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FOOD WEBS: ROAD MAPS OF INTERACTIONS OR GRIST FOR THEORETICAL DEVELOPMENT?

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Introduction

Darwin (1859:59) envisioned natural assemblages as "bound together by a web of complex relations." The resultant trophic interaction can be presented as food chains or cycles (Elton 1927), now termed webs. These linked arrays of species are basic to ecology: all organisms consume and are themselves consumed, meaning that all organisms are embedded in food webs, with trophic links identifying the pathways of energy and matter transfer within the community. Recent interest in webs has been catalyzed by two innovative theoretical analyses: May's monograph (1973) emphasizing the dynamics of species-rich communities and Cohen's (1978) monograph concentrating on the static aspects of web structure and pattern. Since these pioneering efforts, an excellent review (Pimm 1982) has further promoted the subject. Collectively, these works heralded the arrival of food web theory, which attempts to distill rules of nature from general patterns of trophic interconnections. The primary data base for this theory is collections of food webs: an original 14 (Cohen 1977), increased to 31 (Cohen 1978), expanded to 40 by Briand (1983), with a further yet unpublished expansion to 62 (Briand and Cohen 1984), and now 113 (J. E. Cohen, F. Briand, and C. M. Newman, *personal communication*).

Food web theory centers around the idea of connectance. This idea is given some quantitative rigor by first calculating the maximum number of possible binary connections in an assemblage of S species, or $S(S - 1)/2$. The number of observed trophic links (t_L) is then converted to a connectance measure:

$$C = \frac{t_L}{S(S - 1)/2},$$

or the fraction of total possible trophic connections that are actually observed in nature. A second idea that focuses on connectance was proposed by May (1973); on the basis of local stability analyses of multispecies communities, May suggested that communities would tend to be stable if they satisfied the inequality

$$i(SC)^{1/2} < 1;$$

otherwise they would be unstable. Here i indicates mean interaction strength. This disarmingly simple inequality has been the object of food web analysis (Rejmánek and Starý 1979, Pimm 1982, Briand 1983): if one assumes the assemblages to be stable, and the unknown and perhaps unknowable parameter i to be more or less constant, then the product SC approaches a constant (Pimm 1980, 1982), and plots of C vs. S necessarily assume a hyperbolic form. One reason food web theory has become so popular is because S and C are easily extracted from published studies, and because the theory relates these conveniently obtained descriptors to fundamental dynamic properties. One point of this commentary is to argue that this supposed strength is in reality its Achilles' heel.

I have focused my criticisms on the use of connectance in the development of newer ideas on food webs. In order to avoid appearing critical of webs assembled by other biologists, I mainly discuss aspects of my own research, or that of associated students. First, I argue that the manner in which field biologists such as myself draw linkages is usually informal and idiosyncratic. The spatial scale of observation and the number of potentially separable habitats studied are never stated. Second, I suggest that aggregation of species into larger groups is unwarranted, in that it disguises much tropically important biology. Finally, I argue that mean connectance, rather than being an assemblage trait, is highly variable, with values dependent on a variety of arbitrary decisions. These arguments lead me to conclude that the notion of connectance as typically employed is not a sound basis on which to build a theory. Most important, I am not challenging the subject of the theory (food webs), or the necessity of theory itself, but rather the manner in which theory has been linked to data on natural communities.

