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Spatial and temporal variation in food webs in water-filled treeholes

R. L. Kitching

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Food webs have been drawn for the community of animals found in water-filled treeholes in south-east Queensland, Australia. Such webs have been constructed on a quarterly basis for each of 11 habitat units, using a technique which allows incorporation of relative abundance as well as presence or absence of a species. A significant inverse relationship was identified between the degree of similarity shown in the webs from pairs of treeholes and the intersite distances involved. No significant relationships could be identified between any of the foodweb characteristics – connectance, number of trophic levels, abundance indices or predators of saprophages – and the surface area of the treeholes. There was a significant inverse relationship between the mean relative abundance of the predators and the saprophages, their prey. Explanations for the results are examined, and the interaction of stochastic events and short- and mid-term environmental heterogeneity, it is suggested, best account for the observations. Such 'local' webs, shaped by stochastic events are contrasted with full 'regional' webs for which plausible deterministic explanations are available.

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Introduction

Considerable theoretical interest has been shown recently in the structure and control of food webs (see Cohen 1982, Strong et al. 1984). Although theoretical developments and field evaluation have not proceeded at the same pace, Briand (1983) was able to examine pattern and its environmental correlates across 62 real webs collated from a very scattered literature. The present work contributes to this body of fieldbased information.

Virtually all the studies from which food webs used in the analyses of Cohen (1978), Pimm (1982) and Briand (1983) are drawn, represent the results either of extensive study of a particular ecosystem at a particular time or more lengthy studies through time. By their very nature, these are unreplicated; for example, the food webs of Morgan's Creek, Kentucky or Bear Island are unique statements about particular places. Such summations are useful bases for the generation of general theories

about food web structure but food webs do vary in space and time on a local as well as on a biogeographic scale, and it is this local variation that is described here. For study of such smaller scale variation in web structure, ideally webs should be replicated within a given area. Plant-held waters or 'phytotelmata' provide one of the few situations in which such replication is commonplace and thus are ideal subjects for the study of food web variation (Kitching and Pimm 1985, Pimm and Kitching, in press, Beaver 1985). Phytotelmata are of five basic kinds: leaf and bract axils, bromeliad 'tanks', bamboo internodes, plant pitchers and water-filled treeholes. Each kind contains highly endemic, simple animal communities based, trophically, on the detritus which falls into them (see Frank and Lounibos, 1983, for a general treatment).

The food webs contained in water-filled treeholes have been described from several parts of the world and my own studies have focussed on English, Australian

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and Indonesian examples (Kitching 1971, 1983, in press, Kitching and Callaghan 1981). The full food web for such habitats in subtropical *Tristania* forests in south-east Queensland is presented in Fig. 1. This web, like those referred to earlier, is a summation of work on several sites over several months of sampling and, as such, represents a biogeographical statement about this habitat type for the whole region. It reflects the long-term coevolution of the species which are found within the treeholes with each other, with their physical surroundings and with the chemical and climatic environment within which they occur. However when the same data base is examined in more detail, the 'overall' web is seen to be the product of complex spatial and temporal variation and represents but the template on which the web seen at any one time and place is constructed: only parts of it are present on most occasions. This spatial and temporal variation in web structure is illustrated in this paper.

Methods

The study site

Lamington National Park lies just north of the New South Wales border in south-east Queensland (28° 12'S 153° 07'E). It is a region of tall, open forest and wet closed ('rain') forests with a wide variety of tree species (McDonald and Whiteman, 1979). The particular area studied (referred to as "The Box Forest" on local maps) is dominated by mature *Tristania conferta* R. Br. and *Agyrodendron actinophyllum* (F. M. Bail.) H. L. Edlin, which species contain the treeholes studied. Other particularly common canopy species are *Araucaria cunninghamii* Ait. ex. D. Don. and *Nothofagus moorei* (F. Mell.) Krasser. The region has a subtropical climate with July temperatures fluctuating between a mean minimum of 8°C and a mean maximum of 16°C, and January temperatures between 16°C and 25°C, respectively. Rainfall varies from a mean of about 100 mm in August to 500 mm in March. More than half the mean rainfall occurs in the summer, from December to March. The pattern of litterfall is discussed in Pimm and Kitching (in press). Essentially leaves fall all year, but there is a marked peak in late summer. All holes studied were bark-lined 'pans' (sensu Kitching 1971) located in the emergent buttress roots of the trees.

