

Reliable flows and preferred patterns in food webs

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ABSTRACT

We analyse the structure of food webs from a reliability theoretical point of view. The reliability of the network flow is the probability that sources are connected to sinks. With a fixed number of species and connectance, reliability depends on the pattern of links. We construct all of the possible sink web graphs with given numbers of species and links and calculate the reliability of the network flow for each hypothetical sink web. Patterns favourable for reliable flows are characterized. Having compared our results with real web data, we conclude that the structure of natural webs contains mostly such patterns. Thus, the reliability of the network flow seems to be an important factor governing food web structure. Our results show that short chains, a high level of omnivory, a high prey–predator ratio and a low number of specialists are favourable for reliable network flows. These conclusions support the reticulate nature of food webs and the rethinking of the traditional, linearized view.

Keywords: flow network, food web pattern, reliability theory, sink web.

INTRODUCTION

Patterns in nature are present not only at the level of molecules, cells, organs and organisms, but at higher organizational levels as well. Darwin (1859) emphasized the invariance of certain ecological patterns, including the colonization processes of islands (see also Gould, 1995). Such patterns are present, for example, in the structure of food web graphs of ecosystems. Each described pattern is a mathematical problem requiring an explanation (Stewart, 1995).

The patterns of food web graphs are not random (Cohen, 1978; Pimm, 1979, 1982; May, 1983; Pimm *et al.*, 1991; Begon *et al.*, 1996; but see Kenny and Loehle, 1991). Only a fraction of possible topologies is realized. Many attempts have been made to determine the rules and laws governing food web structure, including from the viewpoints of energetics (De Angelis, 1975, 1992; De Angelis *et al.*, 1978; Hairston and Hairston, 1993; Naeem *et al.*, 1994), population dynamics (Pimm and Lawton, 1977; Lawton and Pimm, 1978), information theory (Ulanowicz, 1980; Hirata and Ulanowicz, 1985; Ulanowicz and Wolff, 1991) and constraints deriving from the structural design of organisms (Pimm, 1982). Despite contradictions, each approach has its merits. We suggest a new framework, which is derived from engineering sciences. It is a reliability theoretical view (Barlow and Proschan, 1965; Harr, 1987; Aggarwal, 1993). We focus on reliable flows of matter and energy in

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ecosystems (Molnár, 1994; Jordán, 1997) and optimal food web patterns favourable to them. MacArthur (1955) noted the importance of 'the amount of choice which energy has in following the paths'; on the one hand he thought of it as a measure of stability, but on the other he did not speak explicitly of reliability. Here, we address two basic questions. First, do patterns optimal for reliable flows dominate food webs? In other words, is the construction of trophic links with patterns favourable for reliable flows an important rule in the development of ecosystems? Second, if it is, what can we say about the most interesting problems of food web theory from the reliability theoretical viewpoint? We analyse the correlation between reliability and various food web characteristics.

In this paper, we introduce our reliability theoretical approach, present a model for analysis and compare our results with real data.

THE RELIABILITY THEORETICAL VIEW

Reliability theory is a branch of engineering sciences. It deals with the successful operation of complex systems and machines under given conditions, over a given period of time. Reliability is the probability of a successful operation (Barlow and Proschan, 1965). Reliability theory describes reliability determinants (Molnár, 1995), which are various ways to improve the reliable operation of a given system. Reliability determinants include redundancy, repair, storage, feedback and replacement by which the system is capable of reducing the effects of perturbations.

We examined the reliability of matter and energy flows in ecosystems. We analysed sink web graphs and determined the probability that, in the sink web graph, the sink (the point representing the sink species) and one or more sources (points representing source species or producers) are connected to each other. This probability depends on the deletion probabilities of graph points and the pattern of edges. Points represent species or trophic species, whereas edges represent trophic links between them (we do not take into account interactions in the broader sense, such as competition). The concept of reliability is close to those of resistance, resilience, fragility and robustness, but has the merit of being the central concept of an exact, statistical approach.

We search for patterns favourable to reliable flows. Pattern may be described as a combination of series and parallel ways (Aggarwal, 1993). We introduce a new reliability determinant called 'pattern-dependent combinatorial reliability'. A special case of pattern-dependent combinatorial reliability is bridge structure (Barlow and Proschan, 1965; Aggarwal, 1993; Jordán and Molnár, 1996), which consists of two parallel ways with crosslinks between them.

THE MODEL

Matter and energy flows in an ecosystem can be represented by a food web graph (Fig. 1). We only consider simple directed graphs (digraphs), without loops or multiple edges. If the direction shows who eats who, the arrowhead marks the consumer species (in the figures, we present undirected graphs for simplicity; the upper point always represents a consumer). In sink web graphs, there is only one sink and one or more sources. If the graph represents the whole community, it is called a 'community web graph'. If there is only one source but more sinks, the graph is called a 'source web graph' (Cohen, 1978). We introduce 'source/sink web graphs', in which there is only one sink and one source point.

