

A STOCHASTIC THEORY OF COMMUNITY FOOD WEBS.
V. INTERVALITY AND TRIANGULATION IN THE
TROPHIC-NICHE OVERLAP GRAPH

JOEL E. COHEN AND ZBIGNIEW J. PALKA*

Rockefeller University, 1230 York Avenue, New York, New York 10021-6399

Submitted April 25, 1988; Revised November 28, 1988; Accepted December 11, 1988

When the diets of different organisms overlap in natural communities, the possibility arises that the different consumers may compete for food (Grant 1986) or may interact mutualistically (Kawanabe 1986, 1987). Competitive or mutualistic interactions over food may influence the evolution of the competing or cooperating consumers. Hence, overlaps in the diets of different organisms are of both ecological and evolutionary interest.

The diets of organisms, and the relations among the diets of different kinds of organisms, vary greatly from one ecological community to another. The minimum number of variables required to describe or represent the overlaps among consumers' diets has been called the dimension of trophic-niche space (Cohen 1978). A priori, the dimension of trophic-niche space would be expected to vary among communities. If, in a particular community, this dimension were one, then intervals of some single variable, perhaps food size, would be necessary and sufficient to describe when the diet of one species overlaps that of another. If the dimension were greater than one, then intervals of no single variable, such as food size alone, would suffice to describe when the diets of consumers overlap. That is, if the dimension exceeded one, then it would be necessary to consider at least two variables, perhaps food size and time of day, to account for or describe the presence or absence of overlaps in the diets of different organisms. The dimension of trophic-niche space is one measure of the complexity of the dietary relations among consumers in a given community.

This paper reports new theoretical and empirical information about the overlaps among the diets of organisms in natural communities. On the basis of mathematical calculations, computer simulations, and new analyses of 113 community food webs, we show that, in nature and in theory, the larger the number of trophic species in a web, the larger the probability that the dimension of a community's trophic-niche space exceeds one. Equivalently, the larger the number of species in a web, the smaller the probability that it is an interval web.

* Permanent address: Institute of Mathematics, Adam Mickiewicz University, Matejki 48/49, (60-769) Poznań, Poland.

In addition to intervality (formally defined below), the overlaps among the diets or among the consumers of organisms in natural communities may possess another property (also defined below) called *triangulation* (Sugihara 1982). Again on the basis of mathematical calculations, computer simulations, and new analyses of 113 community food webs, we show that the larger the number of trophic species in a web, the smaller the probability that either the overlap graph or the resource graph of the web is triangulated. The mathematical calculations and computer simulations use a stochastic model of community food webs called the *cascade model* (Cohen and Newman 1985).

The remainder of this introduction gives further details on the background of this work. The terms used in this paper are defined, including community food web, trophic species, trophic link, consumer or niche overlap graph, resource or common-enemy graph, interval graph, interval web, link-species scaling law, and triangulated web. None of these terms is new; readers familiar with theoretical developments in food webs over the last decade could jump directly to the section on intervality. There, the data and theory on the frequency of intervality are described and compared. The description of theoretical results is meant to be intelligible to those who are willing to deal with quantitative concepts but are not interested in the details of proofs, which are provided in the Appendix. The following section compares the observed and predicted frequency of webs with triangulated overlap graphs and triangulated resource graphs. The final section summarizes the results and relates them to previous work. In the Appendix, we analyze mathematically the cascade model's implications for overlap and resource graphs.

Background

The ecological niche of a species has been defined as "a region of hyperspace, every point of which corresponds to a set of values of the variables permitting the organism to exist" (Hutchinson 1965, p. 32). In Hutchinson's usage, and here, *dimension* refers to the minimum number of variables needed to describe the niche and should not be confused with the physical dimension (e.g., flat, or two-dimensional, vs. solid, or three-dimensional) of a habitat (Silvert 1984, pp. 158–161; Briand and Cohen 1987). Hutchinson's definition raises several questions. What is the minimum number of variables required to describe the factors that influence species in a community? Is the dimension the same or different in different communities?

Food webs offer information about the number of *trophic* dimensions in the niches of species in a community (Cohen 1977, 1978). If two species eat a common food species, then their niches must overlap along the trophic dimensions; otherwise, the two consumers would not have access to the same food. If the dietary overlaps among consumers in a community can be described by the overlaps among intervals of a single variable, the web of the community is said to be an *interval* web and to have the property of *intervality*. If intervals of more than one variable are required to describe the dietary overlaps among consumers in a community, the web is said to be a *non-interval* web.

In the first collection of webs assembled to investigate the trophic dimension of

ecological niches, 22 or 23 of 30 webs were found to be interval (Cohen 1977). The exact number (22 or 23) depended on how the data in the web were edited. The observed numbers of interval webs exceeded markedly the numbers of interval webs predicted by seven simple models of food webs (Cohen 1978; Cohen et al. 1979). These findings provoked further analyses of the available data (see, e.g., MacDonald 1979; Critchlow and Stearns 1982; Pimm 1982; Sugihara 1982; Yodzis 1982, 1984). We discuss these analyses later.

Two recent changes now make it opportune to reexamine the question of intervality. First, more data are available. Second, a better food-web model is available, and can be analyzed.

As for data, the number of webs from the original study (Cohen 1977) is small. Sugihara analyzed Briand's collection of 40 webs (including 13 of those assembled in Cohen 1978) and reached conclusions consistent with those of the first study (Cohen 1977). Briand has now assembled and edited 113 community food webs (published in full in Cohen et al. 1990) and has kindly informed us which of these 113 webs show intervality. Other aspects of these webs have been analyzed elsewhere (Cohen et al. 1986; Briand and Cohen 1987).

The earlier models considered (Cohen 1977, 1978) were constructed ad hoc to match the mean number of dietary overlaps. Some of those models also matched the variance of the number of dietary overlaps. Recently, a better food-web model, the cascade model, has been discovered. The term "cascade" used here refers to a specific formal model (proposed in Cohen and Newman 1985) described below; it should not be confused with other uses of the term, for example, by Carpenter et al. (1985). The cascade model describes qualitatively and quantitatively the numbers of top, intermediate, and basal trophic species and the numbers of basal-intermediate, basal-top, intermediate-intermediate, and intermediate-top trophic links, when all food webs are considered together (Cohen and Newman 1985) or individually (Cohen et al. 1985). The cascade model also describes the numbers of food chains of each length (Cohen et al. 1986) and explains Hutchinson's (1959) observation that food chains are typically much shorter than the number of species in a web (Newman and Cohen 1986). It is natural to ask (as in Cohen and Newman 1985, p. 460; Cohen et al. 1986, p. 350) whether the cascade model can account for the observed frequencies of intervality and triangulation. (For further background on food webs, see Pimm 1982; DeAngelis et al. 1983; MacDonald 1983.)

Terminology

A food web is a guide to who eats whom in a community. More formally, a *food web* is a set of kinds of organisms and a relation that shows which kinds of organisms, if any, each kind of organism in the set eats. A *community food web* is a food web obtained by picking, within a habitat or set of habitats, a set of kinds of organisms on the basis of taxonomy, size, location, or other criteria, without prior regard to the eating relations among the organisms (Cohen 1978, pp. 20–21). Hereafter, "web" means "community food web."

Unless otherwise specified, a "species" here means a *trophic species*, that is, a class of organisms that consume the same kinds of organisms and are consumed

by the same kinds of organisms (Sugihara 1982, p. 19; Briand and Cohen 1984). A trophic species may result from lumping together kinds of organisms that were identified as separate by a reporting ecologist but were recorded as having the same sets of prey and the same sets of consumers. A trophic species bears no necessary relationship to a biological species. Yodzis (1982, p. 568) introduced the term "trophic species," but the exact sense in which it is used here is that of Sugihara's (1982) "trophic equivalence" or Briand and Cohen's (1984) "trophic species." A *predator* or *consumer* is a species that eats at least one species in the web. A *prey* is a species that is eaten by at least one species in the web.

By a *link*, we mean any reported feeding or trophic relation between two species in a web. Observers use various criteria to decide how much feeding justifies the reporting of a link and how much failure to observe feeding justifies reporting the absence of a link (Cohen and Briand 1984).

A web may be represented in two equivalent ways: by a directed graph (or digraph) (Harary 1961; Gallopín 1972) or by a predation matrix. A good drawing of the digraph of a web is easier to comprehend visually, but a predation matrix is less prone to error and facilitates the communication of quantitative information about the web.

In the representation of a web by a digraph, the vertices of the digraph correspond to the set of species in the web. We sometimes use the words "species" and "vertex" interchangeably. There is an arrow, directed edge, arc, or link from vertex i to vertex j in the digraph if and only if species j feeds on species i , that is, if food flows from species i to species j . Though often present in nature, cannibalism (i.e., a link from a vertex to itself) was systematically excluded from our data because of the uneven quality of the reporting of cannibalism (Cohen and Newman 1985). Sometimes we use "web" to mean a digraph that represents a web.

To describe the representation of a web by a predation matrix, let S denote the total number of species (vertices) and L the total number of links. The predation matrix \mathbf{A} of a web (or of any digraph) is an $S \times S$ matrix in which the element a_{ij} in row i and column j equals one if species i is eaten by species j and equals zero if species i is not eaten by species j . The matrix \mathbf{A} has L nonzero elements and $S^2 - L$ elements equal to zero.

Instead of using an entry of one to show that j eats i , some ecologists record an estimate of the quantity of i that j eats in row i and column j of a predation matrix. Here, we always assume that nonzero matrix elements equal one.

The dietary overlaps of the consumers in a web are described by an *overlap graph*, short for "trophic-niche overlap graph," which is constructed as follows (Cohen 1977). Given the web W (whether W is represented as a digraph or a predation matrix), the vertices of the overlap graph $G(W)$ are the same as those of W , that is, one vertex for each species in the community. In $G(W)$, there is an undirected edge between distinct vertices i and j (representing an overlap between the diets of species i and species j) if and only if there exists some third vertex k such that, in W , i eats k and j eats k . Thus, two vertices are joined by an edge in $G(W)$ if there are arrows in W from k to i and from k to j , for at least one k , or if at least one row of \mathbf{A} has elements equal to one in both column i and column j . The overlap graph of a web was originally called the competition graph (Cohen

1968), a name still used by graph theorists, and has also been called the consumer graph (MacDonald 1983, p. 32).

The *resource graph*, in the terminology of Sugihara (1982), describes which prey share a common predator. The vertices of the resource graph $H(W)$ are the same as those of the web W . In $H(W)$, there is an undirected edge between distinct vertices i and j if and only if there exists some third vertex k such that, in W , k eats i and k eats j . Thus, two vertices are joined by an edge in $H(W)$ if there are arrows in W from i to k and from j to k , for at least one k , or if at least one column of \mathbf{A} has elements equal to one in both row i and row j .

The resource graph of a web W is the dual of the overlap graph of W , in the sense that the resource graph equals the overlap graph of the web W^* obtained from W by reversing the direction of every link in W ; that is, $H(W) = G(W^*)$. The resource graph was simultaneously and independently invented by Sugihara (1982) and by Lundgren and Maybee (1985, in a paper prepared for a 1982 conference), who called it the "common enemy" graph. Independently, and before either of these graph-theoretic constructions, Holt (1977) introduced the notion that two species are in "apparent competition" if there is a consumer that preys on both of them and if a change in the abundance of one species induces a numerical response in the other. The resource graph presents necessary but not sufficient conditions for the relation of apparent competition in a community.