Sampling programme

Eleven treeholes were sampled monthly over the period September 1982 to August 1983. The holes were chosen to represent a variety of sizes (as measured by their surface area) and localities within the forest. Although two species of host tree were involved, earlier work had established that there were no differences in the species occurring in holes across the two species (Kitching and Callaghan 1981). On each sampling occasion, detritus

was removed from the holes first and then, following agitation, a sample of water present was dipped from each. Solid and liquid samples from each site on each occasion were mixed. I have discussed elsewhere the difficulties inherent in sampling repeatedly from a small unit of habitat and the necessary variation one must accept in so doing (but see below) (Kitching 1971). The total volume of the samples varied from 80 ml to 550 ml. In the laboratory, the volumes of the samples were measured by displacement before each was sieved to extract the animals present. Sieved animals were hand-sorted and counts made of the numbers of each type of animal present. All material was preserved for subsequent use. Counts were converted to numbers l⁻¹.

Interhole distances were calculated following mapping of the sites by triangulation and surface areas of the holes were estimated by regarding each as a sum of appropriate geometrical figures.

Construction of food webs

The web shown in Fig. 1 is based on actual observations of what eats what, strong inferences based on knowledge of closely related organisms, and information from the literature on particular species. It is drawn to be maximally connected: that is, if any doubt exists about the presence of a particular link, then it has been included.

For each treehole included in my twelve-month sampling programme, I have constructed four webs, each representing a summary of the presence or absence and levels of abundance of those species present in each three-month period of study. I chose to combine the twelve monthly estimates of densities into four quarterly measures to minimise the effects of the unavoidable

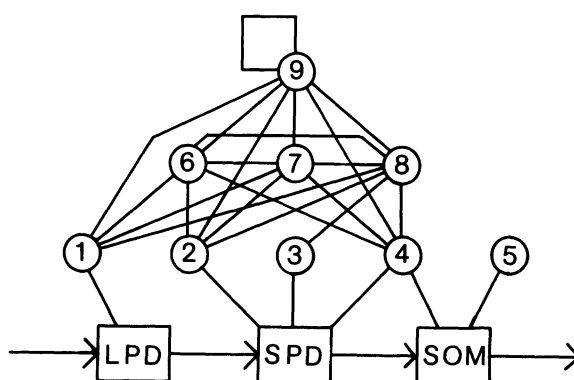


Fig. 1. The full 'regional' food web for the treehole community studied. Key: LPD – large particle detritus, SPD – small particle detritus, SOM – suspended organic matter, 1 – *Prionocyphon niger* (Scirtidae), 2 – *Clogdia* sp. (Psychodidae), 3 – algophagid mites, 4 – mosquito larvae, 5 – ostracods, 6 – *Anatopynia pennipes* (Chironomidae), 7 – *Culicoides angularis* (Ceratopogonidae), 8 – *Arrhenurus* sp. (Arrhenuridae), 9 – *Lechriodus fletcheri* (Leptodactylidae).

Tab. 1. Density ranges (l^{-1}) used in indexing the levels of abundance of species occurring in treehole food webs. The four ranges of abundance used are quartiles based on the log densities of the species over the four three-monthly periods of sampling (see text).