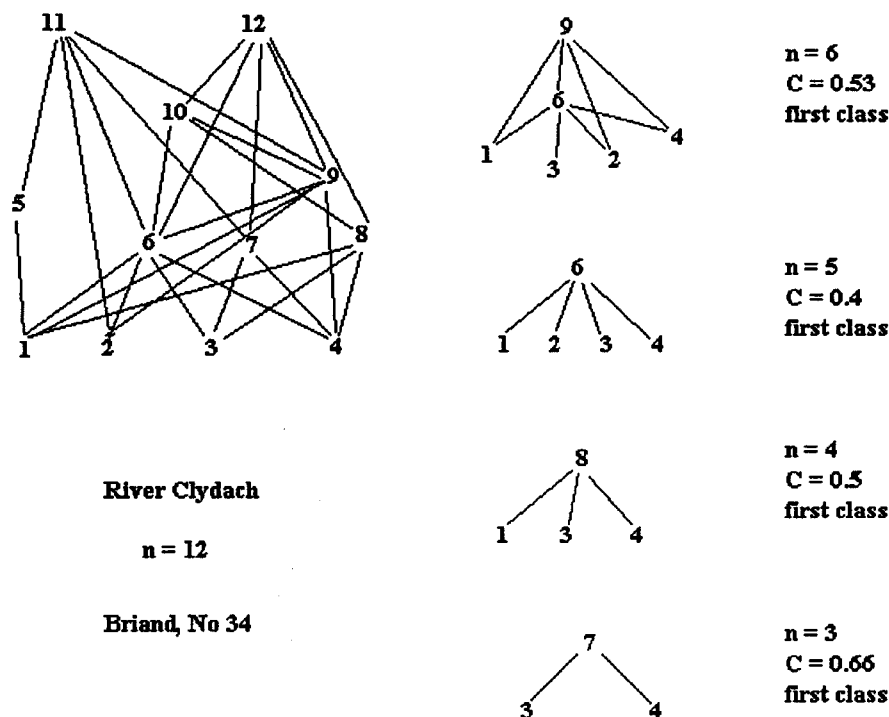


Fig. 1. Food web graph of the River Clydach, Wales. The food web matrix of this community is described by Jones (1949) and collected by Briand (1983). The number of species is 12, within our first limit ($n < 14$). We constructed the sink web subgraph for each species and found that there are four sink webs within our second limit ($2 < n < 8$). These four sink web graphs are shown on the right. We determined the number of species (n) and the connectance (C) for the subwebs. We compared the graphs with the possible sink web graphs similar in terms of n and C and determined which class of reliability they belong to. Numbers correspond to species. For further details, see Briand's (1983) collection.

In digraphs, the in-degree of a point is the number of edges incident to that point as an end point. The out-degree is the number of edges incident to a given point as a start point. We define the sink as a point with an out-degree of zero and the source as a point with an in-degree of zero. Sources represent producers. Sinks represent chosen species, not necessarily top predators. The sink web graph includes the chosen species and all other species and trophic links through which matter and energy can reach it. A sink web can be constructed to each species of an ecosystem, as well as to decomposers and parasites. The sink web of producers is a single point. The sink web of specialist herbivores contains only two points and one edge. Because of their uniformity, the latter webs are not considered here.

We assume that, in the sink web, each point (except the sink) may be deleted with a given and equal probability ($p = 0.01$, $q = 1 - p$). For sink species (and source species in source/sink webs), $p = 0$ and $q = 1$. In our model, only points can be deleted with edges incident to them. Elsewhere (Jordán and Molnár, 1996), we have analysed the case of deleting edges only. In food webs, point deletions seem to be most important; however, trophic links can also change with a constant composition of species. The deletion of a point may correspond

to the extinction of a population or its temporarily very low density because of emigration, epidemics, predators, catastrophes and so on (Pimm, 1982). Deletion can be caused by an effect specific to the deleted species (or trophic species); for example, pollution, sudden changes in environmental factors (pH, temperature, etc.) or biological interactions. Moore and Hunt (1988) have shown for an underground community that the members of the fungal compartment show a similar response to disturbances but a dissimilar response to that of the members of other compartments. We consider the simultaneous deletion of all members of a trophic species to be realistic.

The deletions of points are independent events. Depending on the pattern, the deletion of one or more points may result in disconnectedness between the sink and the sources. We can calculate this probability (P) and the reliability of the sink web flow ($R = 1 - P$; see Appendix for a detailed explanation). We calculate the reliability of flows in flow networks (see Busacker and Saaty, 1969; Harary, 1969; Fulkerson, 1975). We assume that, after the deletion of points, there is no reorganization of links.

We characterize a sink web by counting its points (number of species, n), by calculating its connectance (the fraction of existing and possible links, C) and determining the reliability value of its network flow (the probability that, after deletions, the sink will be connected to at least one source, R).

HYPOTHETICAL FOOD WEB GRAPHS

In flow networks, the reliability of the network flow can easily be increased by adding new edges. Nevertheless, in the case of food webs, it can be shown on population dynamical grounds, that high connectance results in instability (Gardner and Ashby, 1970; May, 1972; McMurtrie, 1975; Rejmánek and Stáry, 1979; Yodzis, 1980; Hogg *et al.*, 1989). However, the reliability of the network flow can be increased without increasing connectance, by constructing a favourable pattern of links. For a given number of species (n), connectance (C) has a minimal value for the web to be connected. In this case, the food web graph is a tree. It is not preferred from a reliability theoretical viewpoint because a tree contains only series ways (a series-organized system fails if any of its points fails). Keeping n constant, if C is very high, stability decreases. In the optimal range of C , the network flow is reliable enough and instability is tolerable. With given n and C , reliability depends strongly on the pattern of edges.

For fixed values of n and C , we constructed all of the possible sink webs (Fig. 2). For each sink web, we determined the value of reliability (R). Examining these R values, it can be shown that differences occur only in the fourth and second decimals. Therefore, we classified our graphs into reliability classes. In a class, differences are approximately 100 times less than between classes. We compiled tables for some n/C pairs containing each possible sink web ranked into classes of reliability (Table 1).

