Geographical variation in food web structure in *Nepenthes* pitcher plants

R. A. BEAVER School of Natural Resources, The University of the South Pacific, Suva

ABSTRACT. 1. Relative to *Nepenthes* species in West Malaysia near the evolutionary centre of the genus, outlying species of *Nepenthes* in the Seychelles, Sri Lanka and Madagascar have fewer species of both prey and predator living in them, fewer and smaller guilds of species, much apparently empty niche space, less complex food webs, and a greater connectance. The ratios of prey to predators, and of connectance (C_1) to the total number of trophic types present remain approximately constant.

2. Differences between the food webs appear to be related in a complex way to the size of the country and its degree of spatial and temporal isolation, the size of the local species pool capable of colonizing the pitchers, and the number of *Nepenthes* species present. However, the maximal length of food chains in the richest and most complex food webs is probably limited by energetic constraints or environmental predictability.

3. The data may illustrate how food webs change to become more complex, both by the addition of new guilds of species and the addition of species to existing guilds, while at the same time certain properties of the food web are kept approximately constant.

Key words. Food webs, geographical variation, species guilds, food chain lengths, predator–prey ratios, connectance, *Nepenthes*.

Introduction

Although food web ecology is a rapidly expanding area of research (Cohen, 1978; Pimm, 1982), there have been few attempts to compare community food webs in the same habitat in different geographical areas (Briand, 1983; Kitching, 1983). Briand (1983) suggested that, regardless of geographical location and taxonomic composition, food webs from similar habitats tended to be more similar to each other than to food webs from contrasting habitats. Using data on the communities living in five species of *Nepenthes* pitcher plants in four widely separated tropical countries, I show here that there are considerable differences between geographical areas in certain food web parameters within the same habitat type.

The pitchers of *Nepenthes* are well known to attract insects which fall into the pitchers and drown. Their remains are partly absorbed by

Correspondence: Professor R. A. Beaver, School of Natural Resources, The University of the South Pacific, P.O. Box 1168, Suva, Fiji.

17

Seychelles (*N. pervillei*)

Sri Lanka (*N. distillatoria*)
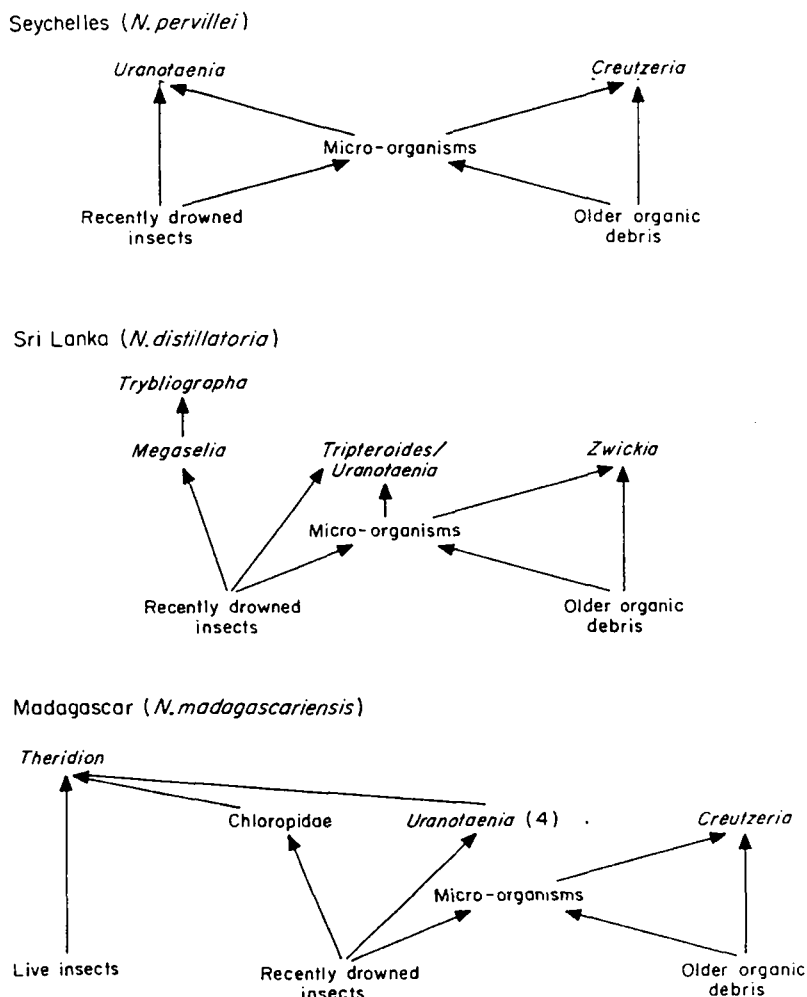
Madagascar (*N. madagascariensis*)