Species	Quartile 1	Quartile 2	Quartile 3	Quartile 4
<i>Prionocyphon niger</i> Kitching and Allsopp	25.1–73.4	73.5–214.6	214.7–627.6	627.7–1627.0
<i>Anatopynia pennipes</i> Freeman	0.0–3.4	3.5–11.9	12.0–41.4	41.5–143.1
<i>Culicoides angularis</i> Lee and Reye	0.0–3.3	3.4–11.2	11.3–37.8	37.9–126.8
Mosquito larvae	0.0–3.7	3.8–13.7	13.8–49.5	49.6–181.8
<i>Clogdia</i> sp.	0.0–3.5	3.6–12.4	12.5–44.1	44.2–155.9
<i>Arrhenurus</i>	0.0–2.0	2.1–4.0	4.1–8.1	8.2–16.4
Algophagid mites*	0.0–5.1	5.2–25.9	26.0–132.0	132.1–671.9
Ostracods	0.0–5.9	6.0–35.7	35.8–214.8	214.9–1278.5
<i>Lechriodus fletcheri</i> Boulenger			presence (+) or absence, only, recorded	

* This designation also includes small numbers of an undescribed, predatory ascid mite.

able variation in results associated with the sampling technique used. Mean abundances for each species present in each quarter were calculated. In order to incorporate a measure of the level of abundance of each species in the webs, I divided the full range of quarterly densities across all holes and time periods into four quartiles based on the logarithms of the numbers concerned. Tab. 1 shows the actual densities involved for each species in this process of simplification. The occurrence of the leptodactylid frog, *Lechriodus fletcheri*, was noted simply as presence or absence, as the sampling technique is not well suited to provide density measures of either the eggs or tadpoles of this species. Webs were then drawn using the full web (Fig. 1) as a template, but drawing in only those links defined by the particular set of species present at the place and time. The nodes were drawn using different sized symbols, depending into which abundance quartile the calculated densities fell. (Note that in the figures the smallest non-zero density is represented simply by the intersection of the appropriate trophic links: higher densities as solid circles of increasing size).

Analyses of the webs

A number of summarising statistics were derived from the webs constructed as described. For each site and time, the number of species present, the number of trophic levels, and the number of predatory and top predatory species were calculated. In addition, an abundance index for all the species in the web and the saprophagous and predatory segments of it could be computed. These indices were arrived at simply by summing the quartile measures described (1–4 in each case). The presence of *L. fletcheri* was incorporated into these indices by recording its presence as unity in the sum. A measure of connectance was calculated based on the ratio of the actual number of links present in a web for a particular site and time, to the total number of links

possible (as shown in Fig. 1). This statistic was calculated for each quarter and as an overall mean for each site. These measures, as well as the estimations on which they are based, have been used to describe spatial and temporal variation in web structure. The demography of the constituent species will be discussed elsewhere.

Although the primary aim of this paper is to develop and present *descriptions* of variation in food webs, the results of two subsidiary exercises which use some of the derived statistics, are included. The first of these tests the hypothesis that the patterns of variation among the 11 sites is related to the distance between them: that is, the pattern in any hole will be most similar to that in adjacent holes and the degree of similarity will fall off with distance. To test this hypothesis a correlation matrix was drawn up for the 44 data sets represented by the webs (11 sites \times 4 quarters). Correlation coefficients were drawn from this matrix for selected pairs of holes and the mean values across the four quarters calculated. Selection of pairs of holes was made on the basis of nearest neighbour distances, but without reusing the same pairs. Because eight of the eleven sites fell into sets of three, three and two respectively based on their close proximity one to the other, this meant that eight pairs of holes represented all the independent information usable in this analysis. The extracted correlation coefficients were used as data points to test the null hypothesis that there is no relationship between degree of similarity (as measured by the correlation coefficients) and inter-site distance. Secondly, I examined the possible role of the surface area of the treeholes in determining pattern or structure in the observed webs. I used surface area rather than volume as a measure of hole size firstly because it is impossible to measure hole volume with any accuracy without destroying the community it contains and, secondly, because, it can be argued, surface area is likely to be more important as the interface between the community and the rest of the world, through

which all invasion and energy input takes place. Essentially, I looked for significant relationships between the various abundance indices and structural measures with the surface areas of the holes sampled.