REAL CASES

We do not discuss in detail the problems of describing food webs, for example trophic resolution, the binary nature of links or the completeness of data (Paine, 1988; Polis, 1991; Polis and Strong, 1996; Goldwasser and Roughgarden, 1997). Although databases are far from perfect, theoreticians are able to use them (Pimm and Kitching, 1988). We believe mills can work better with a better grist but that they can also produce something from a

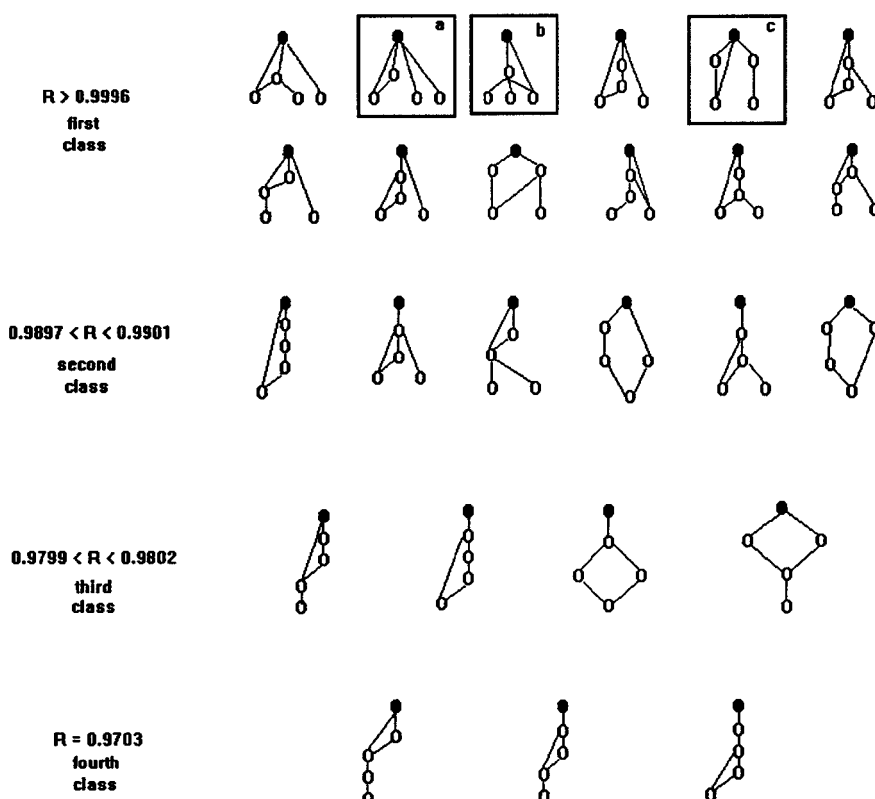


Fig. 2. If a sink web contains five species ($n = 5$) and five trophic relations ($C = 0.5$), we can construct these possible patterns. Solid circles represent sinks. The graphs are directed but, for simplicity, we do not sign the direction of edges. Upper points always represent consumers. On the left, we present the value of reliability (R) for each class of graphs. We found four graphs with $n = 5$ and $C = 0.5$ at Briand and Cohen, within our limits. Graphs 'a' and 'b' correspond to two subwebs of web 21 at Briand (Ross Sea; Patten and Finn, 1979), while graph 'c' corresponds to two sink subwebs of web 4 (California Salt Marsh; Johnston, 1956). The four sink subwebs belong to the most reliable class.

grist of poor quality, when used carefully (Paine, 1988). We collected food webs from the classical papers of Joel Cohen (1978) and Frédéric Briand (1983). From community and sink webs, we constructed sink subwebs for each species. Source webs were excluded as they were inconvenient for the construction of perfect sink subwebs of the community. After the characterization of these sink subwebs (determining n and C), we compared them with our hypothetical webs to determine which classes of reliability they belong to (Fig. 1).

We restricted our work to small webs and subwebs introducing two limits. There were two methodological reasons for this: first, the criteria of qualitative stability (May, 1973a; Jeffries, 1974) are valid only for small webs and we used these criteria; second, as Cohen (1978) stated, the bigger the web the less information we can obtain from mere analysis of the graph. We discuss the problems of analysing small graphs later.

We analysed community and sink webs only below the limit $n(\max) = 13$, and sink subwebs only below $n(\max) = 7$. Of 58 described food webs, we used 18 because of our first limit. In these 18 webs, there are 120 species for which sink webs can be constructed

(they are not producers with $n = 1$, nor specialist herbivores with $n = 2$). We constructed the sink web to 75 of these 120 species based on our second limit. Our real sink subwebs contain $2 < n < 8$ species. They are subwebs of community and sink webs containing $n < 14$ species.

RESULTS OF COMPARING REAL AND HYPOTHETICAL WEBS

We conclude that the most reliable patterns dominate the structure of real food webs (Table 1). This suggests that the development of patterns favourable to reliable flows may be a strong rule shaping the structure of food webs.

There are three reasons not to expect perfect agreement between our predictions and reality. First, the organization of ecosystems is extremely complex. There are many more or less important rules. These rules act together, sometimes against each other. Patterns preferred for reliable flows only obey one of the rules. Second, as May (1977) pointed out, taking the history of ecosystems into account, we may expect more stable states. He emphasized the importance of contingency. Third, scale dependence may affect the validity of our predictions (Havens, 1993; to be discussed later).