Some Generic Problems Concerning the Raw Data

Information on trophic links is readily assembled: direct observation of the predation act, stomach analysis, indirect evidence such as bored holes or scrape marks, immunological techniques, scatology, and even plausible guesses, all suffice. The assembled evidence, presented as a pictured web or, better, as a matrix of predator and prey interactions, can produce an illusion of completeness. Only the original collector really knows, but four problems are probably rampant. (1) Not all species are equally observable or interesting. In the rocky intertidal communities I've examined, small, highly cryptic or ecologically subtle species (flatworms, amphipods, and small chitons, for instance) are often poorly known and underrepresented. (2) Species may be observable but so highly mobile that their residence time within the study area may be limited. As a result, organisms such as birds, fish, and certain crabs are surely underrepresented in food webs, although their trophic influences may be substantial. (3) Occasionally a transient species, one that should not be considered a member of the local assemblage, will be observed within the site. Should this event be recorded and portrayed? I would guess not, but the temptation is to err on the side of completeness at the expense of biological significance. Wandering starfish and, under the correct circumstance, humans are examples. (4) Species that exhibit size, age, or ontogenetic stage-related changes in diet are widespread and are not easy to position in a fixed food web. Starfish, chitons, and fishes all make such dietary shifts. Most or all of this detail is lost in summary statistics, yet its presence embodies very real web complexities that remain totally invisible to web analysts.

CONNECTANCE AND THE SPATIAL SCALE OF OBSERVATION

Food webs for particular communities are often amalgamated from several different study sites. At first glance this might seem like a wise decision since it overrides the small scale of much ecological research. However, the spatial scale of this procedure (metres?, kilometres?) bears major implications for the calculation of connectance. I argue here that, for webs that are dominated by relatively sessile marine invertebrates, dietary variations in space are apt to be greater than those produced by seasonal or interyear events at a site. This is because many marine invertebrates are long-lived, and even if their local dynamics are influenced by substantial numerical variation, they usually can be found and found feeding. Thus food web construction by an experienced observer within a site should not be hampered by temporal variation. On the other hand, major shifts in habitat characteristics associated with changes in the spatial location of the observations are apt to embrace some new resources and exclude others previously present. Species diets, then, should change qualitatively geographically, and no amount of local observation will serve to generate a complete web.

Data sets illustrating such geographic shifts are commonplace, and I have published two: Paine (1980) showed that the observed diet of the starfish *Pycnopodia* changed from five species in Washington state to 23 in Alaska, 10° of latitude to the north. In coastal Chile, the diet of another starfish (*Heliaster*) ranges from 18 to 29 known species. However, at any particular site, from 2 to 4 prey dominate the list, and their identities can change radically between sites (Paine 1983). A third example is given in Table 1, drawn from previously published work on the opisthobranch gastropod *Navanax* (Paine 1963, 1965). This sea slug tends to feed on shelled prey in sandy or muddy environments (Crown Point and the Flood Control Channel), and on nudibranchs at more exposed, rocky sites (Dike Rock). There is little ecologically meaningful overlap in the observed diets between sites. Clearly, a more synthetic view of the number of potential links leading from *Navanax* to its prey would be generated by combining the data sets.

TABLE 1. Differences by location in the natural diet (prey individuals fed on) of *Navanax inermis*. Dike Rock is a rocky area exposed to ocean swells; both of the other sites are protected soft-sediment environments. See Paine (1965) for more detail.

	Dike Rock		Flood Control Channel and Crown Point	
Taxa	*N*	% prey ind.	*N*	% prey ind.
Shelled opisthobranchs				
Bulla	0	0	223	30
Haminoea	0	0	284	39
Aglaja	0	0	56	8
Other (4 spp.)	9	3	87	12
Navanax	9	3	24	3
Nudibranchs				
Hermissenda	77	25	6	1
Polycera	104	34	0	0
Dirona	37	12	0	0
Triopha	10	3	0	0
Dorids (2 spp.)	10	3	0	0
Crustaceans	53	17	2	0
Fish	0	0	49	7
Total	309	100	731	100

However, I do not believe such spatial lumping to be justified: vacancies in diets (visually represented by holes in the web matrix) are bound to have both ecological causes and consequences. Generalizing the diet by combining observations from a variety of habitats disguises these locally important features and interactions. If web theory is to become predictive, for instance about the impact of deletions or additions of species on stability (Pimm 1982), it must be sensitive to the biological nature of species vacancies. Composite webs would disguise such detail. Further, experimental tests of web dynamics (e.g., Paine 1966, Pimm 1980) will surely be done at a very local scale. Spatially aggregated pictures of the distribution of links in whole webs will obscure or be insensitive to local dynamics and ignore such attributes as interaction strength (May 1973) or the presence or absence of critical species (Paine 1980). I suggest that local, process-oriented studies, as opposed to larger scale web amalgamations, will continue to be the best source of insights regarding food web patterns.