Results

Fig. 2 shows a selection of the 44 webs constructed as described. Each has been overlain on the full potential web for the region (shown as dashed lines in the figure). Tabs 2 to 4 contain summarising statistics on the food webs themselves and the trophic levels within them.

Food web statistics

The number of species present in the webs varied from three to seven (Tab. 2). No hole contained all nine species, either at any one time or through time. Only two sites achieved eight species through time although eight of the remaining sites did have seven of the nine species through time. Site 10 was the poorest overall, having but six species. There was much less variation in the number of trophic levels present over sites and times (as would be expected for a variable of such restricted range of values). Eight of the holes had three levels present on each occasion, whereas the remaining three had four levels on some occasions and never less than three such levels (Tab. 2). The numbers of species of predators and top predators present varied from one to four, with all sites having at least two present through time. The maximum number of predators present at one time was four, the maximum possible value (Site 2, Quarter 1)

The scores for the species' abundance indices within each web can be used as a guide to the numbers as well as the presence or absence of species (Tab. 3) (and bearing in mind that these statistics have the following ranges: all species, 0-33; saprophages only, 0-20; predators and top predators, 0-13). Overall abundance levels totalled in this fashion ranged from 5 (Site 1, Quar-

ter 2) to 20 (Site 4, Quarter 1), whereas the means per hole varied from 8.0 (Site 1) to 16.5 (Site 8). The indices for saprophages alone varied in value from 4 (Site 1, Quarter 2) to 15 (Site 5, Quarter 2). These two holes also showed the smallest (3.25) and largest (11.75) mean values. Lastly, predators and top predators varied in abundance, using this index, from 3 (several sites and occasions) to 12 (Site 2, Quarter 4). Site 2 also had the maximum mean value of abundance (9.0), whereas Site 5, one of the five showing the overall minimum value, had the minimum mean value of 4.0. Overall the saprophage index is more closely linked to the total abundance index, with a rank difference across sites of only 2.1 (Spearman's $R_s = 0.7159$, $0.05 > p > 0.01$), whereas a comparison between the rank order of means across sites for predators and top predators with total species shows a mean difference of 4.3 ($R_s = -0.1159$, n.s.). This contrast is not simply a reflection of the number of species involved within the two trophic designations, as there is but one more saprophagous species than there are predators and top predators. In addition, there is a weak but significant inverse relationship based on these ranks, between the abundance index of the predators and top predators and that for the saprophages ($R_s = 0.7072$, $0.05 > p > 0.01$).

Connectance scores defined as indicated in the "Methods" section, are presented in Tab. 4. The mean values across time range from 0.31 at Site 5 to 0.59 at Site 6, with an overall mean value of 0.42. Within site values range from a grand minimum of 0.15 (Site 1, Quarter 2) to a grand maximum of 0.77 (Site 2, Quarter 1). Within site ranges, a measure of temporal change in site-to-site quality ranged from 0.08 (Site 11) to 0.46 (Site 2) with an overall mean of 0.29. There is no obvious seasonality in connectance scores across all sites.

Comparing the connectance scores with ranked values for the abundance indices (see above), there is no relationship of note with the indices, either for total species or saprophages alone. A significant positive relationship does exist, however, between connectance and

Tab. 2. Summary statistics for quarterly food webs from eleven water-filled treeholes.