Table 1. Comparison of our hypothetical graphs with reality^a

<i>n</i>	<i>C</i>	Number of classes	Sink subwebs reported by Briand and Cohen	Sink subwebs belonging to the:					
				First class	Second class	Third class	Fourth class	Fifth class	Sixth class
3	0.66	2	27	24	3				
3	1.00	1	3	3					
4	0.50	3	7	4	3	0			
4	0.66	3	4	1	3	0			
4	0.83	2	1	0	1				
5	0.40	4	5	4	1	0	0		
5	0.50	4	4	4	0	0	0		
5	0.60	3	4	4	0	0			
5	0.80	2	1	1	0				
6	0.33	5	3	2	1	0	0	0	
6	0.40	5	2	2	0	0	0	0	
6	0.47	4	1	1	0	0	0		
6	0.53	3	2	2	0	0			
6	0.60	2	2	2	0				
7	0.28	6	4	3	1	0	0	0	0
7	0.33	6	1	1	0	0	0	0	0
7	0.38	5	1	1	0	0	0	0	
7	0.43	4	1	1	0	0	0		
7	0.47	3	1	1	0	0			
7	0.71	1	1	1					

^a With given values of n and C , we determined the possible sink web graphs. For example, Fig. 2 corresponds to the seventh row. Here we present only the number of reliability classes. In the fourth column, we give the number of sink subwebs with n and C , found at Briand and Cohen. How many subwebs belong to the classes are shown on the right. Most sink webs found in the literature are appropriate for very reliable transport of matter and energy. Sink webs with unreliable flow patterns are rare in nature.

RELATIONS BETWEEN RELIABILITY AND VARIOUS FOOD WEB CHARACTERISTICS

Because reliable patterns appear to dominate real food webs, the reliability theoretical view may be very important for investigating food web structure. In this section, we discuss some problems. Our results derive mainly from the analysis of graphs with three n/C pairs ($n = 5$ with $C = 0.4, 0.5$ and 0.6). These data inform us about the relation between reliability and various food web characteristics.

Chain length

The maximum chain length in food webs is generally three to five (May, 1978; Pimm, 1982; Briand and Cohen, 1987; Hastings, 1988a; Pimm *et al.*, 1991), although there are a few exceptions. For example, in intertidal ecosystems, food chains are longer (Schoener, 1989) and there are also differences in chain length between marine and continental food webs (Cohen, 1994). As chain length increases, flow reliability decreases (Fig. 3). We plot the average of maximal chain length against reliability. Short chains are preferred. Our results support the general view derived from dynamical and energetical considerations. However, from our point of view, it is unnecessary to dissect communities into discrete levels because it does not affect flow reliability. The existence of levels is a subject of debate (Cohen and Newman, 1985; Oksanen, 1991; Polis and Strong, 1996). The advantages of omnivory discussed below support the reticulate character (without levels) of webs (Polis and Strong, 1996).

Compartments

The existence of compartments in ecosystems has also been debated. On stability grounds, Pimm (1979) argued against their existence. In contrast, May (1972, 1973b) considered compartmentalization to be a mechanism counteracting the destabilizing effect of great complexity. An example of a compartmentalized web is web 11 in Briand's (1983) collection (described by Menge and Sutherland, 1976). Our results suggest that homogeneous and

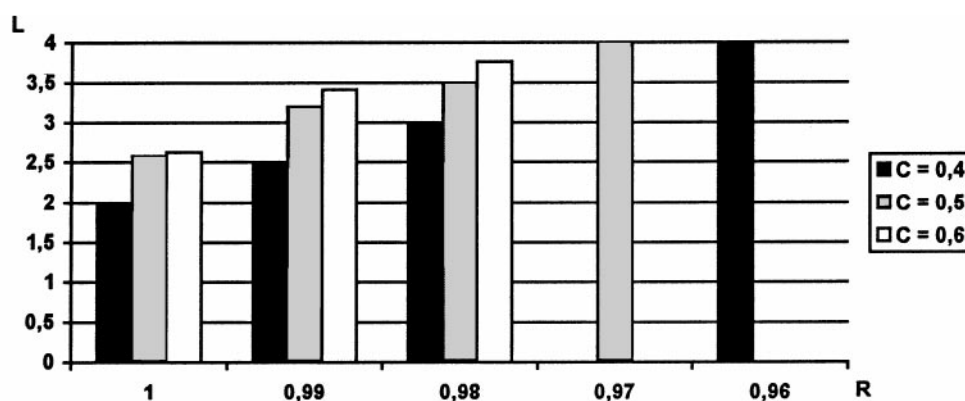


Fig. 3. Average maximal chain length (L) as a function of reliability (R). The data are derived from a comparison of each possible sink subweb with $n = 5$ and $C = 0.4, 0.5$ and 0.6 . Shorter chains result in greater reliability.

compartmentalized webs have the same character in terms of reliability (i.e. compartmentalization is neutral). We can show both compartmentalized and homogeneous webs with both high and low reliability values (Fig. 4). However, the nature of compartmentalization may depend strongly on web size (Pimm, 1982; to be discussed later). In addition, sink webs may not be suitable for analysing compartmentalization (Pimm, 1982). Nevertheless, we feel it useful to investigate the hierarchical nature of sink webs, because it is a characteristic property of pattern.

