However, gross anatomy precedes physiology. This line of work at least offers a coherent theoretical and empirical approach to some aspects of the gross anatomy of webs.

What might be offered by better data and models that will, we hope, replace those we analyse here? Quantitative, predictive models of webs could assist in foreseeing the paths and concentrations of natural and artificial toxins in the environment, and the consequences of the removal and introduction of species. Such models could assist in the design of nature reserves on Earth and closed regenerative ecosystems for supporting humans during prolonged stays in space; the cascade model suggests already that certain proportions of top, intermediate and basal species (or physico-chemical equivalents) need to be provided or else will evolve. Finally, since the webs containing the species man are not notably different in structure from those without man, such models may provide some understanding of man's place in nature. These grand opportunities are an incentive to pursue the hard scientific work that may bring them within reach.

Anne M. Welna assisted in preparing the manuscript. C.M.N. acknowledges with thanks a John S. Guggenheim Memorial Fellowship and the support of U.S. National Science Foundation grant MCS80-19384. J.E.C. acknowledges with thanks the John D. and Catherine T. MacArthur Foundation Fellows Program, U.S. National Science Foundation grant BSR84-07641, and the hospitality of Mr and Mrs William T. Golden.

REFERENCES

- Bollobás, B. & Erdős, P. 1976 Cliques in random graphs. *Math. Proc. Camb. phil. Soc.* **80**, 419–427.
- Cohen, J. E. 1978 *Food webs and niche space*. Princeton: Princeton University Press.
- Cohen, J. E. & Newman, C. M. 1985 A stochastic theory of community food webs. I. Models and aggregated data. *Proc. R. Soc. Lond. B* **224**, 421–448.
- Cohen, J. E., Newman, C. M. & Briand, F. 1985 A stochastic theory of community food webs. II. Individual webs. *Proc. R. Soc. Lond. B* **224**, 449–461.
- Cohen, J. E., Briand, F. & Newman, C. M. 1986 A stochastic theory of community food webs. III. Predicted and observed lengths of food chains. *Proc. R. Soc. Lond. B* **228**, 317–353.
- Esary, J., Proschan, F. & Walkup, D. 1967 Association of random variables with applications. *Ann. math. Statist.* **38**, 1466–1474.
- Harris, T. E. 1960 A lower bound for the critical probability in a certain percolation process. *Proc. Camb. phil. Soc.* **59**, 13–20.

- Hutchinson, G. E. 1959 Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159.
- Newman, C. M. & Schulman, L. S. 1985 Infinite chains and clusters in one dimensional directed and undirected percolation. In *Particle systems, random media and large deviations* (ed. R. Durrett), pp. 297–313. Contemporary Mathematics vol. 41. Providence, Rhode Island: American Mathematical Society.
- Pimm, S. 1982 *Food webs*. London: Chapman and Hall.