# Food web patterns and their consequences

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A food web is a map that describes which kinds of organisms in a community eat which other kinds. A web helps picture how a community is put together and how it works. Although webs were often initially reported in despair at ever understanding ecological complexity, recently discovered widespread patterns in the shapes of webs, and theoretical explanations for these patterns, indicate that webs are orderly and intelligible, and have some foreseeable consequences for the dynamics of communities.

FOOD webs are the road-maps through Darwin's famous 'entangled bank'[1] and have a long history in ecology[2]. Like maps of unfamiliar ground, food webs appear bewilderingly complex. They were often published to make just that point. Yet recent studies have shown that food webs from a wide range of terrestrial, freshwater, and marine communities share a remarkable list of patterns. Current research concentrates on how many independent patterns there are, how they may be described quantitatively, why the patterns are so general, and what are the consequences of these patterns for the dynamics of a community and its constituent species. Just as any map omits details, most published webs omit predation on minor species, the quantities of food consumed, the chemical composition and temporal variation of the flows and many other details. Published webs are also of very variable quality. These omissions and problems are causes of concern, but on present evidence do not present insurmountable difficulties.

## The data

Food web complexity is exemplified in Fig. 1. (This web[3] predates Shelford's study[4], which is often credited as the first published web, by one year.) The community embracing the boll weevil is certainly complex, but not hopelessly so; indeed it raises several issues of contemporary interest. For instance, what level of taxonomic resolution is appropriate for work of this kind (most taxa in Fig. 1 are highly aggregated, but some are identified to species); and how are the boundaries of the studied system to be delineated?

Three kinds of food webs are published. A source web includes one or more kinds of organisms, the organisms that eat them, their predators and so on (for example, the part of Fig. 1 based on the cotton plant). A sink web describes one or more kinds of organisms, the organisms they eat, plus their prey, and so on. A community web is defined by picking, within a habitat or set of habitats, a group of species without regard to the eating relations between them, and working out who eats whom[5]. Reference 6 compiles 113 community webs and most of these webs contain between 5 and 50 species. We focus here on

community webs[5-7], an example of which is shown in Fig. 2. Terms used to describe web features and the information that can be extracted from them are defined in Boxes 1 and 2. Over 200 community webs have been reported in the literature[7] (available in machine-readable form through ECOWeB[7]) embracing a wide variety of habitats, locations and taxa. The analyses of these webs are usually in terms of trophic species—a set of organisms with identical prey species and identical predators, within the level of resolution used in the study. Figure 1 is unusual in that it indicates the number of species grouped into a trophic species; there are, for example, 12 species grouped under the trophic species of 'leaf worm parasite'. In general, a trophic species may correspond to a set of biological species, to a single biological species or to a single life-stage of a species. We shall use 'species' to mean 'trophic species' throughout.

## Features common to all webs

Box 1 explains the statistics commonly derived from a web and also gives the particular statistics derived from the *Nepenthes* web. Two associated graphs, the predator overlap graph (also called the trophic niche overlap graph[5] or, by graph theorists, the competition graph) and the prey overlap graph[8] are derived from an analysis of the web (Box 2 and Figs 3 and 4). Several features are common to the set of webs studied so far, a set that has widely varying numbers of species and contains webs from many different habitats. Common features (see Box 3) include the average proportions of top, intermediate and basal species, the ratio of predatory species to species of prey, the proportions of trophic linkages between different kinds of species, the length of food chains, the absence of compartments within a habitat, and complex patterns in the topological relationships between predators and prey elucidated by the predator and prey overlap graphs.

## Are the patterns real?

Are these general patterns artefacts? There are good reasons for concern about the quality of data in published webs. Communities often contain thousands of species. Because published
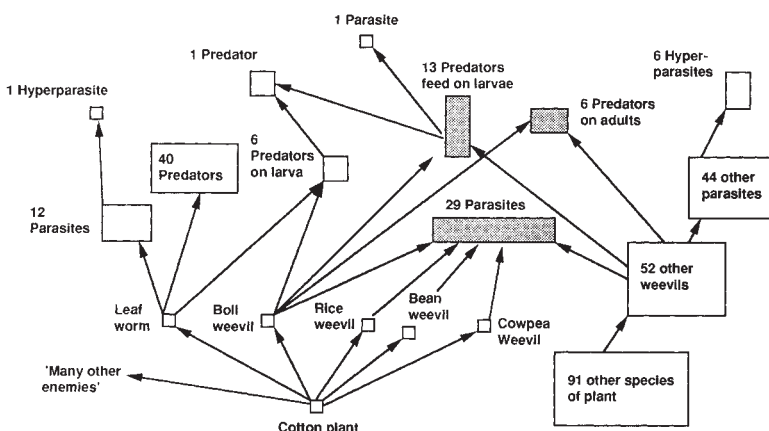