Omnivory

Omnivory means feeding on more than one trophic level. It is thought to be uncommon and especially rare between non-adjacent levels (Pimm and Lawton, 1978; Pimm, 1980). Pimm (1982) stated that dynamical constraints alone predict the pattern of omnivory. However, several authors have described a surprisingly high level of omnivory in some cases (Sprules and Bowerman, 1988). Our work supports these findings: on reliability theoretical grounds, omnivory is favoured. We can illustrate this by comparing the number of non-adjacent omnivores in the web and the reliability of the network flow (Fig. 5). The correlation is not very strong but it does exist. (It is stronger if we fix the number of trophic levels. In this case, within a type of graphs with a given number of levels, the more reliable graphs

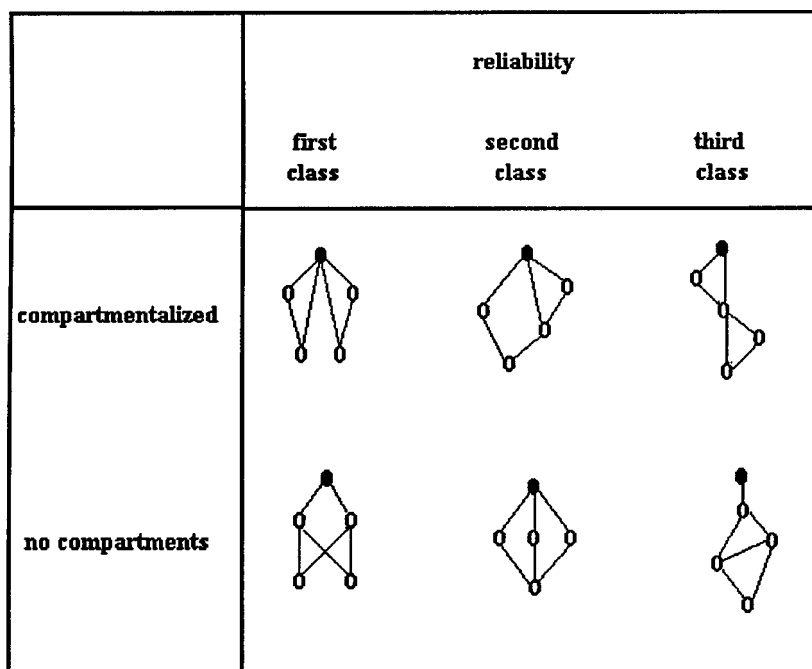


Fig. 4. Examples of variously reliable and compartmentalized sink webs. Compartmentalization means a group of elements in a food web with many connections to each other but few connections to other elements outside the group. Because we can see graphs for each combination, we can conclude that reliability does not depend on compartmentalization, at least in small webs.

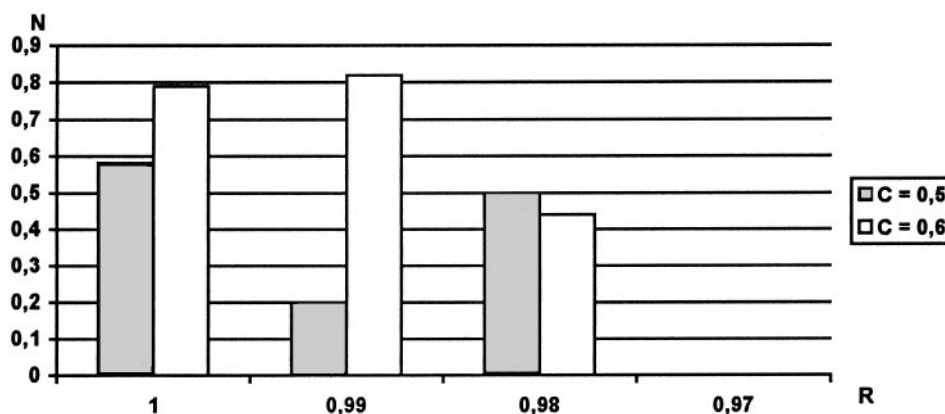


Fig. 5. Relation between average number of non-adjacent omnivores (N) and reliability (R). If $n = 5$ and $C = 0.4$, the graph is a tree. In trees, there are no omnivores, so the diagram shows two columns only for each value of reliability ($C = 0.6$ and 0.5). With higher non-adjacent level omnivory, reliability usually increases, but the relation is not very strong (a stronger correlation can be shown with a fixed number of levels).

have the more non-adjacent level omnivores.) In general, more omnivores feeding on non-adjacent levels results in higher reliability.

Prey–predator ratio

The ratio of the number of prey species to predators is generally thought to be around 3:4 in community webs (Pimm, 1982; Hastings, 1988a; Pimm *et al.*, 1991). In sink webs, this ratio must be modified, because of the reduced number of predators (in sink webs there is only one top predator). Nevertheless, it is possible to compare the prey–predator ratio of various sink webs. From the viewpoint of matter and energy fluxes, parasites can be treated as predators (for a review on parasites, see Marcogliese and Cone, 1997).

We determined the number of species eating others, and being eaten by others, in each of our sink web graphs. We conclude that, as the ratio of prey increases, reliability also increases (Fig. 6). So with fixed values of n and C , it is preferable to contain more prey (including producers) for the ecosystem. This is favourable for short return times after perturbation as well (Pimm and Lawton, 1977). This fact may support the possible dominance of bottom-up regulation processes in the dynamics of ecosystems (Wiegert and Owen, 1971; Polis and Strong, 1996) without detracting from the importance of top-down processes (Hunter and Price, 1992). The analysis of the bidirectional effects of species deletions would help to understand some aspects of dynamic regulation (S. Pimm, personal communication).