On the Choice of Biological or "Trophic" Species

A developing and seemingly useful convention among food web users is aggregating trophically similar biological or true species into trophic species. Briand (1983: 253) succinctly discusses his use of "kind or organism," a definition that encompasses food web entries ranging from individual species to "collections of functionally or taxonomically related species." Cohen (1988) similarly defends his use of aggregations termed "trophic species." In most cases, the original data have been scrutinized, edited, or sanitized, and then reworked in some fashion before being aggregated.

One major drawback of this practice is that most ecological theory requires that populations or species be segregated as n_1, n_2, n_3, ... Identification of the individual dynamics requires such specification. Aggregation of taxa into more inclusive and convenient units ("plankton," trophic species, guilds, functional groups, even trophic levels) must either remove treatment of web dynamics from web structure, or require mathematical approaches independent of the recognition of species individuality. May's (1973) classic study retains the sanctity of the species: it is an appropriate example to emulate, and one that most field observers appreciate.

One consequence of aggregation has already led to fascinating, though perhaps spurious, prediction. Cohen (1978) and Briand and Cohen (1984) have discovered scale-invariant structure in the collection of webs: specifically, predator : prey ratios remain constant at $\approx$4:3 over the range of web entries employed. Such results will surely depend on persistent biases in the practice of aggregation. I concur with Pimm (1982: 168) that aggregation is commonplace at the bottom of webs, because the species tend to be smaller, less observable, less well known ecologically, and perhaps more similar, and rarer at the higher trophic levels. Such procedure is certain to minimize the number of prey categories. Predator : prey ratios may very well be scale invariant, but until the above bias is examined closely the hypothesis that it and especially its numerical value is just a procedural artifact remains unchallenged.

There is probably no reasonably sized community in which the trophic architecture has been completely described. Thus all portrayals are incomplete and will only be made more so by the dual processes of aggregating species into larger units and "editing" webs. I believe that analysis of such biased and massaged data does not provide a convincing basis for development of predictive theory. An argument supporting this view is that analyses reveal comparable patterns in webs composed primarily of identified species and in webs whose nodes are generated by aggregating species into taxonomically vague, inclusive units; this suggests that pattern is a product of the analysis and is insensitive to the biology (Cohen 1988). Alternatively, of course, it could suggest that some robust and unifying rule has been discovered.

Two Examples of Food Web Construction and Analysis

Arbitrary decisions to delete or add species to webs and to aggregate species into guilds or even trophic groups are common to all field studies and are dictated by necessity and by the author's interests. They are useful in the sense that they set bounds to the study, and they are totally arbitrary in that no guidelines or rules are applied.

Example 1.—Menge and Sutherland (1976) illustrated a web for protected shores of New England. Much of the supporting biological and experimental detail is available in Menge (1976). Subsequently some of these conclusions were challenged by Edwards et al. (1982), which elicited an effective rebuttal (Menge 1982). This body of papers portrays the changes in connectance values introduced by aggregating species or by adding new consumers. Five views of the same assemblage are given in Table 2. In the simplest form, when *Littorina* is located as a single entry, $C = 0.36$. When each of the three *Littorina* species is recognized, C decreases to 0.31. If a crab (*Carcinus*), fish (*Tautoglobarus*), and a complex of birds-mammals-fish are added to the original web, as suggested by Edwards et al. (1982), C increases to 0.44. When both birds-mammals-fish and *Littorina* spp. are distinguished within their respective groupings, $C = 0.46$. Another decision, not in the original papers, could have been made to exclude consideration of the obviously complex, heterogeneous groupings of "algae," "detritus," and "plankton." If this were done, C would equal 0.61.