FIG. 1 The food web associated with the cotton plant and the boll weevil (after ref. 3). The cotton is attacked by 'many other enemies' than those specified. Moreover, the predators shown in the three shaded boxes are known to attack species other than those shown in the figure.
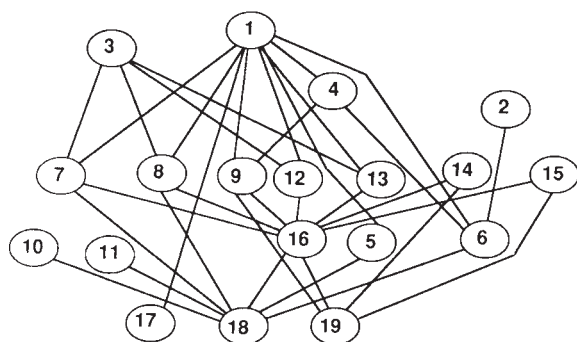
FIG. 2 A food web of the insects in the pitcher plant *Nepenthes albomarginata* in West Malaysia (from ref. 16). Each line represents a trophic linkage; predators are higher in the figure than their prey. Key: (1) *Misumenops nepenthicola*; (2) Encyrtid (near *Trachinaephagus*); (3) *Toxorhynchites klossi*; (4) *Lestodiplosis syringopais*; (5) *Megaselia* sp. (?*nepenthina*); (6) *Endonepenthia schuitemakeri*; (7) *Triperoides tenax*; (8) *T. bambusa*; (9) *Dasyhelea nepenthicola*; (10) *Nepenthosyrphus* sp.; (11) *Pierretia urceola*; (12) *Culex curtipalpis*; (13) *C. lucaris*; (14) *Anotidae* sp. 1; (15) *Anotidae* sp. 2; (16) bacteria and protozoa; (17) live insects; (18) recently drowned insects; (19) older organic debris.

webs include only tens of trophic species (>100 is exceptional), they are either highly aggregated or represent only a tiny part of the entire system. Aggregation is rife in many published webs; moreover, aggegation varies in extent from web to web, and at different positions in the same web[9]. Even when webs are detailed enough for most of their elements to be single biological species (for example Fig. 2), the linkages are less often based on experimental evidence than on casual observations; only

those linkages that are 'artistically convenient'[10] may appear in the figure. In recent studies we detect a counter-tendency to report every linkage, no matter how minor. We appeal for studies where the frequencies of feeding encounters are reported, so that objective criteria may be used to include or exclude linkages.

There are a number of rejoinders to the criticisms that the data are too aggregated and unreliable to reveal meaningful patterns. Possible artefacts ought not to apply equally to webs from special microhabitats described in detail and to those more aggregated webs summarizing interactions throughout larger communities. Present evidence suggests that most patterns appear across all webs. Moreover, artefacts should be more obvious in the highly aggregated webs. Indeed, the ratio of species of predators to species of prey is sensitive to the greater aggregation of species at lower trophic levels[9], and the ratio itself has dropped as better data have become available[11,12]. Nevertheless, the average proportions of species at different levels change only slowly or not at all across webs differing widely in numbers of species and degree of aggregation, though the variation in these proportions is large. Detailed webs can be progressively aggregated. For instance in Fig. 2, the three pairs of biological species (10 and 11; 12 and 13; 14 and 15) that have the same sets of predators and prey could be joined into three trophic species. The web could be further aggregated by joining 7, 8, 12 and 13, which share similar species of predators and prey. Aggregation of webs using trophic criteria affects webs' properties only slightly[13]; in contrast, progressive aggregation by taxonomic affinities alters webs' properties more rapidly (K. Schoenly and G. Sugihara, manuscript in preparation).