Many other graphs can be constructed from a web (Sugihara 1982; Roberts, in press; C. Cable, K. Jones, J. Lundgren, and S. Seager, MS). We discuss primarily the overlap graph and, to a lesser extent, the resource graph.

A graph (with undirected edges) is said to be an *interval graph* whenever, for each vertex of the graph, there exists an open interval of the real line such that there is an edge between any two vertices if and only if the two corresponding intervals intersect, that is, overlap. In an interval graph, it is possible to find an interval of the real line corresponding to each vertex of the graph, and the connections among the vertices are exactly represented by the overlaps among the intervals of the line.

A web W is said to be interval if its overlap graph $G(W)$ is an interval graph (Cohen 1977, 1978). In an interval web, the dimension of trophic-niche space could be one, because the range of variation in the diet of each consumer could be identified with an interval of the real line (e.g., the range of sizes of food eaten by a consumer), and overlaps among diets of consumers in the web would correspond to overlaps of the intervals on the real line. Lumping trophically equivalent kinds of organisms into trophic species has no effect on whether a web is interval: an unlumped web is interval if and only if the corresponding lumped web is interval.

The *link-species scaling law* is the name given (in Cohen and Briand 1984) to the empirical observation that in a scatterplot of species and links, with one data point for each web and species on the abscissa, the points are reasonably well described by a straight line passing through the origin and having a slope of nearly 2. Thus, independent of the scale (or number of species) of a web, the ratio of links to species is about 2. This observation, originally based on 62 webs, was subsequently confirmed (Cohen et al. 1986) with the 113 webs used here.

Substantively equivalent but superficially different forms of the link-species

scaling law were discovered at least twice before it was named (Cohen and Briand 1984). First, MacDonald (1979, p. 586) showed that the ratio of links to species (using the species as originally reported, not using trophic species) was 1.88 ± 0.27 (sample mean \pm fractional root-mean-square deviation) for 30 webs (assembled in Cohen 1978) and that community webs and sink webs did not have significantly different ratios (for the definition of a sink web, see Cohen 1978; MacDonald 1979). Second, Rejmánek and Starý (1979) plotted $L/[S(S - 1)/2]$, a quantity they called the *connectance*, as a function of S for plant-insect-parasitoid webs, one data point for each web. They found that the points fell around a hyperbolic curve of the form $4/S$. This is equivalent (as pointed out in Cohen and Briand 1984), when $(S - 1)/S$ approximates one, to $L = 2S$. This hyperbolic form of the link-species scaling law has been confirmed by Pimm (1982) and Auerbach (1984).

INTERVALITY

Data

The sources and principal characteristics of the 113 webs analyzed here have been presented already (Cohen et al. 1986; Briand and Cohen 1987). These webs come from 89 distinct published studies and 2 unpublished studies. They cover most of the world's biomes. There are 55 continental (23 terrestrial and 32 aquatic), 45 coastal, and 13 oceanic webs, ranging from arctic to antarctic regions. Only webs partially defined, presented too sketchily, or based on information explicitly drawn from different locations were excluded from this collection. The webs were not screened by rejection of outliers or by any other statistical procedure based on the data. Only obvious biological errors were amended in editing the data.

A few minor corrections of previously published numbers of species and links are required. The original numbers of species and links for web number 37 (from Cohen et al. 1986) were corrected in a later paper (Briand and Cohen 1987); the corrected values are used here. In webs numbered 6, 7, 24, 45, 51, 65, and 93, the possibility of lumping two consumers into a single trophic species was overlooked (Briand and Cohen 1987). Hence, the correct number of trophic species for these webs is one less than the number originally given, and the correct number of trophic links is, respectively, 2, 3, 2, 3, 3, 5, and 7 fewer than published (Briand and Cohen 1987). In calculating these values of species and links in the webs taken from Cohen (1978), matrix elements reported as -1 are replaced by 1 and matrix elements reported as -2 are replaced by 0.

According to F. Briand (pers. comm.), all but 16 of the 113 webs have interval overlap graphs. The non-interval webs have serial numbers 3, 6, 18, 20, 22, 26, 27, 33, 39, 41, 60, 67, 98, 99, 100, and 106. We have not repeated his calculation.

The proportion of all webs that are interval webs is $97/113 = 0.86$. This proportion is higher than the proportion of interval webs among the community webs in the original collection (Cohen 1977), namely, $9/14 = 0.64$ or $8/14 = 0.57$, depending on the version of the webs used. Using the 40 webs collected by Briand (1983) (which included 13 of the community webs in Cohen 1978), Sugihara (1982,

TABLE 1

OBSERVED RELATIVE FREQUENCY OF INTERVAL OVERLAP GRAPHS AND OF TRIANGULATED OVERLAP AND RESOURCE GRAPHS IN 113 COMMUNITY FOOD WEBS AS A FUNCTION OF THE NUMBER OF SPECIES

NO. OF SPECIES	NO. OF WEBS	FRACTION OF WEBS THAT ARE INTERVAL	FRACTION OF GRAPHS THAT ARE TRIANGULATED	
			Overlap	Resource
SPECIES DIVIDED INTO FOUR INTERVALS OF NEARLY EQUAL LENGTH				
3-14	56	1	1	1
15-24	40	0.775	0.975	0.875
25-34	15	0.667	0.800	0.800
35-48	2	0	0	0.500
SPECIES DIVIDED INTO FOUR INTERVALS OF NEARLY EQUAL FREQUENCY				
3-11	28	1	1	1
11-14	28	1	1	1
15-21	28	0.857	1	0.929
22-48	29	0.586	0.793	0.759

NOTE.—Presence or absence of intervality was computed by F. Briand. We computed the presence or absence of triangulation in the overlap and resource graphs from predation matrices furnished by Briand.

chap. 4) identified 73 connected components with more than one species and found that only 10 of these 73 had overlap graphs that were not interval. The proportion of interval webs in Sugihara's collection of components is $63/73 = 0.86$. The 40 webs of Briand (1983) are among the 113 webs analyzed here, and a web is interval if and only if its components are interval; thus, Sugihara's proportion of intervality and the proportion just found here are not independent. However, excluding the first 40 webs of Briand's collection (those in Briand 1983 and Sugihara 1982), only 7 of the remaining 73 ($113 - 40$) complete webs (not components, as in Sugihara 1982) failed to be interval. The proportion of intervality among these 73 webs, namely, $66/73 = 0.90$, is independent of the proportion of intervality among the 73 components studied by Sugihara (1982). Thus, in this collection of 113 webs, the proportion of webs that are interval is as high as, or higher than, the proportion of interval webs observed previously.

Because of the large number of webs now available, it is possible to examine how the proportion of intervality co-varies with other characteristics of webs. The most fundamental characteristic, which is examined here, is the number S of species. All webs with S of 16 or fewer are interval. Of the five webs with the largest numbers of species (ranging from 32 to 48 species), none is interval. When the observed range in the variation of S , from 3 to 48, is divided into four nearly equal intervals, the fraction of interval webs declines steadily from one among webs with 3 to 14 species to zero among webs with 35 to 48 species (table 1). However, there are only two webs with 35 to 48 species. When the frequency distribution of S is divided by quartiles, so that each group contains, as nearly as possible, one-quarter of all the webs, the fraction of interval webs again declines steadily from one among webs with 3 to 11 species to 0.59 among webs with 22 to 48 species. In summary, the fraction of webs that are interval is strongly associ-

ated with the number of species in the webs, declining from one for small webs toward zero for large webs.

Though quantitative documentation of this finding seems to be new, hints of it appeared earlier. For example, webs that incorporate multiple habitats were found to be much less likely to be interval than webs from single habitats (Cohen 1978, p. 40); multiple-habitat webs also tend to have more species. More explicitly, MacDonald remarked that “[t]he non-interval community webs . . . are the webs with the largest” numbers of species (1979, p. 586). In neither case (Cohen 1978; MacDonald 1979) did the authors analyze the relation between species number and intervality any further, empirically or theoretically.

Our empirical finding that intervality is less frequent among larger webs is consistent with data presented by Sugihara (1982, pp. 73–74, table 4.1). The numbers of consumers in his 73 components of overlap graphs range from 2 to 34 species. According to our tabulation of his data, of the 52 component webs with 2 to 10 species, 50 are interval (96%); of the 14 component webs with 11 to 14 species, 12 are interval (86%); and of the 7 component webs with 15 to 34 species, 1 is interval (14%).

Theory

This section describes the cascade model and its predictions regarding the probability that a web is interval.

The cascade model assumes that species in a community are ordered in a cascade, or hierarchy, such that any species can consume only those species below it in the ordering and can be consumed only by those species above it. Operationally, if there are S species in the web, the cascade model assumes a labeling of the species from 1 to S in such a way that whenever a species labeled i is eaten by a species labeled j , then i is smaller than j . This assumption excludes the possibility of trophic cycles, for example, cases in which i eats j and j eats i . Moreover, the cascade model assumes that for any two species i and j with i smaller than j , the probability that j actually eats i is p , and whether j eats i is statistically independent of all other eating relations in the web. The positive probability p is independent of the particular pair of species i and j . When webs with different total numbers of species, S , are compared, the cascade model assumes that p depends inversely on S according to $p = c/S$, where c is a positive constant independent of S .

In summary, the cascade model assumes (1) ordering, the prior existence of a labeling or cascade of species that limits the possible feeding relations; (2) equiprobability, a constant probability of a link between any two species for which a link is possible; (3) independence between the existence of a link for any given pair of species and the existence of a link for any other pair of species; and (4) reciprocal scaling, the probability that a link between any pair of species for which a link is possible depends on the number of species in the web, S , according to c/S .

Under these assumptions, the probability of a link, p , is just the expected or average value of the connectance defined by Rejmánek and Starý (1979): $p = E\{L/[S(S - 1)/2]\}$.

We calculated explicit formulas for the probability P that a web W is interval—

that is, the probability that the overlap graph $G(W)$ of W is an interval graph—for extremely small S and extremely large S (Appendix, theorem 5). The probability P that a web is interval depends on, and should not be confused with, the probability p of a link between any two species i, j with $i < j$ in the web.

If $S = 3, 4,$ or 5 , then $P = 1$. If $S = 6$ or $S = 7$, a lower bound on P is the difference between 1 and a sum of high powers of p (the link probability) times high powers of $1 - p$ (see the Appendix). Because the product of high powers of p times high powers of $1 - p$ must be small, one expects (and numerical results below confirm) this lower bound on P to be very close to one. Thus, for low values of S , the probability P that a web is interval is one or close to one.

At the other extreme, the larger S gets, the closer P gets to $\exp(-\lambda)$ where $\lambda \doteq 0.0025[2L/(S - 1)]^9 S$ (see the Appendix, theorem 5). According to the cascade model, the expected number of links in a web is $pS(S - 1)/2 = c(S - 1)/2$; thus, the average of $2L/(S - 1)$ is just c . The best current estimate of c , based on aggregate data for all webs, is approximately 4. If we replace $2L/(S - 1)$ by 4 in the expression for λ , we obtain approximately $\lambda = 660S$. Thus, for average webs according to the cascade model, P is expected to decline exponentially fast with increasing S , and the coefficient of S in the exponent is large, in excess of 660. Hence, for large S , the cascade model predicts a frequency of intervality near zero.