FIG. 1. Food webs found in five species of *Nepenthes* in four countries. (For further details of taxonomic composition see references cited. Figures in parentheses indicate number of species present where greater than one.)

the plants, but also support communities of insects (mostly mosquitoes) and other organisms living in the pitcher fluid or on the upper walls of the pitcher (Beaver, 1983). Detailed studies of the fauna and food webs of different *Nepenthes* species are few, but there is sufficient information available to compare various parameters of the food webs of species in the Seychelles (Mattingly & Brown, 1955; Nesbitt, 1979), Sri Lanka (Guenther, 1913; Oudemans, 1915; Disney, 1982), Madagascar (Fage, 1930; Paulian, 1961; Grjebine, 1979), and West Malaysia (Beaver, 1979, 1980, 1983). Indomalaysia is the centre of evolution of the genus

Nepenthes; twenty-eight species are known from Borneo, nineteen from Sumatra and eleven from West Malaysia (Steenis & Balgooy, 1966). Areas at the edge of the range of the genus have only one (Seychelles, Sri Lanka) or two (Madagascar) species.

Methods

The food webs for the five species of *Nepenthes* studied are shown in Fig. 1, and the food web matrices derived from them in the Appendix. The components of the food webs are
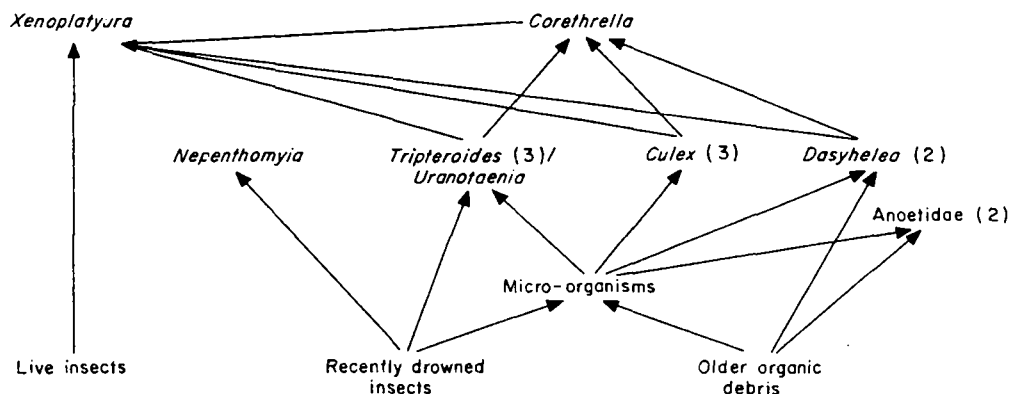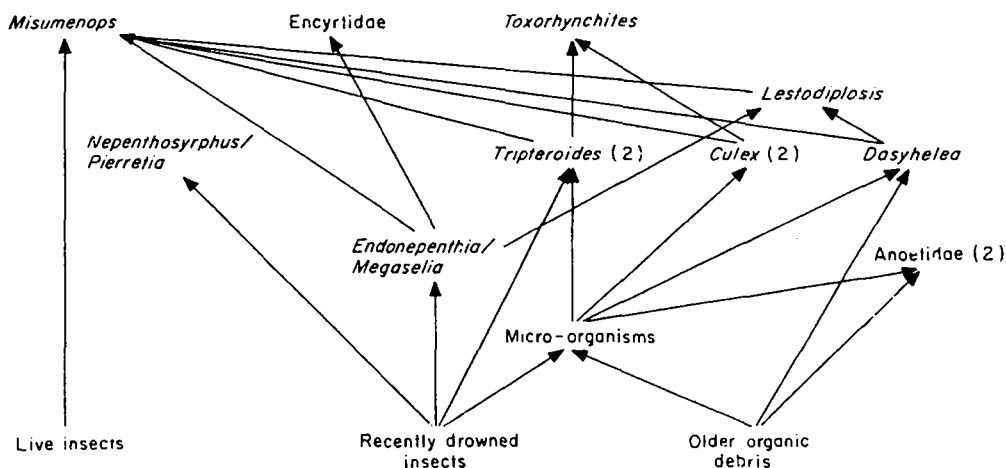
West Malaysia (*N. ampullaria*)