Recent studies to address limitations in the data (for example, refs 14–18) have generally confirmed the patterns. The pattern

## BOX 1. Definitions of web features and analysis of the *Nepenthes* web

Top predators are species on which nothing else in the web feeds, basal species feed on nothing within the web, and intermediate species have both predators and prey within the web. Linkages are trophic connections between species.

Cycles occur where, for example **j** eats **i** and **i** eats **j**, or **i** eats **j**, **j** eats **k** and **k** eats **i**. Cannibalism is a cycle where one species feeds upon itself.

Connectance is the number of realized trophic interactions divided by the number of possible interactions. Within this definition are several closely related variants. The number of possible interactions may be $S^2$ if cannibalistic interactions are counted, $S(S-1)$ if only inter-specific interactions are counted. We may assume that for each linkage between predator and prey there are two interactions: the effect of the predator on the prey, and the effect of the prey on the predator. Alternatively, we may assume that either of these two effects are dynamically zero. Typically, connectance is calculated from twice the number of observed linkages divided by $S(S-1)$ for the number of possible interactions. Hence, when the number of links per species (linkage density, $d$), is constant, connectance declines approximately hyperbolically with increasing number of species.

The trophic level of a species in webs of linear structure is one more than the chain length, that is, the number of linkages between it and the basal species in the web (which may be plants or detritus). In reality, species may trace linkages to basal species along food chain pathways of different lengths.

Omnivores are species that feed on more than one trophic level[9]. Omnivores blur the distinction between trophic levels, because top predators may trace linkages to basal species through food chains of different lengths. Omnivory can involve either different food chains or the same food chain. In the latter case, for example, an omnivore may feed on both a prey species and that prey species' prey species. Other definitions of omnivory are possible[20].

Compartments exist when linkages are few (or weak) between groups of species and common (or strong) within those groups.

*Species analysis*
Number of top predators is 7: species **1, 2, 3, 10, 11, 14, 15**.
Number of basal species is 3: species **17, 18, 19**.
Number of intermediate species is 9: the rest.
Number of linkages: intermediate to top 14; basal to top 4; intermediate to intermediate 8; basal to intermediate 7.

*Cycles.* There are no cycles in this web.

*Connectance and linkage density.*
Connectance = 0.19 (calculated as twice the number of linkages divided by $S(S-1)$). Linkage density = 33/19 = 1.74.

*Chain lengths*
Minimum 1: for example, species **1** to **17**, **15** to **19**. Maximum 4: species **1** to **4** to **9** to **16** to **19**.
Modal number for each top predator: species (Mode)
**1** (3); **2** (2); **3** (3); **10** (1); **11** (1); **14** (2); **15** (2).

*Omnivory.* In this web omnivory occurs via different chains, for example, species **1** to **17** and **1** to **18** and **19** via longer pathways, and also within chains, for example, species **1** to **5** and **1** to **4** to **5** or species **9** to **19** and **9** to **16** to **19**.

*Compartments*
None in this web.

There may be a correlation between the number of species of prey each intermediate species exploits and the number of species of predators that exploit the intermediate species

| Intermediate species | 4 | 5 | 6 | 7 | 8 | 9 | 12 | 13 | 16 |
|---|---|---|---|---|---|---|---|---|---|
| No. of prey | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 2 |
| No. of predators | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 7 |

least likely to survive detailed scrutiny involves the linkage density, $d$, which is the number of trophic linkages $L$ per (trophic) species $S$. Averaged over webs in the range from 3 to 48 species, the average number of linkages ($E(L)$) is roughly twice the number of species[6] in any given web (that is, $E(L) = 2S$; $d = 2$). This is equivalent to a hyperbolic relation between connectivity $C$ and species richness $S$ (see linkage density in Box 3). In the original description of this pattern[6] it was noted that a power-law $E(L) = kS^{1+\varepsilon}$, for some small positive $\varepsilon$, was also a viable description of the data, and that future data on webs with large numbers of species would have to distinguish the alternatives. With a few larger webs in hand, a power law with $\varepsilon$ probably between 0.3 and 0.4 indeed seems reasonable[6,19].