Number of specialist species

We define a specialist species as a species which can be represented in the graph by a point with an in-degree of 1. We excluded herbivorous specialists because of their uniform sink webs, but this did not cause any systematic bias in our results. We conclude that, as the

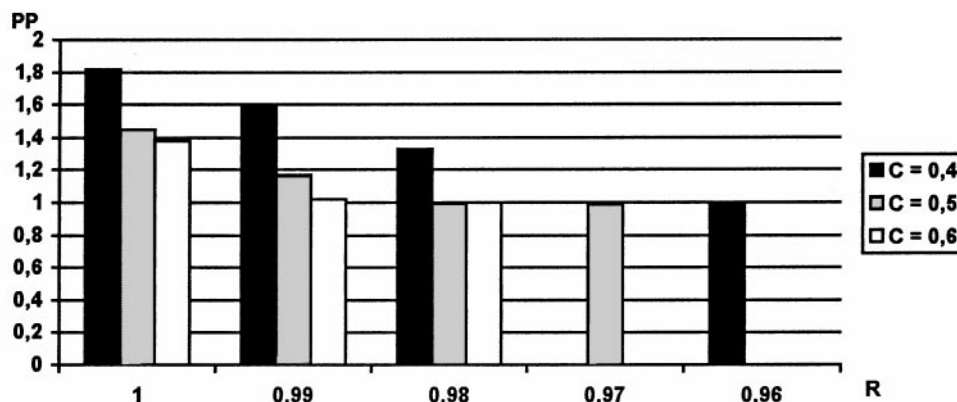


Fig. 6. Relation between the prey-predator ratio (PP) and reliability (R). As the ratio of prey species to predators increases, reliability also increases.

number of specialists increases, reliability decreases (Fig. 7). This result supports the reticulate nature of food webs (Polis and Strong, 1996). It is important to note that specialists may also have a positive effect on reliability by increasing the efficiency of transports.

After calculating the in-degrees for each point of each graph, we noted that the standard deviation of in-degrees increases as reliability increases (Fig. 8). This means more producers (with an in-degree of zero) and more generalist species (with high in-degrees). This is another interpretation of the low number of specialists and the high number of producers. We have found the standard deviation of out-degrees always to be the same.

Stability and connectance

It is very important to distinguish between stability and reliability. The former is a dynamical concept, while the latter is a statistical one. Stability is one of the most important topics in food web studies (Leigh, 1965; Rosenzweig, 1971; May, 1972, 1973a,b; Roberts, 1974; Gilpin, 1975). Reliability is an important factor of stability (and perhaps of ascendancy; Ulanowicz, 1986), but their relation is not simple. Greater reliability may cause less stability if connectance increases. Maynard Smith (1974) noted that long chains alone do not lead to instability, and we can show their lower reliability (Fig. 2, lower graphs). Thus, graphs with unreliable flows can be stable. However, an examination of three graphs from Pimm (1982) shows an example of a positive correlation between reliability and stability. Here, the more reliable graph is the more stable.

The relation between reliability and connectance is not strict. If we compare the R and C values for the three possible graphs containing three species ($n = 3$), we see that the most and the least reliable have low connectance ($C = 0.6$), while the middle one has high connectance ($C = 1.0$). In general, higher connectance results in higher reliability, because with more links more points must be deleted to cause disconnectedness. This is why specialists have a negative effect on reliability (specialists reduce connectance).

Stability does not necessarily depend on connectance (Siljak, 1974, 1975). Nevertheless, greater connectance generally causes instability (May, 1973b; McNaughton, 1978, 1988; Pimm, 1984), in contrast to earlier views (MacArthur, 1955; Elton, 1958). Some authors

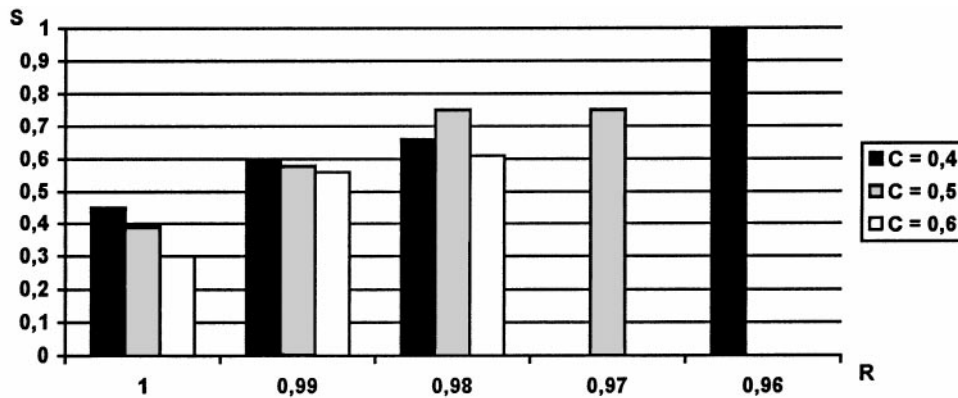


Fig. 7. Relation between the average number of specialists (S) and reliability (R). As the number of specialists decreases, reliability increases.

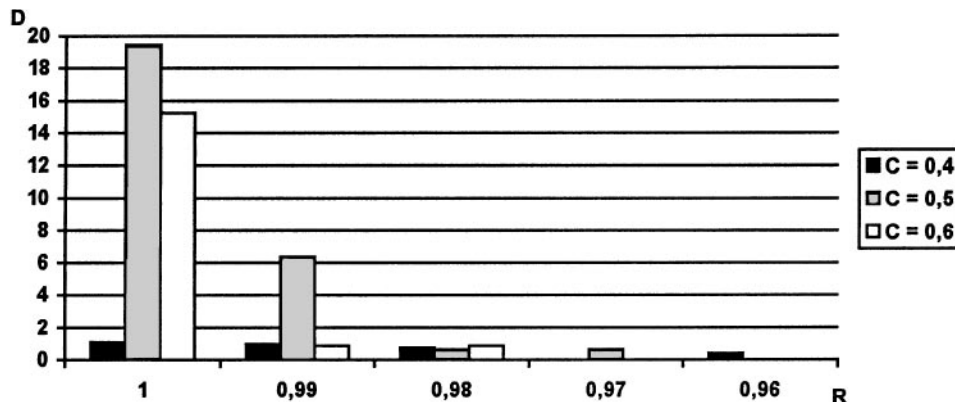


Fig. 8. Relation between the standard deviation of the in-degrees of the graph points (D) and reliability (R). As the standard deviation increases, reliability also increases. In more reliable sink webs, there are more generalists (high in-degree) and producers (zero in-degree).

think that connectance is not adequate for analysing stability (Hastings, 1988b; Paine, 1988).