These are the principal results of the Appendix about the probability that a web is interval. In addition, the Appendix establishes other important structural properties predicted by the cascade model for the overlap graphs of large webs. The cascade model predicts that the overlap graph should contain a complete subgraph on n vertices, for any finite n , with probability one as S becomes large. The cascade model predicts that the overlap graph should contain an induced tree on n vertices, for any finite n , with probability one as S becomes large. The probability that the overlap graph is a unit-interval graph approaches zero as S becomes large.

The section on triangulation reports simulations that establish an upper bound on the probability that a web is interval when S is 10, 20, 30, 40, and 50 species. These simulations establish that the probability of intervality predicted by the cascade model is essentially zero by the time S is as large as 40.

Because of the duality between the overlap graph and the resource graph, with a corresponding duality in the probability distribution of edges according to the cascade model (see the Appendix), all the preceding analytic and numerical results in this section remain valid if “overlap graph” is replaced by “resource graph.”

Confronting Data and Theory

This section compares the data on intervality with the cascade model’s quantitative predictions about the probability that a web is interval.

To do so, it is necessary first to estimate either of the parameters $p = c/S$ or $c = pS$ of the cascade model. The parameters may be estimated in two ways: using data on all webs simultaneously (Cohen and Newman 1985; Cohen et al. 1986) and using data from each web separately (Cohen et al. 1985, 1986).

Using data on all webs simultaneously, c is twice the estimated slope of a

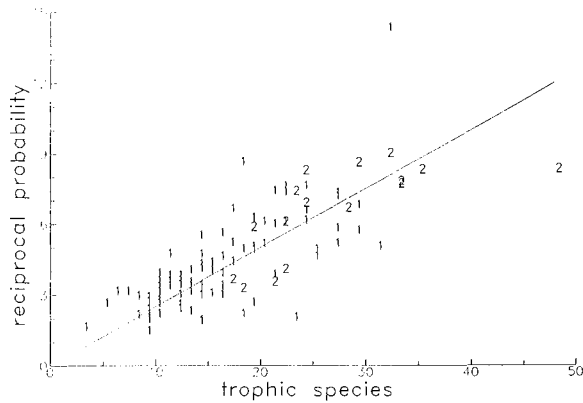


FIG. 1.—Reciprocal of the link probability or reciprocal of connectance as a function of the number of species in 113 community food webs. If S is the number of trophic species and L is the number of trophic links in a web, the ordinate is $S(S - 1)/(2L)$ and the abscissa is S . 1, The web is interval; 2, the web is not interval. *Solid line*, The plot of $S/4$ as a function of S .

straight line through the origin fitted to the data points (S, L) , where L is the number of links in a web with S species. In the 113 webs analyzed here, that slope is 1.99 ± 0.07 (standard error); thus, c is very nearly 4 (Cohen et al. 1986, p. 335). With this value of c , the cascade model makes sense only for webs with S of 4 or more, since by definition $p \leq 1$.

Using data from a single web with S species and L links, a reasonable estimate of p is $L/[S(S - 1)/2]$, which is the connectance; the numerator is the observed number of feeding relations, and the denominator is the number of possible feeding relations given the assumption of ordering. (Estimating p by the connectance $L/[S(S - 1)/2]$ overlooks the omission of isolated species from the data. A more complex estimate [Cohen et al. 1985, pp. 460–461] allows for the omission of isolated species. Since the number of isolated species is small, the error introduced by estimating p from connectance is also small.)

As a preliminary, we now check the cascade model's assumption that the link probability, p , depends on the number of species, S , according to c/S . This assumption implies that if the connectance or p is estimated separately for each web, then the points $(S, 1/p)$ should fall around the straight line $S/c = S/4$ derived from the aggregated data. The agreement in figure 1 between the individual points and the predicted straight line justifies further testing of the cascade model. Each web in the figure is represented by the symbol "1" (for one dimension) if the web is interval or by the symbol "2" (for two or more dimensions) if the web is not interval.

When the link probability, p , is estimated separately for each web, the cascade model predicts a probability of intervality $P = 1$ for $S = 3, 4, \text{ or } 5$, as already mentioned, $P \geq 0.9999$ for $S = 6$, and $P \geq 0.9986$ for $S = 7$. All webs with $S \leq 16$ (the webs plotted in the left third of fig. 1) are interval. Thus, for very small numbers of species, S , the data are consistent with the predicted probability P that a web is interval.

For intermediate numbers of species, the observed fraction of webs that are interval declines as shown in table 1. An upper bound on the predicted probability that a web is interval is given by the predicted probability that a web is triangulated (see the next section). Table 2 reports estimates of the probability of triangulation for $S = 10, 20, 30, 40,$ and 50 , based on 100 simulations for each value of S . The predicted probability of triangulation (table 2), and therefore the predicted probability of intervality, appears to decline with increasing S more rapidly than does the observed frequency of intervality. That is, there is still an excess frequency of intervality not explained by the cascade model. But the cascade model does predict correctly the existence and the location of a range of S over which the probability of intervality declines smoothly from near 1 to near 0.

For very large S , the cascade model predicts asymptotically a probability of intervality, P , lying between $\exp(-39)$ and $\exp(-3.2 \times 10^8)$, according to the theory developed in the Appendix. In these calculations, the link probability, p , is estimated separately for each web. The simulations in table 2 suggest that the asymptotic theory becomes relevant when the number of species is between 30 and 40. Consistent with these analytic and computational predictions, the five largest webs, with S ranging from 32 to 48, are all non-interval.

Overall, there is good qualitative agreement, and reasonable quantitative agreement, between the observed frequency of interval webs and the frequency of interval webs predicted by the cascade model. For intermediate numbers of species, more interval webs are observed than are predicted by the simulations of the cascade model. It remains to be determined whether this excess identifies a deficiency of the cascade model or a deficiency of the data on trophic links or both.

An upper bound on the fraction of webs with interval resource graphs is given by the fraction of webs with triangulated resource graphs. The relative frequencies of triangulated resource graphs are given in table 1 and are discussed in the next section.

TRIANGULATION

A web is said to be triangulated if its overlap graph is triangulated. A graph is triangulated if it has no induced cycles of four or more edges; that is, whenever four or more vertices in the overlap graph make a cycle, there is an edge that cuts across the cycle, reducing the cycle to a composition of triangles. Lekkerkerker and Boland (1962) showed that a graph is interval if and only if it is triangulated and it contains no asteroidal triples. Thus, the probability that a graph is triangulated is an upper bound on the probability that it is interval.

Sugihara (1982) showed that the frequency of intervality in simulated webs could largely be accounted for by requiring the overlap graphs to be triangulated. As part of a more extensive theory that is not reviewed here, he proposed that triangulation is a more fundamental property of webs than is intervality.

Sugihara (1982, p. 118) simulated a dynamic Lotka-Volterra model with random interaction coefficients and allowed species to become extinct until the hypothetical community was "feasible." His model communities started with 15 species,

and the final number of species ranged from 6 to 9. In 18 of 20 simulations, the final communities had triangulated niche overlap graphs. Sugihara noted that "the high frequency of rigidity [equivalent to triangulation] may simply be an artifact of generating relatively small final communities," that is, communities with a small number of species. Though it was not Sugihara's preferred interpretation of the high frequency of triangulation, this possibility is consistent with the following analyses of data and the cascade model.

Data

We determined the triangulation of the overlap graph and the resource graph of each of the 113 webs in Briand's collection by constructing these graphs from the predation matrices (Cohen et al. 1990). The most efficient algorithms to determine whether a graph is triangulated are LEX P and FILL of Rose et al. (1976), based on lexicographic breadth-first search. We programmed their algorithms using a description by Booth (1975, p. 126) and verified the performance of our program in numerous examples.

All of the webs with non-triangulated overlap graphs (numbers 6, 18, 33, 39, 60, 99, 100, and 106) are also non-interval, as is logically required by the theorem of Lekkerkerker and Boland (1962). This consistency provides a check, albeit weak, on our independent computations. Nine webs have non-triangulated resource graphs (numbers 6, 18, 33, 60, 63, 67, 69, 99, and 100).

Sugihara (pers. comm.) provided proposed corrections to several of Briand's predation matrices. When these corrections are made, webs 6 and 18 have triangulated overlap graphs. This change does not alter the general trends in the data. For consistency, we use the predation matrices furnished by Briand.

Table 1 shows the relative frequency of triangulated overlap graphs and triangulated resource graphs in 113 community food webs as a function of the number of species. For both overlap and resource graphs, the frequency of triangulation declines from 1 for the smallest observed webs to much smaller values for the largest observed webs. All 4 webs of more than 32 species have non-triangulated overlap graphs, and 2 of those 4 webs have non-triangulated resource graphs.

Theory

The predictions of the cascade model regarding triangulation are obtained by mathematical analysis (see the Appendix) and simulation. Analytically, the probability that an overlap or resource graph is triangulated is one whenever the number of species in the web is five or less, and is very close to one for six and for seven species. For large numbers of species and a link probability $p = 4/S$, the cascade model predicts asymptotically that the probability that a resource or overlap graph is triangulated is very near zero (Appendix, theorem 7). For intermediate numbers of species (table 2), the simulated probability of triangulation according to the cascade model declines rapidly with an increasing number of species, S .

Confronting Data and Theory

The cascade model's predictions are consistent with observation for very small numbers of species and for large numbers of species. For intermediate numbers of

TABLE 2

SIMULATED RELATIVE FREQUENCY OF TRIANGULATED OVERLAP GRAPHS OR RESOURCE GRAPHS PREDICTED BY THE CASCADE MODEL, ACCORDING TO 100 SIMULATIONS FOR EACH NUMBER OF SPECIES

No. of Species	Fraction of Triangulated Overlap or Resource Graphs	Lower 95% Confidence Limit	Upper 95% Confidence Limit
10	0.91	0.85	0.97
20	0.26	0.17	0.35
30	0.03	0	0.07
40	0	0	0.005
50	0	0	0.005

NOTE.—The 95% confidence interval incorporates the correction for continuity, and negative lower confidence limits for 30, 40, and 50 species were set to zero.

species, the simulated probability of triangulation appears to decline with increasing numbers of species more rapidly than does the observed relative frequency of triangulation. But the cascade model does predict correctly the existence and location of a range of S over which the probability of triangulation declines smoothly from near one to near zero. The difference between the observed and simulated relative frequencies of triangulation for intermediate numbers of species may be due to imperfections of the data or of the cascade model.

DISCUSSION AND CONCLUSIONS

Major Findings

The main accomplishments of this paper are three. First, while confirming empirically the overall high relative frequencies of interval and triangulated overlap graphs found previously, we observe that the relative frequencies of interval and triangulated webs are strongly associated with web size, as measured by the number of species. All overlap graphs of webs with small numbers of species (16 or fewer in our data) are observed to be interval and triangulated, and no overlap graphs of webs with large numbers of species (33 or greater in our data) are observed to be interval or triangulated. Between these extremes, a steady downward trend is observed in the fraction of interval and triangulated overlap graphs. The pattern of triangulated resource graphs is similar. Broadly, the larger the number of species in a community, the less likely it is that a single dimension suffices to describe the community's trophic-niche space, and the less likely it is that there are no "holes" in the overlap graph or resource graph.