## What the patterns do not show

Although most analyses ignore the problem, web structure varies over time and space[15,20]. A useful distinction[21] is between cumulative webs gathered over many occasions (the majority of the published webs) and time-specific webs. In most of 16 habitats with reported time-specific webs, the percentages of top, intermediate and basal species fluctuated widely, generating appreciable variation in predator-to-prey ratios, mean chain length, and linkage density[21]. Within any one habitat, cumulative webs usually overestimate linkage density and underestimate the percentage of basal species relative to time-specific snapshots[21]. Web statistics are sensitive to occasional rare species (typically large, generalized predators) encountered on only some sampling occasions.

Comparable systems involving related taxa and/or similar habitats reveal differences in web statistics from place to place within one region[15] and locally within a single habitat[14]. The significance of these differences is not well understood.

The question of how to define the boundaries of a web is particularly vexing. Most investigators tacitly admit that members of most webs, particularly those higher in the food chain, feed outside the system studied. Published webs are reticulate, with no evidence of compartments (Box 3) except, possibly, fuzzy ones at habitat boundaries[9]. Given the apparently arbitrary nature of the boundaries of most studies, one conclusion must be that web statistics are roughly independent of spatial scale. This leaves open the question of whether spatial and temporal variation in web structure are interchangeable[21]. In certain physical systems, a single system observed over a long time period reveals variation that is identical to that observed in many systems of the same kind simultaneously but at different places. Interchangeability of temporal and spatial variability is called ergodicity; we do not know whether web statistics are ergodic.

## Differences between systems

Although webs have common features across a wide range of habitats and taxa, there is some variation. Counter to earlier predictions, average food-chain lengths do not seem to differ greatly among ecosystems with very different primary productivities[6,9]. There are only slight differences in chain lengths between communities where the consumers are often vertebrates compared with those where the consumers are all invertebrates[22,23]. Chains may be shorter in small habitat patches. Thus, on very small islands predators present on larger islands may be absent, and small ponds may lack the predators of larger lakes[19]. In some special microhabitats, chains are shorter in areas with frequent natural or experimental disturbances[24]. Reported chains are shorter in two-dimensional habitats such as grasslands and the intertidal than in three-dimensional habitats such as forests or the water column of lakes or oceans[6]. Intertidal ecologists, however, do not record the predatory fish that visit their systems at high tide, whereas those working below the low tide mark do. Hence, different average chain lengths may be an artefact of different academic traditions or, as discussed in ref. 19, a genuine difference in the effects fish have on bottom-living versus free-swimming prey. We caution against

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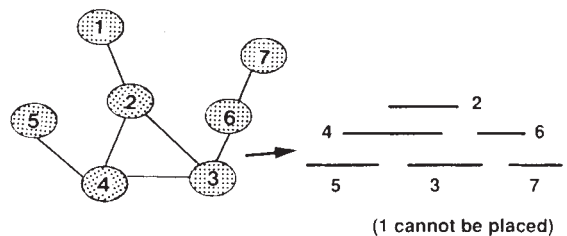**BOX 2. Predator and prey overlap graphs**

From a given web, we can obtain another graph, called the predator overlap graph. In this graph, an edge connects predatory species that share one or more species of prey in their diets. There may be more than one set of connected predators: these sets are called components.

Predator overlap graphs are rigid circuit, when every circuit around four or more predators is divided into triangles by one or more edges across the circuit. Below is a hypothetical overlap graph that is not rigid circuit, it would be if an edge joined predators **1** and **4**, **2** and **3**, or both.



(3 cannot be placed)
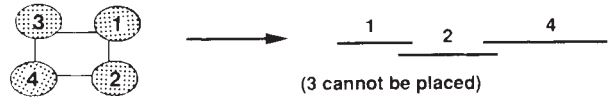
A web is defined to be interval if each predator can be represented by a line segment and the overlaps in the predators' diets are exactly represented by the overlaps among the line segments. The hypothetical graph above left is not interval because the interval that represents predator **3** cannot overlap the intervals that represent predators **1** and **4** without also overlapping the interval that represents predator **2**, contrary to the graph.

For many arrangements of predator overlap graphs, the rigid circuit property ensures that the overlaps will have an interval representation. Yet the rigid circuit property does not guarantee that food webs are interval. Below is a non-interval, rigid-circuit predator overlap graph. There are no circuits around four or more species. It is still not possible to express the overlaps as overlapping segments of a line, because any segment for predator **1** that overlaps the segment for predator **2** must also overlap the segment for predator **3** or **4**, contrary to the graph. This pattern is called asteroidal and the example comes from 7 species of gastropods in the genus *Conus*, from ref. 29 and original work by ref. 55.