Grounds can be found to justify each of the above modifications. Thus, trophic connectance values for this one community range from 0.31 to 0.61, which spans about half the range of 0.05–0.60 given by Yodzis (1981) for the 40 webs presented in Briand (1983).

Example 2.—Animals inhabiting marine rocky shores are readily observed and hence facilitate the

TABLE 2. The effect on connectance values (C)* of the subjective decision to add consumers or to disaggregate them. N = number of entries; t_L = number of trophic links observed; max t_L = the calculated maximum number of possible trophic links. See Two Examples of Food Web Construction and Analysis: Example 1.

Treatment	N	t_L	max t_L	C
Original MS† food web, with 3 *Littorina* species aggregated	8	10	28	.36
Original MS† food web, but with 3 *Littorina* species disaggregated	10	14	45	.31
Edwards et al.‡ reconstruction of original MS web	11	24	55	.44
Edwards et al.‡ reconstruction with birds-mammals-fish and 3 *Littorina* species all disaggregated	15	48	105	.46
As above, but with heterogeneous groups (plankton, algae, and decomposers) removed	12	40	66	.61

* $C = \dfrac{t_L}{S(S-1)/2}$.

† Menge and Sutherland 1976.

‡ Edwards et al. 1982.

assembly of feeding records in this environment. At least five views of food webs from the Pacific shores of North America have been published, all in graphical rather than matrix form. Despite its geographic extent, the biota on exposed rocky shores is remarkably comparable throughout. Thus, in some sense, each web represents a subsample. These five are discussed individually below, both to provide some anecdotal detail about how personal idiosyncrasies influence web construction, and also to illustrate the high between-study variation in connectance values (see Table 3).

Hewatt's (1937) study was executed in Monterey Bay, California, from 1931 to 1934 at the site of the Hopkins Marine Station. His purpose was to determine the "nature and causes" of zonation on a rocky shore. He paid special attention to feeding relationships, and summarized his observations on an exposed point as a food cycle, using Elton's (1927) terminology.

I have given two views of the food web on the Washington state outer coast. In one (Paine 1966), my intentions were to focus on the community role of the starfish *Pisaster ochraceus* and to illustrate, using a web, that proportions of the diet differed depending on whether numbers of items or units of energy were considered. No attempt was made to be comprehensive; focus was on one specific subweb. Observations were assembled over the period November 1963–November 1964, solely at Mukkaw Bay. A more extensive view of the major feeding pathways of the same community was given in Paine (1980). The resultant webs were drawn as "idealized pictures," and were generated by observations from 1963 to 1979 at three outer coast sites in Washington and from more limited observations in coastal Alaska.

The exposed coast web portrayed in Menge and Sutherland (1976) was based in part on Paine (1966) but also on Menge's doctoral research (Menge 1972*a*, *b*) on the small carnivorous starfish *Leptasterias.* Its inclusion enriches the web slightly, and illustrates the strong subjective element characteristic of all food web construction: Menge probably wished to portray "his" starfish as coequal to "mine."

I have calculated some of the standard food web statistics (Table 3) for these five views of the same community. Note that these sorts of webs provide the fundamental data base, and one has actually been examined for patterns. I have, again, not included links to the highly aggregated primary producers or plankton. Two sets of calculations have been made: in the one based on aggregated categories, as provided in the original presentations, connectance varies from 0.07 to 0.40; in the maximally disaggregated view, in which most of the nodes are biological species, connectance varies from 0.08 to 0.30. When these are added to Fig. 5.1 of Pimm (1982) they are seen to fall along the same hyperbolic trend (Fig. 1). Although other hypotheses are available (Pimm 1982), the one I prefer for the hyperbolic relationships that have fascinated food web theorists is what I call "artistic convenience." When S

TABLE 3. Food web statistics for the Pacific Coast rocky intertidal assemblage on exposed shores. N = number of entries, t_L = number of trophic links observed, max t_L = calculated maximum number of possible trophic links, and C = connectance value.