After discussing the fuzzy relations between connectance, stability and reliability, we can conclude that greater connectance generally results in greater reliability but less stability, while greater reliability generally results in greater stability. Contradictions may derive from loose definitions or oversimplified models; for example, May (1973b) admits that high connectance results in greater stability in the real world, despite his models. A detailed analysis of the reliability–stability relation is in preparation.

Keystone species

We deleted some points from our graphs and found that the position of the points greatly affects the change in reliability. Here, we present a summary of the results only. Some

highly reliable graphs are very sensitive to certain deletions. If we delete some of their points, reliability is drastically reduced. However, from some not so reliable graphs, certain points can be deleted without any serious effects. These findings suggest that, from a reliability theoretical view, keystone species are very important in network flows (Leibold, 1996). We can define a keystone species as a species whose deletion results in a serious effect on the ecosystem (Pimm and Gilpin, 1989). A keystone species is generally the single food source of more specialist species. Such a species can be seen in web 13 in Cohen (1978, species 3). The low abundance of keystone species may contribute to their special, risky position. In the context of conservation biology, it is sometimes better to delete (to let go extinct) more, not so crucial species, than a very important keystone species (at least from the view of reliable flows).

Source/sink webs

We define source/sink webs as food webs with only one top predator and one producer. Source/sink webs have no large biological significance but they may be typical for some very special (e.g. man-made) ecosystems. In this case, there is a single producer who is eaten by a whole community, including a single top predator. This special situation may result in new rules for the optimal organization of trophic links. We analysed source/sink webs ($n = 5$ with $C = 0.5$ and 0.6) and conclude that there is no special feature of their graphs. The same rules as for sink webs are valid.

Prohibited patterns

Finally, we present a food web graph that is consistent with most organizational rules described by others but which appears to be rare (or absent) in nature. It can be characterized by short chains, a prey–predator ratio near to 3:4, a tolerable connectance ($C = 0.25$), a predator overlap graph that is an interval graph (Cohen, 1977, 1978) containing only rigid circuits, a prey overlap graph with no holes (Sugihara, 1984), the absence of non-adjacent level omnivory and qualitative stability (May, 1973a; this conclusion is derived from the analysis of the interaction matrix of the graph). However, its structure does not obey the link scaling law (Cohen and Newman, 1985), for instance. We explain its absence or rarity by its unreliable flow pattern (Fig. 9). It belongs to the $n = 6$, $C = 0.33$ row of Table 1, in the third class of reliability.

SCALE DEPENDENCE

The sink web graphs we have analysed so far have been small. Some properties of food webs are thought to be scale-invariant, others not (Briand and Cohen, 1984; Sugihara *et al.*, 1989; Martinez, 1994; Bersier and Sugihara, 1997). For example, Cohen's cascade model (Cohen and Newman, 1985) predicts scale invariance. The food web graphs of larger webs are not interval graphs (Fulkerson and Gross, 1965; Cohen, 1978); as size increases, a sharp transition occurs (Pimm, 1988). Havens (1992, 1993) presents one scale-dependent property out of eight, but a reanalysis of his work suggests six properties to be scale-variant (Martinez, 1993). Havens admits that small webs are more variable, so their structure is less predictable. We have limited our analysis to small webs for two methodological reasons, as mentioned above. Thus, it is important to bear in mind the possibility of scale dependence.

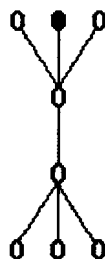


Fig. 9. An example of a graph for which most of the rules described by others are valid (see text for details). Its rarity or absence may be explained by its unreliable network flow. The solid circle indicates one of the sinks. This sink web is of the $n = 6$, $C = 0.33$ type and belongs to the third class of reliability.

Reliable patterns intuitively seem to be scale-invariant; for example, series ways are less reliable than parallel ways, independently of size. However, the relation between reliability and other food web properties may be scale-dependent. For example, compartments may have positive or negative effects on reliability in larger webs. Nevertheless, we have shown that there is no such effect in small webs. The numbers in Table 1 show a better fit to our predictions as web size increases but the lower rows represent smaller samples. Thus, we agree with Havens in terms of small webs and hope that our predictions are robust for larger webs.

Although community webs may be much more complex than the ones described so far, it is not too serious a problem if one analyses sink webs only. Because of short chains, sink webs cannot be much larger than the webs analysed by us; larger food webs are not higher but wider. Scale dependence may be an important factor, especially in the case of community webs.

SUGGESTIONS FOR FURTHER STUDY

As field studies are perfected, theories will be based on more robust ground (Cohen *et al.*, 1993; Goldwasser and Roughgarden, 1993). In the meantime, we can suggest some developments to our model.

After the deletion of points, we did not take the reorganization of links into account. Some papers have discussed reorganization and deletion stability (Pimm, 1982; Yodzis, 1988); they should be incorporated in our model. We have only considered point deletions; our model would be closer to reality if we also considered the deletions of edges (trophic links).