(1 cannot be placed)

Prey overlap graphs are formed by connecting prey species sharing one or more predators. Two prey sharing predators form a line, three a triangular plane, four a tetrahedron, and so on. Some prey species will be used by more than one predator and this allows us to assemble the individual graphs into a complete picture describing the relationships between predators and prey. Now consider a physical analogy of this overlap graph with the objects formed by connecting the various prey species that share a particular predator being considered to be solid. It is possible for this physical analogy to have holes; topological holes are their equivalent in the graph. Topological holes are rare in webs with small numbers of species[8], but Fig. 4 provides an example.

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hasty and uncritical comparisons of web features, especially now that the availability of a collection in machine readable format[7] makes such comparisons easy. More convincing contrasts in patterns will be revealed within sets of webs specially collected for the purpose by the same scientists[11,14–18,20].

In web studies, omnivory has a special meaning (Box 1). Webs are said to contain omnivores when species can trace the energy they obtain through pathways of different lengths. Although still poorly studied critically by a single investigator, the extent of omnivory apparently varies between systems[9,19]. Omnivory is statistically rare in some webs, but there are at least three important exceptions. Aquatic webs often have as their top predators fishes that start their lives as very small

zooplanktivores and thus 'eat their way up the food chain' as they grow. Detritivores often pay little attention to the former trophic position of species now dead. Finally, webs composed of insects and their parasitoids often contain species that feed facultatively on many different species at different trophic levels.

## What causes the patterns?

How many independent web patterns are there? Which patterns are the consequences of others? What causes the patterns? A variety of evolutionary and natural history explanations have been put forward for particular web properties (reviewed in refs 9 and 25). Although we do not dismiss these explanations (most have been poorly investigated), we wish to focus on two more general explanations: the cascade model and web dynamics.

## The cascade model

The cascade model[6] focuses on the static patterns of trophic interaction and assigns linkages at random subject to two constraints. First, the model assumes that species can be arranged *a priori* into a cascade or hierarchy such that a given species can feed only on species below it, and itself can be fed on only by species above it in the hierarchy. This ordering automatically precludes cycles (Fig. 2; Boxes 1 and 3) and decomposer loops. It does not specify whether any particular species must be top, intermediate, or basal (except the lowest and highest species in the cascade). Second, the model requires two parameters obtained empirically: $S$ and $d$. By assumption, connectance declines hyperbolically.

By assigning linkages randomly within these constraints, the cascade model generates quantitative predictions that can be compared rigorously with observed patterns. It correctly predicts the average and variance of the fractions of all species that are basal, intermediate, and top predators (Box 3); the average fractions of linkages that are basal–intermediate, basal–top, intermediate–intermediate and intermediate–top (Box 3); the modal length of chains from basal to top species (Box 3); and the decline in the frequencies of interval and rigid-circuit predator overlap graphs (Box 3) as webs get larger.

The cascade model has not yet been used to explore some features of webs that merit attention, such as omnivory, compartments (Box 3), and the ratios of how many prey species a species exploits to how many predatory species that species suffers (Box 3). It also gets some of the fine details wrong though, again, problems in the quality of the data may be partly responsible for the discrepancy. For example, predicted declines in interval and rigid-circuit predator overlap graphs as $S$ increases are too rapid, and the predicted frequencies of very short and very long food chains within a given web are too high.

The assumption of constant linkage density is challenged by data on species-rich webs (above). An increase in linkage density with the number of species has been incorporated in a variant of the cascade model[12] which, surprisingly, produces a poorer fit to some other observed patterns than the original model. Obviously, the cascade model is very simple, making it easy to refine in various ways, while retaining the essential feature of a trophic cascade. Of 13 such variants[12] only one does as well as or, in some cases, better than the original model in predicting observed web properties. This variant has yet to be tested in detail.

The original formulation of the model offered no explanation for the postulated trophic cascade. Body size is a likely candidate[26] because typically predators are larger[27] than their prey, and parasites are smaller[25,26]. The relationship between the size of a predator, the size of its prey, and their positions in the web is important[28] and not fully explored.