Source	Categories*				Species†			
	N	t_L	max t_L	C	N	t_L	max t_L	C
Hewatt 1937	5	4	10	.40	25	55	300	.18
Paine 1966	7	8	21	.33	11	14	55	.25
Menge and Sutherland 1976	10	16	45	.36	15	32	105	.30
Paine 1980 (Washington)	27	23	351	.07	42	67	861	.08
Paine 1980 (Alaska)	19	26	171	.15	30	79	435	.18

* Aggregated units.

† Entries disaggregated to the lowest possible taxonomic unit.

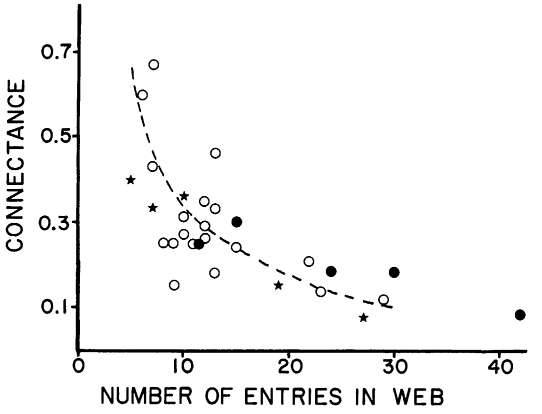

FIG. 1. The hyperbolic relation between connectance values (*C*) and the number of entries in the web. ○ points from Fig. 5.1 (Pimm 1982:90); ★ data from "categories," ● data from "species," in Table 3. The ★ and ● points suggest the potential magnitude of within-assemblage variation of these two webs' parameters.

is small, more links can be portrayed; when *S* is substantially higher, only the links that are deemed to be most meaningful are drawn, and connectance is correspondingly reduced. Necessity for graphical clarity, then, results in the omission of some links: Paine (1980: Fig. 2b) illustrates two links for *Pycnopodia,* whereas five are mentioned in the text. The numbers, respectively, for *Pisaster* are 17 and 41 and for *Leptasterias* 4 and 19. Such pruning for artistic purposes renders obscure the meaning of further elaborations based on connectance measures.

LINKAGE AND WEB STABILITY PROPERTIES

The relationship between connectance, or complexity, and the stability properties of webs has been much debated. This tie, of potential ecological significance, suffers in at least three ways. First, I have presented my views on the arbitrary nature of determinations of *C* in one assemblage (Fig. 1, Table 3). If this variability in *C* (0.08–0.30 or 0.07–0.40) characterizes most of the webs assembled by Cohen and Briand, prior to being sanitized, then any conclusions about whether stability can or cannot exist are tenuous.

Second, stability of intertidal assemblages in Washington State and New Zealand, where stability is defined on the basis of community change subsequent to starfish removal, seems more related to the competitive status of certain prey than to the linkage patterns of the entire web (Paine 1971, 1974, 1980). For example, *Pisaster* is linked to a minimum of 41 prey, whereas *Stichaster* connects with many fewer, yet their influences on stability are comparable because both appear capable of controlling the distribution and abundance of a superior competitor for space. Thus, assemblage stability appears to bear little relation to *C*. The reason is that *C* glosses over the single biological detail most important to the effect of these predators: the competitive status of their prey. If food web theory is to become predictive in a dynamical sense, it must incorporate competitive status.

Finally, as often noted, what the field ecologist recognizes as stability following application of brute force manipulations to the assemblage is vastly different from the local or global stability analyses performed by a mathematician. Although field ecologists are hammering out descriptive details of their nomenclature for stability (Sutherland 1981), and identifying constraints (Connell and Sousa 1983), there is little evidence that empirical and theoretical stability terminology share a common operational basis.