Site	number of species		number of trophic levels		numbers of predators and top predators	
	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum
1	5	3	4	3	3	1
2	7	4	4	3	4	2
3	6	4	3	3	3	2
4	7	4	3	3	2	1
5	7	4	3	3	2	1
6	7	5	3	3	3	3
7	6	5	3	3	3	2
8	6	5	4	3	3	2
9	7	5	3	3	3	2
10	6	4	3	3	2	1
11	6	4	3	3	2	1
Overall	7	3	4	3	4	1

abundance indices of predators and top predators ($R_s = 0.7114$, $0.05 > p > 0.01$), due of course to the fact that the presence of predators can contribute up to 75% of the possible value for connectance.

Inter-site distances and web structure

There was an inverse relationship shown between inter-hole distance and the average degree of similarity shown across webs from eight pairs of sites selected as described above (Fig. 3). There is a significant negative linear regression relationship evident in these data ($y =$

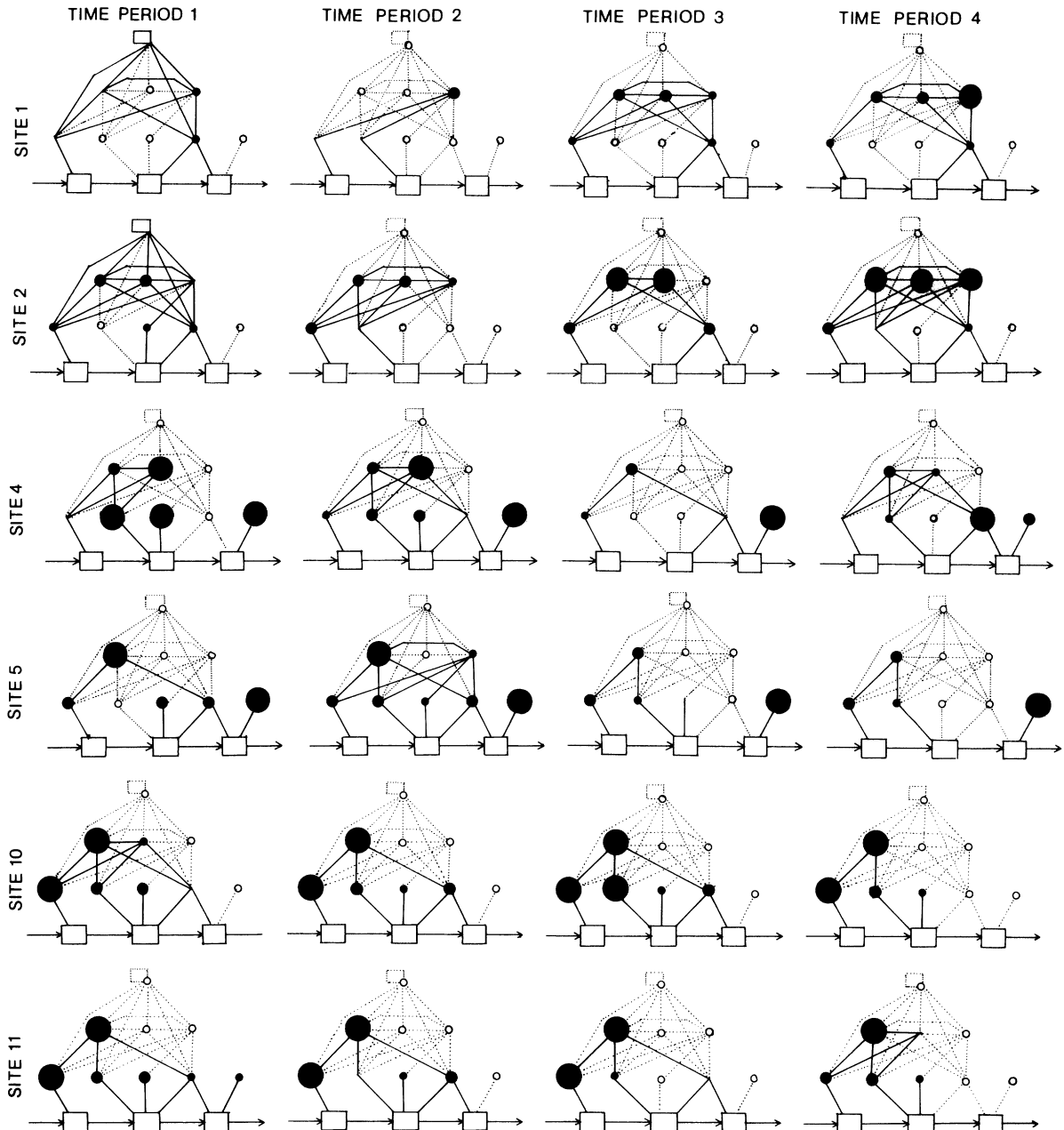


Fig. 2. Local food webs constructed quarterly for six of the eleven sites studied. Unrepresented parts of the 'regional' food web are indicated by dashed lines. The four levels of abundance for each organism (except *Lechriodus fletcheri* – see text) are represented by symbols of increasing size. (Note that abundance in the first, lowest, quartile is represented simply as the point of intersection of the appropriate trophic links). Time period 1 – January to October to December 1982, Time period 2 – January to March 1983, Time period 3 – April to June 1983, Time period 4 – July to September 1983. For further details on web construction and interpretation, see text.

Tab. 3. Summary statistics based on abundance indices of species within quarterly food webs from eleven water-filled treeholes

Site	All species (33*)			Saprophages (20*)			Predators and top predators (13*)		
	Min.	Mean	Max	Min.	Mean	Max.	Min.	Mean	Max
1	5	8.00	14	2	3.25	4	3	6.25	10
2	12	14.50	18	4	5.50	6	8	9.00	12
3	10	12.50	15	4	6.00	7	8	6.00	8
4	10	16.25	20	7	10.75	13	3	5.50	7
5	12	15.75	17	9	11.75	15	3	4.00	6
6	12	15.75	19	4	7.25	11	7	8.50	10
7	12	13.25	17	7	8.25	9	3	5.00	8
8	15	16.50	18	9	10.50	13	5	6.00	7
9	11	13.50	17	6	8.50	12	4	5.00	6