What determines the linkage density? Quantitative theory to explain why the average species apparently utilizes, and is utilized by, a predictable and fairly small number of other species is crucial to a deeper understanding and ultimately testing of the model. We offer one explanation below.

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### BOX 3. Features common to published community webs and their associated graphs

Features of the web itself
- Cycles are rare[5]. (The definitions of cycles and of other terms in this box are in Boxes 1 and 2.)
- The average proportion of top predators, intermediate species, and basal species remains roughly constant (but with high variance)[5] in webs with widely differing numbers of species and from different habitats.
- The average proportion of trophic links that are between intermediate and intermediate species, intermediate species and top predators, basal species and intermediate species, and basal species and top predators remains constant[5] (with large variance) in webs with widely differing numbers of species and from different habitats.
- Linkage density seems to be approximately constant for webs with few species, but may increase with large numbers of species (see text).
- For top predators, the modal food chain lengths are typically 2 or 3, with lengths of only 1 being less common (and perhaps representing incomplete information) and those greater than 3 being uncommon[5,9]. Correspondingly, the modal number of trophic levels is 3 or 4.
- Omnivory is rare in some webs, though there are many exceptions (see text).
- Habitat boundaries sometimes impose compartments on food webs. Compartments are not usually observed within habitats[9].
- For intermediate species, how do the numbers of species they exploit correlate with the numbers of species exploiting them? Studies of species at the same trophic levels in different systems (for instance insect herbivores or parasites) typically do not find a significant correlation[9,54]. Within a food web, species at higher trophic levels tend to have more prey and fewer predators than species at low trophic levels, an observation predicted by the cascade model[5].

Features of the predator overlap graphs
- Webs with small numbers of species only rarely have predator overlap graphs that are not rigid circuit[5].
- Food webs with small numbers of species usually have interval overlaps in the predators' use of prey species[5].
- For many arrangements of predator overlap graphs, the rigid circuit property ensures that the overlaps will be interval. Yet the rigid circuit property does not guarantee that food webs are interval because of the asteroidal pattern. Such asteroidal patterns of overlap are unusual in webs with small numbers of species[5].

Features of the prey overlap graphs
- Topological holes are rare in webs with small numbers of species[8].

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## Web dynamics

Most webs are static descriptions, but the communities they describe are not static. Some species are successful at invading a community whereas others are not and the successes may or may not cause extinctions of former residents. This process of assembly and disintegration may explain many of the empirical web patterns[9,29]. It is not incompatible with the cascade model because it suggests general mechanisms that limit linkage density and species richness, while making specific predictions about the details of web patterns.

The idea that web patterns are shaped by dynamic constraints on assembly and disintegration was first formulated using Lotka–Volterra equations[9,25]. (These are sets of quadratically nonlinear first-order constant coefficient differential equations. Each equation determines the rate of change of a species in the web, from the density of every species with which it interacts, as well as its intrinsic birth and death rates.) Such analyses distinguished stable (persistent) from unstable web structures and so concentrated on the disintegration of webs. In general, these models predict that systems with high linkage density $d$ will be unstable; the critical value of $d$ declines with increasing $S$. Recent models assembled complex communities from simpler ones and found comparable results: models with low $d$ for a given $S$ are more likely to be invaded[30–32]. Moreover, once $d$

and $S$ have come into dynamic equilibrium, each successful invasion makes subsequent invasions less likely[32,33].

Although based on extremely simple models, the processes uncovered are often intuitively sensible, as can be seen from their specific predictions. Consider the difficulties of entering highly connected webs. If invading predators overlap in their prey use with existing predators, levels of interspecific competition will increase, reducing the chance of successful invasion or making the persistence of competitors already in the web less likely. Either way, this process limits species richness and linkage density. Less familiar is the process of apparent competition[34] between species of prey that share the same predators. An increase in one prey species may cause an increase in the shared predator and a consequent decrease in the other prey species. High linkage density makes shared predators more likely, apparent competition stronger and webs harder to invade as a consequence. Competition and apparent competition acting in concert may generate constant predator-to-prey ratios in webs[35].

Species may enter the top of existing food chains. Long chains, however, reduce the rate at which population densities recover from environmental disasters[9] making the persistence of species in long chains unlikely and invasion more difficult. This argument explains why chains appear shorter in unpredictable systems and conceivably explains why insect-dominated chains are short[22]. Insects have particularly variable population densities and may therefore have much larger minimum viable population densities than vertebrates[29].