CONCLUSION

Food webs are too central to ecology, community and ecosystem studies especially, to be dismissed summarily. Whenever as few as two species interact, a link is formed: natural communities, however defined, obviously are characterized by scores if not hundreds of links, which generate the basic structure of connectedness food webs (Paine 1980). They are what naturalists have observed and assembled to provide a convenient, qualitative guide or road map to those relationships that fascinated them. Food webs are guides to relationships, and scanning them allows a reader to assimilate much complex information rapidly. Quite literally, the picture is worth a thousand words. Food webs are of necessity always incomplete; most if not all are idiosyncratic to some degree. Most important, these qualitative descriptions were never intended to be data, to serve as grist for the theoretician's mill.

I do not believe that clever theory can overcome this handicap and generate testable, interesting predictions about web structure and dynamics. Profitable theory can be done, and often is, for theory's sake. However, when theory is developed in concert with data, the partnership should be more or less equal. This has not been the case with food webs, where theory seems far ahead of the data, often to the theory's detriment. I know of no one who, having assembled a data set on feeding relationships, considers those data to constitute much more than an incomplete preliminary description.

I believe a fresh start is called for. My own view (Paine 1980, 1983) is that connectance is too arbitrary a measure to be useful. Thus, future, connectance-based development, even from sanitized webs, will not be enormously profitable. We should abandon aspects of the theory that relate connectance to stability or that emphasize invariant predator : prey ratios.

Natural systems are dynamic and continually changing, with distance from equilibrium being an important unknown. To me, this implies that focus on dynamic rather than static (= completely descriptive) properties would constitute a primary desideratum. I wish to make three suggestions that, although they do not make the study of webs easier, might ultimately yield more convincing or inspiring results.

1) At the least, theoreticians should ask whether the web under consideration is a biologically realistic representation of that community. Common sense is probably the best guide here. For examples: web number 11 in Cohen (1978) employs such aggregate terms as "invertebrates" and "fish," and has major marine and terrestrial components; in matrix 29 (in Briand 1983) the top species are individually treated ("right whale," "bearded seal") while the bottom ones are extensively aggregated ("clupeid fishes," "benthonic invertebrates"); and the aspen parkland web in Sugihara (1984) is based on excessively general interpretations of consumer prey categories.

2) Whenever possible, species should be identified rather than aggregated so that individual roles can be identified and ties to mainstream ecological mathematics facilitated, and especially, to represent more fairly the nature and quantity of links at lower trophic levels.

3) May (1973) identified three independent features of webs and their incumbent species that could influence trophic properties: the number of species (*S*), their average connectance (*C*), and mean interaction strength (*i*). Only the role of the last remains relatively unexplored, both empirically and theoretically. However, its exploration promises substantial simplification to current approaches. If species can be scored on the basis of their interaction "strengths," weakly interacting species can be ignored. I believe most species will eventually fall into that category, leaving the field to a few essential and dominant players. Such scores cannot be derived without experimentation (Paine 1980). However, once made, they offer a defendable criterion for inclusion and a tie to the concept of stability, itself requiring a rapprochement between empiricist and theoretician. A second rationale for examining interaction strength is that if it is not normally distributed within webs, then simulation models that employ average values could be misleading. And last, qualitative understanding of trophic cascades (Paine 1980, Carpenter et al. 1985), which clearly imply major shifts in all static web properties, or interaction-dependent community structure (Kerfoot 1983) are based on the concept of varying interaction strength.

Web metrics change in time and space. To ignore this feature alone, and the fact that species exert varying influences on web membership depending on both their density and specific identity, is to deny that natural systems are dynamic. Future web study, guided by theory, should seek dynamical solutions to patterns as, for instance, the hypothesis supported by field data that dynamics, not energetics, limits the number of trophic levels in a community (Pimm 1982). Such insights, however, constitute the barest of beginnings; newer developments not based on connectance will be required if ecologists are to continue a profitable exploration of the properties of food webs.

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