10	13	15.75	17	9	11.25	13	4	4.50	6
11	13	14.50	18	7	9.75	14	4	4.25	5

*Maximum possible value in each category

0.423 - 0.00369x, $r = -0.89$, $p < 0.01$). The significance of this relationship is greatly enhanced by the point representing the extreme value of the independent variable. However the point is not an outlier, lying close to the line recalculated without its inclusion. The point lies within the sampling error associated with the recalculated line as tested using the method of Snedecor and Cochran (1967: 157-158). Further there is no a priori reason for excluding the point (quite the reverse in fact as it was chosen to increase the range of the independent variable - the intersite distance) and so I retain the relationship while freely admitting that more data in this area would be most welcome.

Based on this relationship we may conclude that, in general, holes that are close together may be expected to have comparable food webs both in terms of the presence or absence of species and the levels of abundance achieved by these species through time.

Web structure and hole size

The eleven sites ranged in surface area from 0.025 m² to 0.429 m², a seventeenfold variation. Mean surface area

was 0.13 m² with a sample standard deviation of 0.134. No significant relationships are evident over the sites between surface area and the overall abundance index for the species in the food webs ($r = 0.177$, n.s.), the index calculated for saprophages alone ($r = 0.220$, n.s.), for predators and top predators ($r = -0.371$, n.s.), or for the connectivity measured as described ($r = -0.434$, n.s.). Surprisingly there is a significant *negative* relationship between surface area and the number of species present ($r = -0.745$, $0.01 > p > 0.001$). I account this result spurious, largely because the range of values of the dependent variable, which is necessarily an integer anyway, is 6 to 8 inclusive. In addition, it is possible that the sampling technique used is more efficient in smaller holes, in which a larger proportion of the whole contents is represented in each sample, than in larger holes.