The scarcity of omnivory in some systems may be due to the obvious difficulties encountered by a species that is both the prey and the competitor of a resident species. Alternatively, a successfully invading omnivore may locally exterminate a resident species on which it can both feed and with which it competes, so forming a food chain without omnivory. In contrast, when each of the omnivore's life history stages depends critically on resident species at progressively higher trophic levels as the omnivore matures, the omnivore cannot eliminate these intermediate species and still persist[36]. Dynamic models also predict that omnivory will be common in decomposer systems (because the consumers are donor-controlled[25]) and in communities of insects and their parasitoids[25]. Other approaches to dynamic modelling of food webs are under investigation[28].

## Concatenating dynamic and cascade models

Dynamic models contrast in purpose, technique, and accomplishment with the cascade model. The dynamic models attempt to explain why some web features are rarely or frequently observed in nature, without saying exactly how rarely or how frequently. These models rest on several largely untested assumptions[37] but offer insight into large questions of community structure, stability and change that are currently beyond the scope of the cascade model. By contrast, the cascade model aims for quantitative explanation, unification and prediction of observed patterns. It rests on extremely simple assumptions that are susceptible to direct test (possibly after additional interpretation, as when the cascade is supposed to be an ordering by body size).

Careful observations and experiments on spatial and temporal variation in webs may reveal more about the roles of the cascade and the dynamic models. For example, seasonal changes in web structure may differ from successional changes. Dynamic models predict that unstable webs from early successional habitats should depart significantly from the norm, for example, in having unusual and widely fluctuating predator-to-prey ratios[35]. The predictions of the cascade model for this situation have yet to be developed.

In real ecological communities both population dynamics and trophic structure are important. A new hybrid model, the Lotka–Volterra cascade model (LVCM)[37], assumes the population dynamics of the Lotka–Volterra model when the interactions between species are shaped by a refinement of the cascade model. The LVCM displays an ecological phase transition: gradual changes in the probabilities of various kinds of interactions related to feeding produce rapid changes in a community's probability of qualitative stability. The frontier of stability in this model differs from that of a classical model of May[38]. The LVCM makes possible a unified discussion of stability and trophic structure in a single, analytically tractable framework, but inherits the shortcomings shared by its parents, the Lotka–Volterra equations and the cascade model.

## Consequences of web patterns

The shape of food webs has inevitable dynamic consequences for constituent species. Our understanding of these consequences is growing quickly[29,39]. For example, the rate at which populations recover from disasters (resilience) theoretically should depend on food chain length[9], an idea now supported by a limited number of experimental studies[40]. Variability of population density depends on features of the species examined and on the variability of the physical environment. It also depends on web features such as the number of prey the species exploits, and the number of predatory species that exploit it[41,42].

Removal of individuals is a common experimental procedure in ecology[43-45]. Food web theory warns that it may be difficult to predict responses of unmanipulated species. For instance, permanent removal of a species' predator may ultimately cause the species' density to decline if the predator also fed on a powerful competitor. Theory predicts that even when the web is known, slight changes in the parameters that describe interspecific interactions may be amplified or dampened by complex pathways generating indirect effects between any pair of species[46-48]. In contrast to these final consequences of removals, there should be little doubt about the direction of the transient changes[46]. Thus, prey species should initially increase when their predators are removed: it takes time for indirect effects to appear. When we do see changes in density expected from immediate interactions with prey and predators, it may only be because of the typically short duration of field studies. At intermediate time scales, we should see effects rippling through the web, a feature illustrated by the relatively long-term studies of the removals of ants and rodents from desert communities[49].