There are two ways to look at this finding. One possibility is that webs with small numbers of species come from especially simple communities; the simplicity gives the communities a small number of species as well as a very small number of dimensions of trophic-niche space, namely, just one. Another possibility, which we favor, is that most webs with small numbers of species are incomplete descrip-

tions of real communities. When communities are described in detail, reported webs contain larger numbers of species and are less likely to be interval and triangulated.

This interpretation is consistent with the empirical finding of Schoener that the "separation [of species in niche space] appears generally to be multidimensional" (1974, p. 29), although he recognized that "the dimensions that ecologists recognize are rarely independent" (p. 32). In 81 studies of niche relations in groups of three or more species, when the dimensions originally reported are classified into the broad categories of food, space, and time, most niches are separated by two dimensions (Schoener 1974). (Other studies of the dimension of ecological niches were reviewed by Cohen [1978, pp. 97–100].)

This interpretation leads to a concrete prediction. If webs reported in the future are consistent with the trends in the existing data and if they are reported in greater detail than are most present webs, they will display much lower relative frequencies of intervality and triangulation than do the existing webs with small numbers of species, even in the communities with webs currently reported as interval or triangulated. As the fidelity and detail of the description of communities improve and the numbers of species in reported webs increase, we expect the relative frequencies of intervality and triangulation to decline.

Second, we calculate the predictions of the cascade model about the probabilities that the overlap graph and resource graph are interval and triangulated, for both very small and very large numbers of species. For very small webs, the predicted probability that either graph is interval or triangulated approximates one. For a web with a very large number of species, S , and with approximately twice as many links as species (in accordance with the empirical link-species scaling law), the predicted probability that either graph is interval falls as approximately $\exp(-660S)$, that is, extremely rapidly with increasing S . The predicted probability that either graph is triangulated also falls exponentially.

We do not know of any previous analytic (as opposed to numerical) calculations of the probability of interval or triangulated overlap or resource graphs starting from a model of webs. The calculations constitute nontrivial new mathematics.

Third, comparing data and theory, we show that the predictions of the cascade model account quantitatively for the observed relative frequencies of interval and triangulated overlap graphs and triangulated resource graphs for webs with 7 or fewer and 33 or more species. The cascade model also predicts correctly the existence and location of a range of numbers of species over which the relative frequencies of interval and triangulated overlap and resource graphs decline smoothly from near one to near zero. Our simulations of the cascade model reveal, however, that there are more interval and triangulated overlap graphs and more triangulated resource graphs observed than expected in webs with intermediate numbers of species. This difference may be due to imperfections of the data or of the model.

The cascade model's successful prediction of the existence and location (though not the exact rate) of declines in the relative frequencies of intervality and triangulation with increasing numbers of species suggests that the relative commonness or rarity of interval and triangulated webs may be a statistical conse-

quence of the general ecological processes posited in the hypotheses of the cascade model, rather than a consequence of special constraints (of whatever origin) acting directly on the dimension of trophic-niche space or the homological structure of the overlap graph or the resource graph.

Related Prior Work

There have been several previous attempts to explain the relative frequency of intervality. Six simple web models were simulated and found to predict fewer interval overlap graphs than were observed (Cohen 1978). The authors of another study (Cohen et al. 1979) calculated the probability that a random graph is interval when the random graph is constructed with an edge probability that is the same for every pair of vertices, that is, according to the classical model of Erdős and Rényi (1960). That model also failed to account for the observed frequency of intervality. (By contrast with the model of Erdős and Rényi, when the overlap graph is derived from the cascade model, the probability of a dietary overlap between two species, or of an edge between the corresponding vertices in the overlap graph, is much higher for two species high in the ordering than for two species low in the ordering.)

Critchlow and Stearns (1982) showed that the predation matrices of the real webs analyzed in an earlier study (Cohen 1978) were divided into block submatrices much more than were the simulated predation matrices generated by an earlier model (Cohen 1978, model 5) and that, in general, the real webs had fewer dietary overlaps (or edges in the overlap graph) than webs simulated according to the earlier model with the same number of predators, prey, and links. Critchlow and Stearns showed that both the deficit of block submatrices and the excess of dietary overlaps in the simulated webs helped to explain why the earlier model underpredicted the observed frequency of intervality.

Yodzis (1984) formulated assembly rules, based on energetic constraints, for the hypothetical construction of an ecosystem from species that arrive sequentially. These assembly rules generate model webs that describe well many structural features of 25 of the 28 webs from fluctuating environments in Briand's (1983) collection of 40 webs, and 3 of the 12 webs from constant environments in Briand's collection. In particular, when Yodzis' model describes well most other structural features of a real web, it also describes well the presence or absence of an interval overlap graph.

Yodzis reported his model's expected intervality for the 28 webs well described by his assembly rules (Yodzis 1984, p. 122, his table 1). For these webs, we graphed his expected intervality as a function of the observed number of trophic species for all the webs (graph not shown). We found Yodzis' expected intervality near one for the webs with the smallest number of species; a hint, amid much scatter, of a declining trend in Yodzis' expected intervality with an increasing number of species; and the smallest values of Yodzis' expected intervality for the webs with the largest number of species. Yodzis did not remark on this association between his expected intervality and the number of species in a web.

Yodzis' assembly rules provide an alternative explanation for the trend we have reported here in the frequency of intervality as a function of the number of

species. But this explanation may be limited to webs from fluctuating environments. By contrast, the cascade model deals equally well with webs from fluctuating and constant environments. Whereas Yodzis' assembly rules so far have been analyzed only by computer simulation, the cascade model is tractable to explicit analysis. In spite of (what we view as) the advantages of the cascade model, the parallels between its predictions and those of Yodzis' assembly rules suggest that it would be worthwhile in the future to determine whether there are deeper connections between the two models.

Sugihara (1982, p. 65) explained the high frequency of interval graphs in terms of different assembly rules that prevent the appearance of "homological holes" in communities. He considered the highly frequent, but not universal, appearance of intervality in real webs to be a consequence of a more fundamental requirement that real webs be triangulated. The data (table 1) indicate that larger webs are less likely to be interval and triangulated. If these trends are not an artifact of faulty data, then the absence of homological holes in the overlap graph is not a universal feature of food webs. An independent theory, such as the cascade model, is required to explain the frequencies of both intervality and triangulation.

The history of data and theory on the intervality and triangulation of the niche overlap graph may be caricatured simply. Initially, the high average proportion of interval webs came as a surprise and could not be explained by the available models (Cohen 1977, 1978). Subsequently, various explanations were offered for the high average proportion of intervality, including compartmentalization (Critchlow and Stearns 1982), energetic constraints on community assembly (Yodzis 1984), and triangularity (Sugihara 1982). Though, in retrospect, the data then available and some of these explanations hinted at a decline in the frequency of intervality with an increasing number of species, it seems fair to say that any such decline remained unremarked. The data presented here provide unambiguous evidence of a decline in the relative frequency of intervality and triangulation with increasing numbers of species. These data seem to us to weaken or obliterate the claim that trophic-niche overlap graphs and resource graphs are interval or triangulated (always or at a constant high frequency) regardless of the number of species in a web. The cascade model predicts accurately the existence of this decline in intervality and triangulation. The cascade model also predicts the range in the numbers of species where this decline occurs. However, the cascade model predicts that the relative frequencies of intervality and triangulation will decline more rapidly, with increasing numbers of species, than they actually do. Excess proportions of interval and triangulated overlap and resource graphs remain to be explained.

SUMMARY

We report new empirical and theoretical information about the dimension of trophic-niche space and the structure of food webs, as measured by the frequency of intervality and triangulation of overlap graphs and resource graphs in community food webs. Briand assembled and edited 113 community food webs, and informed us of which of those webs have interval trophic-niche overlap graphs. In

this collection of 113 webs, the overall proportion of webs that are interval is as high as, or higher than, the proportion of interval webs observed previously. However, the fraction of webs that are interval is strongly associated with the number of species in the webs. The fraction of interval webs declines from one for small webs (16 or fewer species) toward zero for large webs (33 or more species). According to new mathematical and numerical calculations presented here, the cascade model predicts, as observed, that the probability that a web is interval is near one for webs with fewer than 10 species, declines as the number of species increases from 10 to 30 or 40, and is very near zero for larger numbers of species. However, in the range of 10 to 40 species, the cascade model predicts a more rapid decline in the relative frequency of intervality than is observed.

Using the predation matrices of the same 113 webs, we determined which webs have triangulated overlap graphs and triangulated resource graphs. The empirical, mathematical, and computational results on the relative frequency of triangulation parallel those on intervality.

The broad ecological interpretation of our findings is that the larger the number of species in a community, the less likely it is that a single dimension suffices to describe the community's trophic-niche space and the less likely it is that there are no "homological holes" in the overlap graph and resource graph. Most reported webs with small numbers of species are incomplete descriptions of real communities. If future webs have larger numbers of species and are described in greater detail, we predict that those webs will have smaller relative frequencies of being interval and triangulated.

ACKNOWLEDGMENTS

For comments on earlier versions of the manuscript, we thank D. L. DeAngelis, T. Łuczak, C. M. Newman, S. Pimm, A. Ruciński, G. Sugihara, P. Yodzis, and the referees. We thank K. S. Booth for advice on computation. The Inter-Academy Exchange Program of the U.S. National Academy of Sciences and the Polish Academy of Sciences made possible J.E.C.'s attendance at the "Random Graphs '85" conference in Poznań, which led to this collaboration. This research was partially supported by National Science Foundation grants BSR 84-07461 and BSR 87-05047 and by the hospitality of Mr. and Mrs. William T. Golden.

APPENDIX

MATHEMATICAL ANALYSIS

Basic Concepts

The cascade model W_p assumes that the species (vertices) of a web may be labeled from 1 to S , with $S \geq 2$. If $i < j$, then j feeds on i (there is a link from i to j) with probability p , and j does not feed on i with probability $q = 1 - p$, independently for all $1 \leq i < j \leq S$. The probability that species j feeds on species i is 0 if $j \leq i$. The probability p is assumed to depend on S , such that $p = p(S) \rightarrow 0$ as $S \rightarrow \infty$.

By replacing each link of W_p by an undirected edge, one obtains the usual random-graph model G_p , that is, an undirected simple graph on the vertex set $\{1, 2, \dots, S\}$, in which each edge appears with probability p , independently of all other edges. A simple graph is one

that has neither loops nor multiple edges. The structure of G_p when p changes from 0 to 1 has been studied extensively since the fundamental paper of Erdős and Rényi (1960) (see, e.g., Bollobás 1985). The greatest discovery of Erdős and Rényi was that many important properties of graphs appear quite suddenly. We shall use such facts about G_p here.