The uniform values for p have strong support. Because each point has the same deletion probability, we can focus purely on patterns. Nevertheless, some authors suggest various flows are different in magnitude (Paine, 1980; Platt *et al.*, 1981; Ulanowicz and Wolff, 1991). It is a very rational claim because unweighted edges lead to overemphasis on rare interactions. Deletion probabilities should differ for two reasons. First, as each point has its own deletion probability, upper points of predators could be characterized by a cumulative loss in reliability. The reliability of the success of a third-level predator depends on its deletion probability and on the deletion probability of all of the species below it (predators on the second level, herbivores and producers). Second, the deletion probability of the third-level predator also depends on other reliability determinants, for example on redundancy (the

abundance of individuals also affects flow reliability). It has been shown that, in a specific underground community, the main pathways of energy contain more resistant species, for example bacteria instead of fungi or roots. Predators obtain their diet mainly from the bacterial line (Moore and Hunt, 1988). More reliable pathways are preferred. Weighted edges and differences between the quality of points are crucial. Considering points of different quality and fluxes would make our recent static view more dynamic (Paine, 1988, 1992). We agree that a static representation of a dynamic system is of limited utility (Platt *et al.*, 1981). A dynamical analysis of reliable food web patterns and processes should be performed.

We introduced two limits for choosing food webs and sink subwebs. For testing scale dependence, they can be cancelled out but keeping in mind the statements of May and Cohen. Applying these limits, our sink webs better represent the lower regions of real community webs. At higher levels, maintaining the desired level of reliability is more difficult because of cumulative loss in reliability. Because of cumulative loss in reliability, we should expect preferred patterns to be more important at higher levels. This may be one cause of convergent ways of matter and energy (i.e. of the pyramid-like shape of many community webs).

CONCLUSIONS

With fixed number of species and connectance values, various sink webs can be constructed. The reliability of the network flows differs depending on link pattern. The most reliable patterns of links dominate real food webs. This result supports our conviction that reliability theoretical rules have a strong role to play in shaping the structure of ecosystems. Because the reliability theoretical view seems to be interesting and important, we examined some old and recent problems using this framework.

Short chains, a high level of omnivory, a high prey–predator ratio and few specialists are favourable properties for reliable network flows. The compartmentalized nature of webs seems to be neutral from the reliability theoretical view. The exact relation between reliability and stability remains unclear, but reliability may be an important factor for achieving stability. Keystone species have a central role to play in network flows. Scale dependence may affect our predictions for larger webs but we think that its effects are not too serious for sink webs.

Ecosystems are extremely complex systems, so we have no reason to expect just one organizing rule. Our view is but one of many, but the close fit of our predictions to described web properties suggests these rules to be basic, as far as a rule can be basic in ecology (for discussions, see Gould, 1995; Murtaugh and Kollath, 1997).

We conclude that our results support some modern theories on food web structure. These theories emphasize the reticulate nature of webs and reduce the significance of the traditional hierarchical and linearized view. We also acknowledge the importance of global approaches to food web analyses. Our results suggest that conservation projects should focus not on discrete species but on their compositions (i.e. on communities).

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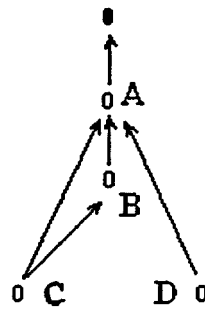
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APPENDIX

Here we present a detailed calculation of the value of reliability for a chosen graph. The graph consists of five points and five edges. For the sake of didactics, we mark the direction of edges by arrows and indicate the points by letters. According to our model, each point has an equal error probability of $p = 0.01$, so the chance of correct operation is $q = 0.99$. The sink is assumed not to be deleted, so we have to consider four deletion probabilities. Because failures are independent, we can easily calculate the probability that one or more points do not work. We use binomial distribution.



With $P(0)$ probability, each point works:

$$P(0) = \binom{4}{0} \times 0.01^0 \times 0.99^4 = 0.9606 \quad (1)$$

The probability of a single failure is:

$$P(1) = \binom{4}{1} \times 0.01^1 \times 0.99^3 = 0.0388 \quad (2)$$

because one point fails with $p = 0.01$ and three points work with $q = 0.99$. For double failures:

$$P(2) = \binom{4}{2} \times 0.01^2 \times 0.99^2 = 0.000588 \quad (3)$$

If three or more points fail, probabilities are small. These cases can be neglected:

$$P(3) = \binom{4}{3} \times 0.01^3 \times 0.99^1 = 0.0000036 \quad (4)$$

$$P(4) = \binom{4}{4} \times 0.01^4 \times 0.99^0 = 0.00000001 \quad (5)$$

In the case of single failures, A, B, C or D may fail. Only the deletion of A leads to disconnection between the sink and the sources. 1:4 is the fatal ratio, $F(1)$. If two points fail, there are six combinations: AB, AC, AD, BC, BD and CD. Four of these (AB, AC, AD and CD) lead to disconnection. If B and C or B and D fail, the sink remains connected to the sources. In this case, the fatal ratio, $F(2)$, is 4:6. Considering the total probability formula, the sum of the products of error probabilities and fatal ratios gives the probability of disconnection:

$$P = P(1) \times F(1) + P(2) \times F(2) = 0.0388 \times 1/4 + 0.000588 \times 4/6 = 0.0097 + 0.00039 = 0.01009 \quad (6)$$

from where reliability is:

$$R = 1 - P = 1 - 0.01009 = 0.9899 \quad (7)$$

It can be seen that single failures that lead to disconnection are of utmost importance. The number of fatal double failures modifies the result only slightly. The graph presented belongs to the second class of reliability (Fig. 2).