Web theory has addressed changes in species composition, and in the total density of a group of species when species are manipulated or removed[29]. Theory predicts that highly-connected (complex) communities should be most sensitive to the loss of species from the top of the web because secondary extinctions propagate more widely than in loosely connected (simple) communities[29]. In contrast, simple communities should be more sensitive to the loss of plant species than complex
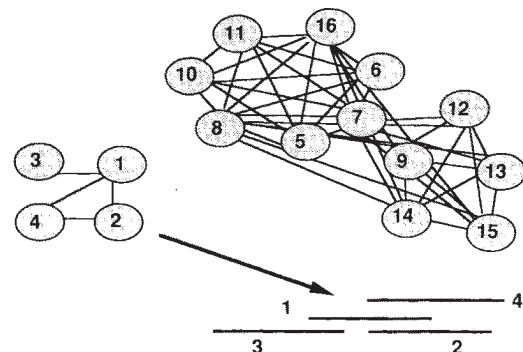


FIG. 3 Predator overlap graph for the *Nepenthes* web. In the *Nepenthes* web there are two connected sets of predators one involving four predators, the other involving the other twelve. The overlap graph in the component of the *Nepenthes* graph involving predators **1** through **4** is rigid circuit. Species **3** in the figure does not violate this condition because it is not part of a circuit around four or more species. In the *Nepenthes* web, the observed predator overlap involving species **1** to **4** is interval—as can be seen from the overlaps of the segments above right. (See Box 2 for terminology).
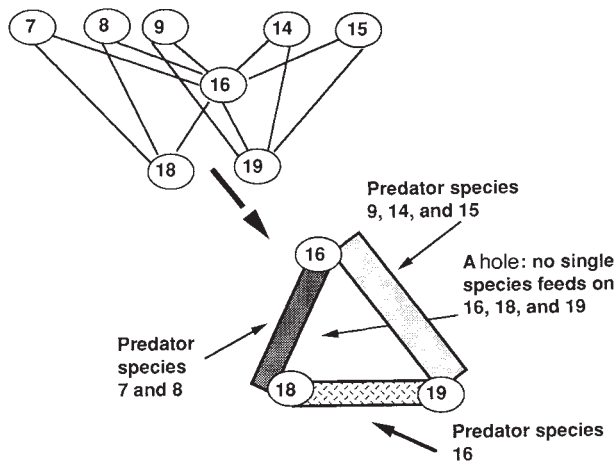
FIG. 4 Prey overlap graph derived from the *Nepenthes* web and the 'topological hole' formed by connecting the various prey species that share a particular predator (see Box 2).

communities, because in simple communities the consumers are dependent on only a few species and cannot survive their loss[29]. 'Keystone' species, those having disproportionate effects when removed, can occur at all trophic levels. Theory[50] has also addressed empirical findings[51] that when grazers are removed from a community, increased plant diversity is associated with large changes in species composition, but relatively small changes in total plant density.

## Whither food webs?

A major obstacle to progress in food web research is the weakness of the available data; this is more severe than a matter of not having enough webs. A bigger problem is the lack of methodological standards; the aim must be to reduce interobserver subjective differences in the way in which field workers observe and report webs. To assess the completeness of observations, Cohen[5] recommended a yield–effort curve, which plots the cumulative number of species and linkages against sampling effort. In a recent example[52], there is little sign of a decrease in the number of new species observed per field day after more than 5,000 hours of observation over 10 years. This finding supports the criticism, often made, that many published webs are grossly incomplete in the species and perforce in the linkages included. In such detailed studies, however, many of the linkages must represent rare and thus possibly dynamically unimportant events. The need to quantify the relative frequency of feeding interactions is crucial.

Despite methodological and theoretical problems, we favour a cautiously optimistic view of the future of food web research. Present shortcomings in theory and data must serve as a spur to refining both; they are not a reason to discard emerging insights and understanding.

Nature presents ecologists with ecological communities as the natural units of analysis. Though boundaries may be drawn in different ways for different purposes, the given primitives of ecology are forests, lakes, watersheds, wetlands, shorelines, deserts, estuaries, oceans, and the like. Populations of a single species, and still more individuals of a single population, are abstractions from communities for the sake of analytical convenience. To a considerable degree, these abstractions have upstaged the communities from which ecologists isolate them. In this time of rapid environmental change, the many endangered species are only a drop in the flood of endangered communities. Although it is by no means the only, or a sufficient approach, a quantitative, predictive understanding of food webs would provide a better basis for solving many problems of applied ecology than is now available. The average proportions of species in different trophic positions is found to be roughly invariant in webs with different numbers of species: this finding has already been used, for example, in an estimate of the total number of species on earth from the number of known plant species[53]. We anticipate increasing use of food web theory in such disparate but pressing problems as the management of multispecies fisheries, integrated pest control, and predicting the effects of climate change on ecological communities. □

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