Accordingly I conclude that there are no relationships between hole size and any of the key characteristics of the food webs they contain.

Tab. 4. Connectance in quarterly food webs from eleven water-filled treeholes (calculated as: the number of trophic links present in the food web/total possible links in the community).

Site	Period 1	Period 2	Period 3	Period 4	Mean	Range
1	0.50	0.15	0.46	0.38	0.37	0.35
2	0.77	0.38	0.31	0.62	0.52	0.46
3	0.35	0.62	0.31	0.31	0.40	0.31
4	0.35	0.50	0.23	0.46	0.39	0.27
5	0.27	0.54	0.23	0.19	0.31	0.35
6	0.42	0.73	0.73	0.46	0.59	0.31
7	0.46	0.62	0.35	0.42	0.46	0.27
8	0.50	0.46	0.35	0.46	0.44	0.15
9	0.50	0.69	0.31	0.35	0.46	0.36
10	0.46	0.31	0.31	0.19	0.32	0.27
11	0.35	0.31	0.27	0.31	0.31	0.08
Overall	0.49	0.48	0.35	0.38	0.42	0.29

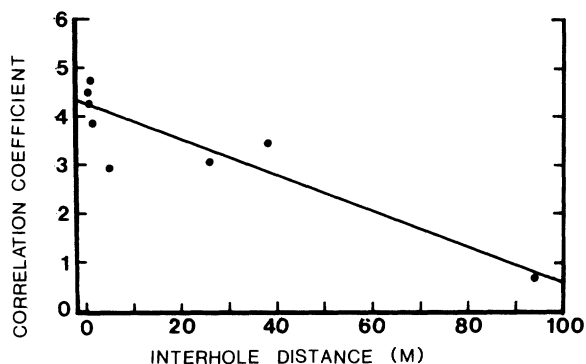


Fig. 3. Relationship between the degree of similarity among the contained food webs and the distance between sites. An appropriate linear regression is $y = 0.423 - 0.00360x$, $r = -0.893$, $0.01 > p > 0.001$.

Discussion

The results and analyses I have presented demonstrate clearly that there is substantial spatial and temporal variation in the structure of food webs within a single type of habitat in a particular ecosystem. The first question this raises is whether the summed webs used in previous analyses by many authors, including myself, are accordingly devalued. On reflection this contention is obviously naive. The 'regional' webs based on the summed and summarised results of studies over several occasions and locations, are entities which represent the suite of organisms which have overlapping ecologies at the level of the population and which have been and remain in contact along an evolutionary time-scale. The trophic interactions incorporated into webs on this longer scale reflect a degree of coevolution (*sensu lato*) among the species concerned. The statement such 'regional' webs make about a community have been, demonstrably, useful for the answering of biogeographical questions (see, e.g., Kitching and Pimm 1985, Beaver 1985) or in the making of habitat to habitat or ecosystem to ecosystem comparisons (cf. Cohen 1978, Pimm 1982, Beaver 1985). It is from such exercises that we may hope to arrive at generalisations at the level of the community. In contrast, what I will call 'local' webs lead to an understanding of the environment/community interactions on a more restricted but no less interesting scale. In addition they reflect and allow comment upon the spatial population dynamics of the constituent organisms.

Beaver (1985), Kitching and Pimm (1985) and Pimm and Kitching (in press) have compared the 'regional' webs from both treeholes and pitcher plants with the available theoretical explanations for food web complexity and food chain length. Such evidence as can be adduced, lends support to Pimm and Lawtons' (1977) hypothesis which suggests that dynamic constraints within the web control the observed structure. They suggest we should expect more complex webs in more