We shall say that almost every G_p has property π if the probability that G_p has π tends to 1 as $S \rightarrow \infty$. If we pick a function $p = p(S)$, then, in many cases, either almost every graph G_p has property π or else almost every graph fails to have property π . More precisely, for many properties there is a *threshold function* $p^* = p^*(S)$ such that

$$\lim_{S \rightarrow \infty} P(G_p \text{ has property } \pi) = \begin{cases} 0 & \text{if } p/p^* \rightarrow 0, \\ 1 & \text{if } p/p^* \rightarrow \infty. \end{cases}$$

As examples, here are two facts from Erdős and Rényi (1960) that we use later.

Fact 1.—The threshold function that G_p contains a complete subgraph K_n on n vertices is $p^* = S^{-2/(n-1)}$.

Fact 2.—The threshold function that G_p contains a cycle on n vertices is $p^* = S^{-1}$ for any fixed $n \geq 3$.

If G is a simple graph on the vertices $V = V(G)$ and F is another simple graph on the vertices $V(F)$, we say that F is an induced subgraph of G if $V(F) \subset V(G)$ and if the edges of F contain all the possible edges from the edges of G ; that is, if $v_i, v_j \in V(F)$ and $\{v_i, v_j\}$ is an edge of G , then $\{v_i, v_j\}$ is an edge of F .

There are some properties of a random graph G_p that suddenly appear, then hold when p increases, and at some point suddenly disappear. For example, consider the property that G_p contains an induced cycle on a fixed number of vertices. By fact 2, such a cycle appears with probability 1 when $p = w(S)S^{-1}$, where $w(S) \rightarrow \infty$ (arbitrarily slowly) as $S \rightarrow \infty$. However, when p is very close to 1, then the cycle is no longer induced. Thus, in our investigations we focus on the *appearance function* of a given subgraph of G_p , which describes when such a subgraph first appears as p increases. Of course, when one considers subgraphs (but not induced subgraphs) of G_p , then the appearance function and the threshold function coincide.

The concepts of threshold and appearance functions also apply to the cascade model W_p and to the overlap graph $G(W_p)$, defined as follows (Cohen 1977, 1978).

The trophic-niche overlap graph $G(W_p)$ is defined as an undirected simple graph on the vertices of W_p . Two consumers are joined by an undirected edge when there is at least one prey that both consumers eat. That is, $\{v_j, v_k\}$ is an edge in $G(W_p)$ if and only if there exists some v_i in W_p such that both (v_i, v_j) and (v_i, v_k) are links in W_p .

Let G be a simple graph on the set of vertices $V = \{v_1, v_2, \dots, v_n\}$. G is an *interval graph* when there is a collection I_1, I_2, \dots, I_n of open, closed, or mixed intervals of the real line such that there is an edge between v_i and v_j , $i \neq j$, if and only if I_i and I_j overlap, that is, $I_i \cap I_j \neq \emptyset$. Thus, G is an interval graph if and only if G is the intersection graph of some family of intervals of the line. If each interval I_1, \dots, I_n has length equal to 1, then G is called a *unit-interval graph*.

Existence of Some Induced Subgraphs in $G(W_p)$

We now establish the appearance functions of induced subgraphs of various types in a random overlap graph $G(W_p)$. We find the appearance functions of the properties that $G(W_p)$ contains an induced tree, an induced cycle, and an induced asteroidal 1-triangle (see fig. A1). These subgraphs determine the intervality of $G(W_p)$ when S is large, which we examine in the following section.

We begin with the existence of a complete subgraph in a random overlap graph $G(W_p)$. There are two reasons for this. First, the threshold function for having a complete subgraph in $G(W_p)$ (which in this case is also the appearance function) is quite different from that in the usual random-graph model G_p (see fact 1). Second, all the proofs in this section rely on the so-called “second-moment method.” It is easiest to present this method in the case of

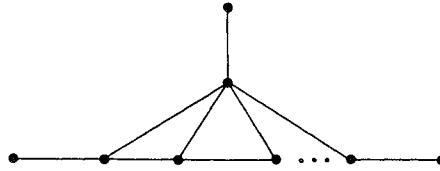


FIG. A1.—An asteroidal k -triangle with $k + 5$ vertices. (An asteroidal 1-triangle contains a single central triangle, each vertex of which is joined by an edge to one outlying vertex.) (From Cohen et al. 1990, p. 190, with permission of the publisher.)

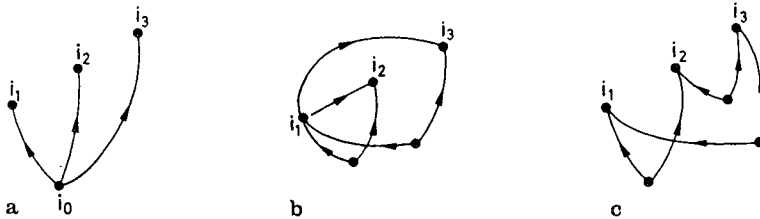


FIG. A2.—Three web configurations that produce the complete graph K_3 in the overlap graph. (From Cohen et al. 1990, p. 191, with permission of the publisher.)

complete subgraphs. Thus, we present first a rather detailed proof of the threshold function for the existence of a complete subgraph of $G(W_p)$ and then state the remaining results, indicating only the crucial points in their proofs.

Theorem 1 (complete subgraphs).—Let $n \geq 3$ be fixed. The threshold function of the property that $G(W_p)$ contains a complete subgraph K_n on any n vertices is $S^{-1-1/n}$; that is,

$$\lim_{S \rightarrow \infty} P[G(W_p) \supset K_n] = \begin{cases} 0 & \text{if } pS^{1+1/n} \rightarrow 0, \\ 1 & \text{if } pS^{1+1/n} \rightarrow \infty. \end{cases}$$

Proof.—Denote by X_n the number of all configurations in the cascade model W_p that produce complete subgraphs on n vertices in $G(W_p)$. As an example, figure A2 presents three types of configurations of W_p that correspond to K_3 in $G(W_p)$.

The graph in figure A2a is called a three-star with root i_0 . Generally, a subgraph of W_p on $n + 1$ vertices $i_0, i_1, i_2, \dots, i_n$ —where $1 \leq i_0 < i_1 < i_2 < \dots < i_n \leq S$, such that (i_0, i_k) is a link for every $k = 1, 2, \dots, n$ —will be called an n -star with root i_0 . Let Y_n stand for the number of all n -stars in W_p . Then, $X_n = Y_n + Z_n$, where Z_n is the number of configurations other than n -stars that produce a K_n in the overlap graph. (If we forget about the orientation of links, then all those configurations contain at least one cycle.) Elementary calculation shows that

$$E(Y_3) = \binom{S}{4} p^3 = O(S^4 p^3),$$

and

$$\begin{aligned} E(Z_3) &= \sum_{2 \leq i_1 < i_2 < i_3 \leq S} (i_1 - 1)(i_1 - 2)p^6 + \sum_{2 \leq i_1 < i_2 < i_3 \leq S} (i_1 - 1)(i_1 - 2)(i_2 - 4)p^6 \\ &= O(S^5 p^6) + O(S^6 p^6) \\ &= O(S^6 p^6). \end{aligned}$$

The first sum in $E(Z_3)$ enumerates the expected number of graphs of the form shown in figure A2*b*; the second sum refers to figure A2*c*. Similarly, for $n \geq 4$,

$$E(Y_n) = \binom{S}{n+1} p^n = O(S^{n+1} p^n),$$

and it is not hard to see that in a formula for the expectation of Z_n , the exponent of p is always greater than the exponent of S (only if $n \geq 4$). Consequently, $E(Z_n) = O(S^m p^k)$ for some $m \geq n + 2$ and $k > m$.

Now, let $p = p(S)$ be such that $pS^{1+1/n} \rightarrow 0$ as $S \rightarrow \infty$. Then, clearly,

$$E(X_n) = E(Y_n) + E(Z_n) = o(1).$$

(We could have proved that $E(Z_n) = o(1)$ from the threshold function for cycles in G_p , because each of these configurations contains a cycle [if we ignore orientation], and from fact 2 we know that there are no cycles in G_p when $pS \rightarrow 0$ as $S \rightarrow \infty$, which is satisfied under our assumption on p .) Since $P(X_n \geq 1) \leq E(X_n)$, it follows that, with probability approaching 1 as $S \rightarrow \infty$, the cascade model W_p contains no configurations producing a complete subgraph K_n in $G(W_p)$; that is, as $S \rightarrow \infty$,

$$P[G(W_p) \supset K_n] = P(X_n \geq 1) \rightarrow 0.$$

Now assume that $pS^{1+1/n} \rightarrow \infty$ as $S \rightarrow \infty$. We show that, under this assumption,

$$P(Y_n \geq 1) \rightarrow 1 \tag{A1}$$

as $S \rightarrow \infty$. Since

$$P(Y_n \geq 1) \leq P[G(W_p) \supset K_n],$$

it follows that, with probability tending to 1, a random overlap graph $G(W_p)$ contains at least one complete subgraph K_n . For $1 \leq i_0 < i_1 < \dots < i_n \leq S$, let S_i denote the indicator random variable of the event that there is in W_p an n -star \mathbf{i} on the vertices $\{i_0, i_1, \dots, i_n\}$ with i_0 as the root. Then,

$$\text{var } Y_n = \sum_{\mathbf{i}} \sum_{\mathbf{j}} \text{cov}(S_{\mathbf{i}}, S_{\mathbf{j}}),$$

where the summations are over all n -stars specified by \mathbf{i} and \mathbf{j} , respectively. If the stars \mathbf{i} and \mathbf{j} share exactly m links, $0 \leq m \leq n$, then

$$\text{cov}(S_{\mathbf{i}}, S_{\mathbf{j}}) \leq P(S_{\mathbf{i}} = 1, S_{\mathbf{j}} = 1) = p^{2n-m}.$$

If $m = 0$ and none of i_0, i_1, \dots, i_n coincides with any of j_0, j_1, \dots, j_n , then $S_{\mathbf{i}}$ and $S_{\mathbf{j}}$ are independent; thus, $\text{cov}(S_{\mathbf{i}}, S_{\mathbf{j}}) = 0$. Let Q_m be the number of ordered pairs (\mathbf{i}, \mathbf{j}) such that \mathbf{i} and \mathbf{j} share m links and at least one vertex. Then, for $m \geq 1$, clearly the roots i_0 and j_0 coincide and $Q_m \leq S^{2n+1-m}$, whereas for $m = 0$, $i_0 \neq j_0$ and $Q_0 \leq S^{2n+1}$. Consequently,

$$\text{var } Y_n \leq \sum_{m=0}^n (Sp)^{2n-m} S.$$

Thus, from Chebyshev's inequality,

$$\begin{aligned} P(Y_n = 0) &\leq \text{var}(Y_n)/E(Y_n)^2 \\ &= O\left[\sum_{m=0}^n (Sp)^{-m} S^{-1}\right] \\ &= o(1), \end{aligned}$$

since under the assumption on p , Sp can be expressed as $Sp = w(S)S^{-1/n}$, where $w(S)$ is a sequence tending to infinity as $S \rightarrow \infty$. Thus, we proved relation (A1).

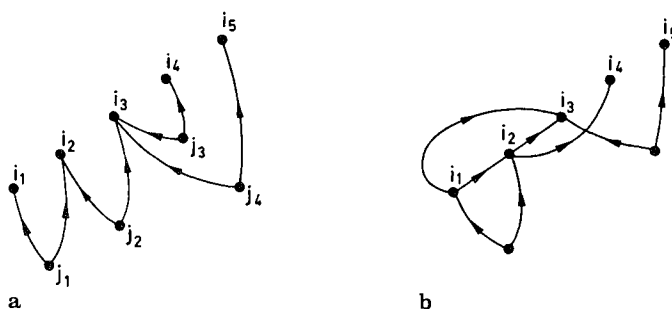


FIG. A3.—Two web configurations that produce the tree shown in figure A4 in the overlap graph. (From Cohen et al. 1990, p. 193, with permission of the publisher.)

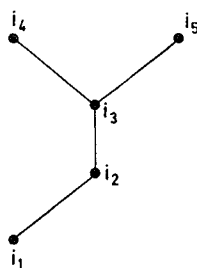


FIG. A4.—Tree in the overlap graph produced by the web configurations in figure A3. (From Cohen et al. 1990, p. 193, with permission of the publisher.)

Theorem 2 (induced trees).—Let $k \geq 2$ be fixed. The appearance function of an induced tree on k vertices in $G(W_p)$ is $S^{-(2k-1)/(2k-2)}$.

Proof.—If $G(W_p)$ contains an induced tree on vertices (consumers) i_1, i_2, \dots, i_k , where $2 \leq i_1 < i_2 < \dots < i_k \leq S$, then there must exist $k - 1$ vertices (prey species) j_1, j_2, \dots, j_{k-1} , where $j_1 < i_1$ and $j_{k-1} < i_k$, such that for every j_m ($m = 1, 2, \dots, k - 1$), there are exactly two links from j_m to two appropriately chosen vertices from $\{i_1, i_2, \dots, i_k\}$. (See fig. A3a.) Some of the consumers may at the same time be prey species. (See fig. A3b.) Figure A3 presents two examples of configurations in W_p that produce a tree in $G(W_p)$ as shown in figure A4.

Each configuration of the web W_p that produces an induced tree on k vertices in the overlap graph $G(W_p)$ must have exactly $2(k - 1)$ links. The configurations are of two types. In configurations of the first type, $\{i_1, i_2, \dots, i_{k-2}\} \cap \{j_1, j_2, \dots, j_{k-1}\} = \emptyset$; therefore, none of the vertices $\{i_1, i_2, \dots, i_{k-2}\}$ is a prey for two consumers from $\{i_2, \dots, i_k\}$. In configurations of the second type, some of the vertices i_1, i_2, \dots, i_{k-2} are at the same time consumers and prey. In the latter case, if we ignore the orientation of links, there is always a cycle in the configuration.

Assume that $p = p(S)$ such that, as $S \rightarrow \infty$,

$$pS^{(2k-1)/(2k-2)} \rightarrow 0. \tag{A2}$$

Since our p is of smaller order than S^{-1} , by fact 2 almost every G_p has no cycles and, consequently, almost every W_p has no configurations of the second type. Moreover, each configuration of the first type forms an induced tree of W_p in which there is no vertex lying below i_k and different from $\{i_1, i_2, \dots, i_{k-1}, j_1, j_2, \dots, j_{k-1}\}$ that is connected with exactly two vertices from $\{i_1, i_2, \dots, i_k\}$; such a vertex would destroy the property that the tree in

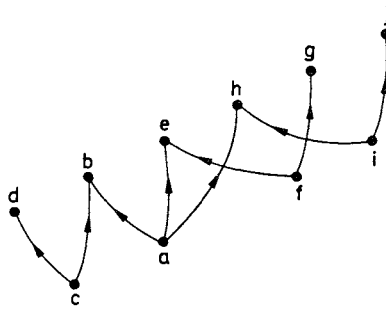


FIG. A5.—A web configuration that produces an asteroidal 1-triangle in the overlap graph. (From Cohen et al. 1990, p. 195, with permission of the publisher.)

$G(W_p)$ is induced. Thus, if T_k denotes the number of configurations of the first type, then

$$\begin{aligned} E(T_k) &= O\left[\sum_{2 \leq i_1 < i_2 < \dots < i_k \leq S} (i_k - 1)^{k-1} p^{2(k-1)}\right] \\ &= O[S^{2k-1} p^{2(k-1)}] \\ &= o(1). \end{aligned}$$

Consequently, under assumption (A2), the overlap graph $G(W_p)$ contains no induced tree on k vertices.

However, if the limit in assumption (A2) is infinity instead of zero, then $E(T_k) \rightarrow \infty$ as $S \rightarrow \infty$. Applying the same approach as in the preceding proof, it can be shown that $P(T_k \geq 1) \rightarrow 1$ as $S \rightarrow \infty$; that is, with probability tending to 1, $G(W_p)$ contains an induced tree on k vertices.

The next result shows that the appearance function of an induced cycle on m vertices in $G(W_p)$ is the same as the threshold function for an m -cycle in the usual random-graph model G_p if $m \geq 4$.

Theorem 3 (induced cycles).—Let $m \geq 4$ be fixed. The appearance function of an induced m -cycle in $G(W_p)$ is S^{-1} .

Proof.—Each configuration of W_p producing an induced m -cycle of $G(W_p)$ must contain exactly $2m$ links. As in the case of induced trees, the configurations most likely to occur are those in which none of vertices i_1, i_2, \dots, i_{m-2} is used in W_p as a prey for any two consumers from $\{i_2, \dots, i_m\}$. Therefore, the expected number of configurations of W_p giving induced m -cycles in $G(W_p)$ is of the order of magnitude $O(S^{2m} p^{2m})$. Now the same ideas as in the proof of theorem 1 imply our result.

The asteroidal 1-triangle plays a special role in the asymptotic probability, as $S \rightarrow \infty$, that a random overlap graph $G(W_p)$ is an interval graph.

Theorem 4 (asteroidal 1-triangle).—The appearance function of an induced asteroidal 1-triangle in $G(W_p)$ is $S^{-10/9}$.

Proof.—Consider a configuration (see fig. A5) in W_p that gives an asteroidal 1-triangle in $G(W_p)$. The expected number of such configurations is $O(S^{10} p^9)$. It is easy to check that the expected number of all other configurations of W_p that produce an asteroidal 1-triangle subgraph of $G(W_p)$ is of an order of magnitude less than $O(S^{10} p^9)$. Thus, the same argument as before applies.

Intervality of $G(W_p)$

Lekkerkerker and Boland (1962) showed that a graph G is an interval graph if and only if it contains no induced subgraph of the forms pictured in figures A1 and A6. This characteri-

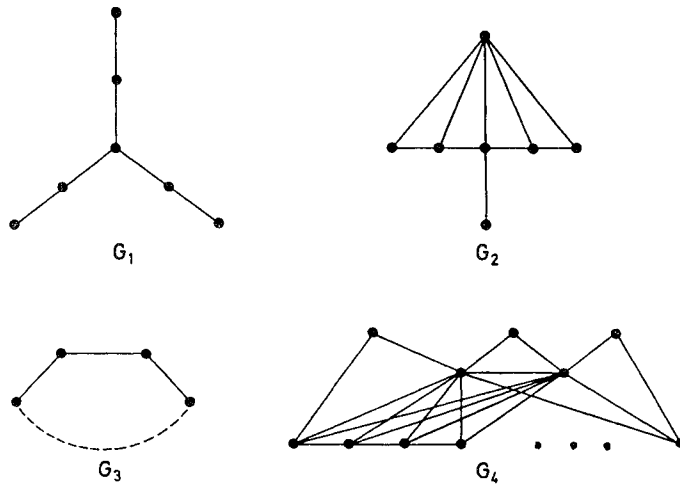


FIG. A6.—Forbidden subgraphs of an interval graph: a graph is an interval graph if and only if it contains none of the subgraphs shown here and in figure A1. G_3 contains k vertices, $k \geq 4$. G_4 contains $k + 5$ vertices, $k \geq 1$. (From Cohen et al. 1990, p. 196, with permission of the publisher.)

zation of interval graphs differs from, but is consistent with, the characterization in terms of triangulation and asteroidal triples, which is mentioned in the text.

We now describe the probability that a random overlap graph $G(W_p)$ is an interval graph for $S = 3, 4, 5, 6, 7$, and $S \rightarrow \infty$. For $S = 3, 4$, and 5 , $P[G(W_p) \text{ is interval}] = 1$, since the web W_p contains no configurations that could destroy the intervality of $G(W_p)$. If W_p has the vertex set $\{1, 2, 3, 4, 5, 6\}$, then the only possible forbidden subgraph of $G(W_p)$ is an induced 4-cycle, which may appear on vertices $\{3, 4, 5, 6\}$ in four different configurations of W_p as shown in figure A7.

Let X_4 be the number of configurations in W_p on $S = 6$ vertices that produce an induced 4-cycle in $G(W_p)$. Then, $P[G(W_p) \text{ is not interval}] = P(X_4 \geq 1) \leq E(X_4)$. Since each configuration in figure A7 contains eight arcs and must exclude five arcs, and since there are exactly four such configurations, $E(X_4) = 4p^8(1 - p)^5$. Thus, $P[G(W_p) \text{ is interval}] \geq 1 - 4p^8(1 - p)^5$, for $S = 6$.

When $S = 7$, the subgraphs of $G(W_p)$ that destroy intervality are induced 4-cycles and induced 5-cycles. There are many different configurations of W_p that produce induced 4-cycles or induced 5-cycles of $G(W_p)$. If Y_4 and Y_5 stand for the number of configurations (of W_p on $S = 7$ vertices) that produce induced 4-cycles and induced 5-cycles, respectively, then a lengthy enumeration of the possibilities yields, with $q = 1 - p$,

$$E(Y_4) = 36p^8q^7(1 - p^2) + 12p^8q^6(2 - 2qp^2 - p^2 - p^3) + 4p^8q^5(6 + 6q^4 + 24q^3p + 24q^2p^2 - 3qp^2 - p^2 - 2p^3) \tag{A3}$$

and

$$E(Y_5) = 8p^{10}q^9. \tag{A4}$$

We leave the proofs of equations (A3) and (A4) to an eager reader as additional entertainment. Consequently, when $S = 7$,

$$\begin{aligned} P[G(W_p) \text{ is not interval}] &= P(Y_4 \geq 1 \text{ or } Y_5 \geq 1) \\ &= P(Y_4 \geq 1) + P(Y_5 \geq 1) - P(Y_4 \geq 1 \text{ and } Y_5 \geq 1) \\ &\leq E(Y_4) + E(Y_5). \end{aligned}$$

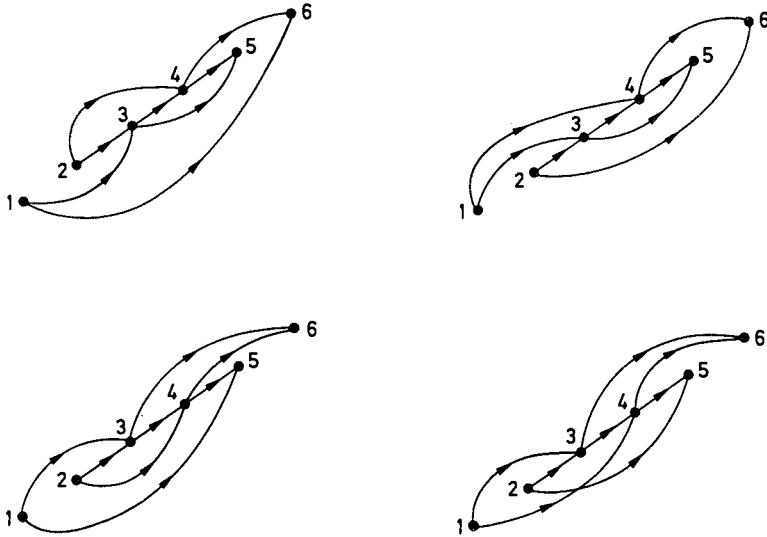


FIG. A7.—Four configurations of a web on six vertices that produce an induced 4-cycle in the overlap graph. (From Cohen et al. 1990, p. 196, with permission of the publisher.)