predictable environments. These works provide little support for the major contending theory that energetic limitations at the base of the food webs are the controls which determine chain length and web complexity (Hutchinson 1959, Slobodkin 1961). Turning to 'local' webs and looking for explanations for variations in structure at this level, it seems at first reasonable to look for correspondence or otherwise with these two basic explanatory ideas. Again there is little support for the energetic constraint idea – if there were, I would expect to find relationships between one or more properties of the food webs and the surface area of the treeholes which contain them as it is through the surface interface that most energy enters the holes. The dynamic constraints hypothesis provides an apparently plausible explanation for the variation observed in the webs in space and time – if web differences reflect environmental differences due to microclimatic or structural heterogeneity across holes, then the associated differences in predictability could produce the variations in web complexity. This argument, however, is flawed fatally. Pimm and Lawtons' (1977) arguments rest on the premise that, on average, more complex webs will have a longer characteristic return time following a perturbation, before the full equilibrium structure is regained. Accordingly, *over evolutionary time*, the regular components of the web will reflect the frequency of perturbations at the site. Rephrased, a given degree of environmental predictability will have an associated equilibrational degree of web complexity. The key phrase in this argument, however, is 'over evolutionary time'. The environment presented on a site-to-site basis by treeholes in a particular patch of forest will vary with season, with the degree of maturity of the trees and as the surrounding vegetation changes. These changes will be superimposed on the shorter term variation due to rainfall patterns, incident radiation and litter input into the holes. Even if we adopt a time scale related to the average lifetime of the trees, this does not allow an *evolutionary* explanation of the sort outlined above for the local variations here described.

I conclude, therefore, that although 'grand' theories based on energetic or dynamic constraints can explain region-to-region pattern in food webs, different tools are needed to explain local variation in structure. Of course, the regional webs are the sums of the local webs but the sums are not simple, cumulative ones. The species involved have behavioural and life-history characteristics which interact with local environmental heterogeneity. Accordingly the web we see at any particular time and place reflects the interaction between stochastic events such as searching and survivorship, with short- and middle-term environmental heterogeneity such as the formation and destruction of treeholes, rainfall events, local variations in litter deposition and the presence of other species at the site. These phenomena will produce ever-changing webs *within the limits set by the full 'regional' web*, which is determined by evo-

lutionary processes operating on a much longer time scale. The inverse relationship between web similarity and intersite distance (Fig. 3) is evidence for the role of spatial heterogeneity, as local peaks in population levels ebb and flow within the forest as habitat availability and quality interact with species vagility.

It is noteworthy that the deterministic 'grand' theories and the stochastic 'local' explanations both have an important role in explaining the food webs observed in the *same* communities, the immediate applicability of each reflecting simply the time scale of the approach taken to the community. I hesitate to extend this idea beyond food webs in phytotelmata but I mention, in passing, the parallel explanations offered by community ecologists to account for observed patterns of species diversity. On the one hand, the data available may be explained by ideas of 'non-equilibrium' assemblage (Sale and Dybdahl 1975, Sale 1978, 1980,) and the importance of stochastic events (Connor and Simberloff 1979, Rathke 1984). In contrast, others see a more deterministic world centred on ideas of competition (Dayton 1971, Underwood and Denley 1984), resource partitioning (Grant 1981, Grant and Schluter 1984, Seifert 1984), or a combination of these with other ecological processes (Paine 1974, Murdoch 1979). In my results at least, I show that both a stochastic and a deterministic view may be necessary to explain observed patterns in a community, each pertaining to a particular scale of observation.

The inverse relationship between the abundance indices of saprophages and predators I suggest, reflects a close-linking of the trophic levels at the population level and further data will be presented on this contention in due course. Its importance in the determination of community structure, however, is probably small.

Lastly, I draw attention to the technique, presented here for the first time, of incorporating relative abundances into food web representation. I suggest the inclusion of such additional information is essential, as the range of variability of webs based solely on the presence or absence of species is likely to be but an insensitive measure of local variation in web structure. I used a four-step classification of abundance levels, but any number of divisions could be used if the data base is sufficiently reliable. I submit that the method developed here is both visually and analytically useful when a richer representation of food webs is required.

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