Note that $P(Y_4 \geq 1 \text{ and } Y_5 \geq 1) = 0$. Thus, $P[G(W_p) \text{ is interval}] \geq 1 - E(Y_4) - E(Y_5)$, where $E(Y_4)$ and $E(Y_5)$ are given by equations (A3) and (A4), respectively.

We do not even try to estimate $P[G(W_p) \text{ is interval}]$ when $S = 8$, since the calculation looks hopeless. Perhaps surprisingly, the calculation becomes much easier when S is large.

Theorem 5 (interval graphs).—Let $p = p(S) \rightarrow 0$, such that $pS^{10/9} = d$. Then,

$$\lim_{S \rightarrow \infty} P[G(W_p) \text{ is interval}] = \begin{cases} 1 & \text{if } d = d(S) \rightarrow 0, \\ e^{-\lambda} & \text{if } 0 < d < \infty, \\ 0 & \text{if } d = d(S) \rightarrow \infty, \end{cases}$$

where $\lambda = 9170d^9/10!$.

Proof.—Let

$$pS^{10/9} \rightarrow 0 \tag{A5}$$

as $S \rightarrow \infty$. By theorems 2, 3, and 4, it follows immediately that a random graph $G(W_p)$ contains no induced subgraphs of the forms of G_1 , G_3 , and asteroidal 1-triangles. For example, in the case of G_1 , if

$$pS^{13/12} \rightarrow 0 \tag{A6}$$

as $S \rightarrow \infty$, then by theorem 2, $P[G(W_p) \supset G_1] \rightarrow 0$. Clearly, condition (A5) implies condition (A6). Next, it is not hard to see that asteroidal k -triangles for $k \geq 2$ and G_2 and G_4 are unlikely to occur when p satisfies condition (A5). One need simply estimate the expected numbers of configurations in W_p that produce those subgraphs in $G(W_p)$ and check that, under the assumption on p given by condition (A5), these expected values tend to 0 as $S \rightarrow \infty$. Consequently, by the Lekkerkerker-Boland characterization of interval graphs, if p satisfies condition (A5), then

$$\lim_{S \rightarrow \infty} P[G(W_p) \text{ is interval}] = 1.$$

Now assume that $pS^{10/9} \rightarrow \infty$ as $S \rightarrow \infty$. Then by theorem 4, with probability tending to 1

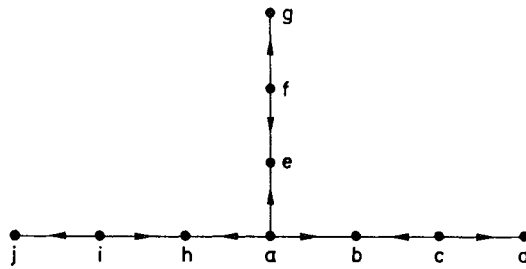


FIG. A8.—A redrawing of the web configuration in figure A5. (From Cohen et al. 1990, p. 199, with permission of the publisher.)

as $S \rightarrow \infty$, a random overlap graph $G(W_p)$ contains at least one induced asteroidal 1-triangle that destroys the intervality of $G(W_p)$.

Finally, let $pS^{10/9} \rightarrow d$, with $0 < d < \infty$. The same argument as in the first part of our proof shows that in this case the only induced subgraphs that destroy the intervality of $G(W_p)$ are induced asteroidal 1-triangles. Let X denote the number of such subgraphs in $G(W_p)$. We show that

$$\lim_{S \rightarrow \infty} P(X = k) = \frac{\lambda^k e^{-\lambda}}{k!}, \quad k = 0, 1, 2, \dots, \tag{A7}$$

where $\lambda = 9170 d^9/10!$; that is, the distribution of X asymptotically approaches the Poisson distribution with parameter λ . Define a configuration of type C to be a configuration of the type presented in figure A5. Let Y be the number of configurations of type C that may appear in W_p as an induced subgraph such that none of the vertices lying below $\{a, b, c, d, e, f, g, h, i, j\}$ is connected with exactly two vertices from $\{b, d, e, g, h, j\}$. Then (cf. the proof of theorem 4), the probability distribution of X is asymptotically the same as the distribution of Y . Replace for a moment each link of W_p by an undirected edge. Clearly, the configuration in figure A5 becomes an ordinary tree on 10 vertices. It is known (see, e.g., Bollobás 1985) that if $pS^{10/9} \rightarrow d$, then the distribution of the number of such trees in G_p asymptotically approaches the Poisson distribution with parameter $\mu = d^9/A$, where A is the order of the automorphism group of a tree on 10 vertices; that is, $A = 10!/10^8$. If we return to the model W_p , then (applying the same approach as in, e.g., Bollobás 1985) it can be shown that the number of configurations of type C also has a Poisson distribution but with a parameter $\gamma = d^9/B$, where $B = 10!/\xi$ and ξ is the number of different ways of labeling 10 given vertices of a configuration of type C . Let us redraw the graph from figure A5 in a different but more useful form (see fig. A8).

Since there are at least three vertices lying above vertex a in W_p , we must have $1 \leq a \leq 7$. Furthermore, b is above a (i.e., $a + 1 \leq b \leq 10$) and c is below b (i.e., $1 \leq c \leq b - 1$) but different from a . Moreover, d is above c (i.e., $c + 1 \leq d \leq 10$) but different from a and b . Continuing this process up to vertex j , we obtain

$$3! \xi = \sum_{a=1}^7 \sum_{b=a+1}^{10} \sum_{c=1}^{b-1} \sum_{d=c+1}^{10} \sum_{e=a+1}^{10} \sum_{f=1}^{e-1} \sum_{g=f+1}^{10} \sum_{h=a+1}^{10} \sum_{i=1}^{h-1} \sum_{j=i+1}^{10} 1,$$

where $c \neq a$, $d \notin \{a, b\}$, $e \notin \{b, c, d\}$, $f \notin \{a, b, c, d\}$, $g \notin \{a, b, c, d, e\}$, $h \notin \{b, c, d, e, f, g\}$, $i \notin \{a, b, c, d, e, f, g\}$, and $j \notin \{a, b, c, d, e, f, g, h\}$. Each author independently wrote a computer program in BASIC to compute ξ , and each independently obtained $\xi = 55020/3! = 9170$.

The probability that a configuration of type C is an induced subgraph of W_p and that none of the vertices lying below C is connected with two vertices $\{b, d, e, g, h, j\}$ tends to 1 as $S \rightarrow \infty$ (since if $pS^{10/9} \rightarrow d$ then almost every G_p has no cycle; see fact 2). Consequently, the

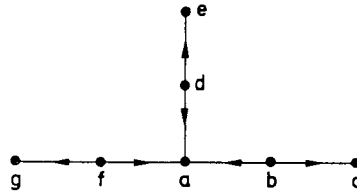


FIG. A9.—A subweb that produces an induced $K_{1,3}$ in the overlap graph. This configuration prevents a web from having a unit-interval graph. (From Cohen et al. 1990, p. 200, with permission of the publisher.)

distribution of the random variable Y asymptotically approaches the Poisson distribution with parameter $\lambda = 9170d^9/10!$ and equation (A7) is proved. Under the assumption on p ,

$$\lim_{S \rightarrow \infty} P[G(W_p) \text{ is interval}] = \lim_{S \rightarrow \infty} P(X = 0) = e^{-\lambda}.$$

The numerical value of λ in theorem 5 may be estimated for an observed web with L links (or arcs) and S species. The maximum-likelihood estimate of p is $p = L/[S(S - 1)/2] = 2L/[S(S - 1)]$. Hence, $d = pS^{10/9} = 2LS^{1/9}/(S - 1)$; hence, $d^9 = [2L/(S - 1)]^9 S$. Since $9170/10! \doteq 0.0025$, we get $\lambda \doteq 0.0025[2L/(S - 1)]^9 S$, and for sufficiently large S , the probability that the overlap graph $G(W_p)$ is interval is arbitrarily close to $e^{-\lambda}$.

Finally, we describe the behavior of the probability that an overlap graph $G(W_p)$ is a unit-interval graph. Roberts (1969) proved that a graph is unit interval if and only if it is an interval graph and does not contain the bipartite complete graph $K_{1,3}$ as an induced subgraph.

Theorem 6 (unit-interval graphs).—Let $p = p(S) \rightarrow 0$, such that $pS^{7/6} = d$. Then,

$$\lim_{S \rightarrow \infty} P[G(W_p) \text{ is unit interval}] = \begin{cases} 1 & \text{if } d = d(S) \rightarrow 0, \\ e^{-\mu} & \text{if } 0 < d < \infty, \\ 0 & \text{if } d = d(S) \rightarrow \infty, \end{cases}$$

where $\mu = 48d^{6/7}!$.

Proof.—The proof follows the same lines as the proof of theorem 5. A subgraph of W_p that produces an induced $K_{1,3}$ in $G(W_p)$ is of the form presented in figure A9. If $pS^{7/6} \rightarrow d$ for some d , such that $0 < d < \infty$, then the distribution of the number of trees on seven vertices in G_p asymptotically approaches the Poisson distribution with parameter $7^5 d^{6/7}!$. Similarly, the distribution of the number of configurations of the form in figure A9 in the cascade model W_p also approaches the Poisson distribution but with parameter $\xi d^{6/7}!$, where

$$3! \xi = \sum_{a=4}^7 \sum_{b=1}^{a-1} \sum_{c=b+1}^7 \sum_{d=1}^{a-1} \sum_{e=d+1}^7 \sum_{f=1}^{a-1} \sum_{g=f+1}^7 1,$$

and $c \neq a$, $d \notin \{b, c\}$, $e \notin \{a, b, c\}$, $f \notin \{b, c, d, e\}$, and $g \notin \{a, b, c, d, e\}$. Again, using computer programs, we obtained $\xi = 48$.

As before, the numerical value of μ in theorem 6 may be estimated for an observed web with L links and S species. Here, $d = pS^{7/6} = 2LS^{1/6}/(S - 1)$; hence, $d^6 = [2L/(S - 1)]^6 S$. Since $48/7! \doteq 0.0095$, we get $\mu \doteq 0.0095[2L/(S - 1)]^6 S$. For sufficiently large S , the probability that the overlap graph $G(W_p)$ is a unit-interval graph is arbitrarily close to $e^{-\mu}$.

Triangulation of W_p

We say that the cascade digraph W_p is *triangulated* if its overlap graph $G(W_p)$ contains no induced k -cycles for all $k \geq 4$. As in the case of the intervality of $G(W_p)$, the probability that W_p is triangulated equals one for $S = 3, 4$, and 5 , whereas

$$P(W_p \text{ is triangulated}) \geq \begin{cases} 1 - 4p^8q^5 & \text{for } S = 6, \\ 1 - E(Y_4) - E(Y_5) & \text{for } S = 7, \end{cases}$$

where $E(Y_4)$ and $E(Y_5)$ are given by equations (A3) and (A4), respectively.

Theorem 7 (triangulated graphs).—Let $p = p(S) \rightarrow 0$, such that $pS = d$. Then,

$$\lim_{S \rightarrow \infty} P(W_p \text{ is triangulated}) = \begin{cases} 1 & \text{if } d = d(S) \rightarrow 0, \\ e^{-\gamma} & \text{if } 0 < d < 1, \\ 0 & \text{if } d \geq 1, \end{cases}$$

where

$$\gamma = \sum_{\substack{k=8 \\ k \text{ even}}}^{\infty} \frac{d^k(-4)^{k/2}}{k!} \sum_{m=1}^{k-1} (-1)^m m! S(k-1, m) 2^{-2-m},$$

and $S(k, m)$ are Stirling's numbers of the second kind.

Proof.—If $d = d(S) \rightarrow 0$ as $S \rightarrow \infty$, then by theorem 3, there is no induced k -cycle for all $k \geq 4$ in $G(W_p)$; thus, W_p is triangulated with a probability approaching 1. Keeping in mind the remarks made in the proof of theorem 3, we can focus on only the very special subgraphs of W_p that form induced k -cycles in $G(W_p)$. Those subgraphs (denote their number by Z_k) have $2k$ vertices and $2k$ links (appropriately joining those vertices) and, after the orientation of links is removed, form induced $(2k)$ -cycles in the usual random graph G_p . Assume that d is a constant, where $0 < d < 1$. It is known (Bollobás 1985) that in this case almost every random graph G_p is a union of tree components and unicyclic components. Thus, each cycle that may appear in G_p is an induced cycle. Let X_k be the number of k -cycles of G_p . Then (Bollobás 1985, p. 79), X_3, X_4, \dots, X_k are asymptotically independent Poisson random variables with means $\lambda_i = d^i/(2i)$, where $i = 3, 4, \dots, k$. No cycle of odd length contributes to forming an induced cycle of $G(W_p)$. The only cycles of even length in W_p that contribute to forming an induced k -cycle of $G(W_p)$ are $(2k)$ -cycles with the property that for each vertex i its neighbors are either both smaller or both larger than i . A. Ruciński (MS) observed that the number of such cycles that may be formed on a given set of vertices is

$$a_{2k} = (-4)^k \sum_{m=1}^{2k-1} (-1)^m m! S(2k-1, m) 2^{-2-m}, \quad k = 2, 3, \dots$$

Furthermore, the same approach as used by Bollobás (1985) shows that the distribution of the random variable

$$Z = \sum_{\substack{k=8 \\ k \text{ even}}} Z_k$$

asymptotically approaches a Poisson distribution with parameter

$$\begin{aligned} \gamma &= \sum_{\substack{k=8 \\ k \text{ even}}} \binom{S}{k} a_k p^k \\ &\sim \sum_{\substack{k=8 \\ k \text{ even}}} \frac{d^k(-4)^{k/2}}{k!} \sum_{m=1}^{k-1} (-1)^m m! S(k-1, m) 2^{-2-m}. \end{aligned}$$

Thus,

$$\lim_{S \rightarrow \infty} P(W_p \text{ is triangulated}) = \lim_{S \rightarrow \infty} P(Z = 0) = e^{-\gamma}.$$

Finally, when $d \geq 1$, almost every graph G_p with $p = d/S \rightarrow 0$ contains a long induced cycle (see, e.g., Bollobás 1985) that can form an induced cycle of $G(W_p)$.

The Resource Graph

The resource graph $H(W_p)$ is defined as an undirected simple graph, with the same vertex set as W_p , such that $\{v_j, v_k\}$ is an edge in $H(W_p)$ if and only if there exists some v_i in W_p such that both (v_j, v_i) and (v_k, v_i) are links in W_p . For $1 \leq i < j \leq S$, define P_{ij} to be the probability of an edge between i and j in the overlap graph $G(W_p)$; then, $P_{ij} = 1 - (1 - p^2)^{i-1}$. Similarly, for $k < l$, define Q_{kl} to be the probability of an edge between k and l in the resource graph $H(W_p)$; then, $Q_{kl} = 1 - (1 - p^2)^{S-l}$. Now define π to be the permutation $\pi(i) = S + 1 - i$, for $i = 1, \dots, S$. Then, $P_{ij} = Q_{\pi(j), \pi(i)}$ for all $1 \leq i < j \leq S$. Therefore, the probability of any configuration of edges is the same in $G(W_p)$ as in $H(W_p)$, after relabeling the vertices by π . Hence, all the results in this Appendix apply equally to overlap graphs and to resource graphs.

LITERATURE CITED

- Auerbach, M. J. 1984. Stability, probability and the topology of food webs. Pages 412–436 in D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, N.J.
- Bollobás, B. 1985. *Random graphs*. Academic Press, London.
- Booth, K. S. 1975. PQ-tree algorithms. Ph.D. diss. Computer Science Division, University of California, Berkeley. Lawrence Livermore Laboratory UCRL-51953, November 14, 1975.
- Briand, F. 1983. Environmental control of food web structure. *Ecology* 64:253–263.
- Briand, F., and J. E. Cohen. 1984. Community food webs have scale-invariant structure. *Nature (Lond.)* 307:264–266.
- . 1987. Environmental correlates of food chain length. *Science (Wash., D.C.)* 238:956–960.
- Carpenter, S. R., J. F. Kitchell, and J. F. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Cohen, J. E. 1968. Interval graphs and food webs: a finding and a problem. Rand Corporation Document 17696-PR. Rand Corporation, Santa Monica, Calif.
- . 1977. Food webs and the dimensionality of trophic niche space. *Proc. Natl. Acad. Sci. USA* 74:4533–4536.
- . 1978. *Food webs and niche space*. Princeton University Press, Princeton, N.J.
- Cohen, J. E., and F. Briand. 1984. Trophic links of community food webs. *Proc. Natl. Acad. Sci. USA* 81:4105–4109.
- Cohen, J. E., and C. M. Newman. 1985. A stochastic theory of community food webs. I. Models and aggregated data. *Proc. R. Soc. Lond. B, Biol. Sci.* 224:421–448.
- Cohen, J. E., J. Komlós, and T. Mueller. 1979. The probability of an interval graph, and why it matters. *Proc. Symp. Pure Math.* 34:97–115.
- Cohen, J. E., C. M. Newman, and F. Briand. 1985. A stochastic theory of community food webs. II. Individual webs. *Proc. R. Soc. Lond. B, Biol. Sci.* 224:449–461.
- Cohen, J. E., F. Briand, and C. M. Newman. 1986. A stochastic theory of community food webs. III. Predicted and observed lengths of food chains. *Proc. R. Soc. Lond. B, Biol. Sci.* 228:317–353.
- Cohen, J. E., F. Briand, and C. M. Newman. 1990. *Community food webs: data and theory*. Springer-Verlag, Heidelberg, W. Germany.
- Critchlow, R. E., and S. C. Stearns. 1982. The structure of food webs. *Am. Nat.* 120:478–499.
- DeAngelis, D. L., W. M. Post, and G. Sugihara, eds. 1983. *Current trends in food web theory*. ORNL-5983. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Erdős, P., and A. Rényi. 1960. On the evolution of random graphs. *Magy. Tud. Akad. Mat. Kutatóintez. Kozl.* 5:17–61. [Reprinted 1973. Pages 574–617 in J. Spencer, ed. *Paul Erdős: the art of counting: selected writings*. MIT Press, Cambridge, Mass.]
- Gallopín, G. C. 1972. Structural properties of food webs. Pages 241–282 in B. C. Patten, ed. *Systems analysis and simulation in ecology*. Vol. 2. Academic Press, New York.

- Grant, P. R. 1986. Interspecific competition in fluctuating environments. Pages 173–191 in J. Diamond and T. J. Case, eds. *Community ecology*. Harper & Row, New York.
- Harary, F. 1961. Who eats whom? *Gen. Syst.* 6:41–44.
- Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. *Theor. Popul. Biol.* 11:197–229.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* 93:145–159.
- . 1965. *The ecological theater and the evolutionary play*. Yale University Press, New Haven, Conn.
- Kawanabe, H. 1986. Cooperative study on the ecology of Lake Tanganyika between Japanese and African scientists, with special reference to mutual interactions among fishes. *Physiol. Ecol. Jpn.* 23:119–128.
- . 1987. Niche problems in mutualism. *Physiol. Ecol. Jpn.* 24:s75–s80.
- Lekkerkerker, C. G., and J. C. Boland. 1962. Representation of a finite graph by a set of intervals on the real line. *Fund. Math. Polska Akad. Nauk* 51:45–64.
- Lundgren, J. R., and J. S. Maybee. 1985. Food webs with interval competition graphs. Pages 245–256 in F. Harary and J. S. Maybee, eds. *Graphs and applications: proceedings of the first Colorado Symposium on Graph Theory*. University of Colorado, Boulder, 1982. Wiley, New York.
- MacDonald, N. 1979. Simple aspects of foodweb complexity. *J. Theor. Biol.* 80:577–588.
- . 1983. *Trees and networks in biological models*. Wiley, New York.
- Newman, C. M., and J. E. Cohen. 1986. A stochastic theory of community food webs. IV. Theory of food chain lengths in large webs. *Proc. R. Soc. Lond. B, Biol. Sci.* 228:355–377.
- Pimm, S. L. 1982. *Food webs*. Chapman & Hall, London.
- Rejmánek, M., and P. Starý. 1979. Connectance in real biotic communities and critical values for stability of model ecosystems. *Nature (Lond.)* 280:311–313.
- Roberts, F. S. 1969. Indifference graphs. Pages 139–146 in F. Harary, ed. *Proof techniques in graph theory: proceedings of the second Ann Arbor Graph Theory Conference*, Ann Arbor, Michigan, 1968. Academic Press, New York.
- . In press. Applications of combinatorics and graph theory to the biological and social sciences: seven fundamental ideas. In F. S. Roberts, ed. *Applications of combinatorics and graph theory in the biological and social sciences*. Springer-Verlag, New York.
- Rose, D. J., R. E. Tarjan, and G. S. Lueker. 1976. Algorithmic aspects of vertex elimination on graphs. *SIAM J. Comput.* 5:266–283.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science (Wash., D.C.)* 185:27–39.
- Silvert, W. 1984. Particle size spectra in ecology. *Lect. Notes Biomath.* 54:154–162.
- Sugihara, G. 1982. *Niche hierarchy: structure, organization, and assembly in natural communities*. Ph.D. diss. Princeton University, Princeton, N.J.
- Yodzis, P. 1982. The compartmentation of real and assembled ecosystems. *Am. Nat.* 120:551–570.
- . 1984. The structure of assembled communities II. *J. Theor. Biol.* 107:115–126.