West Malaysia (*N. albomarginata*)

FIG. 1 (*continued*)

functionally similar groups of taxonomic species, termed here trophic types. In the food web of *Nepenthes albomarginata*, for example, two species of filter-feeding *Culex* mosquito larvae which feed on microorganisms are combined as one trophic type, but separated from two species of *Tripteroides* mosquito larvae which are largely filter-feeders but also browse along the surface of recently drowned insects. These larvae make up another trophic type. This is equivalent to the 'lumping' procedure of Briand & Cohen (1984). Micro-organisms

are considered throughout as one trophic type in the absence of reliable information on the taxonomic composition of the group. Only species which regularly occur and develop in the pitchers are included in the analyses. The basic food resource for the species which live in the pitchers is composed of (1) live insects (mostly ants) falling into the pitchers; (2) recently drowned insects; (3) older organic debris. (In the Seychelles and Sri Lanka, live insects are not utilized.)

In the analyses of food web parameters

(Table 1), I have generally followed the procedures and terminology of Pimm (1982). Most of the trophic types serve as 'prey' for 'predators' which feed on them. Many of the 'predators' may themselves serve as 'prey' for other 'predators' at a higher trophic level. Those which serve only as 'prey' are termed 'basal' trophic types.

The connectance of a food web is the ratio of the actual to the possible number of interspecific interactions (Pimm, 1982). Following Yodzis (1980), I have calculated connectance in two ways. The lower limit to the connectance (C_1) is determined by the actual number of trophic interactions in the food web, ignoring potential interference competition between species for the same species of prey. If these potential competitive interactions are included, a higher value (C_u) of the connectance is obtained. Connectance then is calculated as

$$C = \frac{n}{s(s-1)/2}$$

where n is the number of interactions including (C_u) or excluding (C_1) interference competition, and s is the number of species in the community This formula assumes that cannibalism does not occur (diagonal elements of the matrix are excluded), and that if species A eats species B, the latter cannot also eat the former (only half the matrix is considered). In the calculation of C_u, interference competition interactions are also considered to be asymmetrical. It should also be noted that in the calculation of the connectance for the *Nepenthes* food webs, the basal trophic types, being successive stages in the decay of the basic food resource, can not interact, so links between them are omitted. The maximal number of connections for a top predator (Table 1) is the greatest number of trophic levels through which energy passes between the top predator and the lowest trophic level. It indicates the maximal length of the food chains in the food web.

Results and Discussion

It is evident from Table 1 that the *Nepenthes* pitchers in the outlying areas (Seychelles, Sri Lanka, Madagascar) have fewer trophic types

of prey and predator, and a smaller number of predator–prey interactions than the pitchers of *N.ampullaria* and *N.albomarginata* in West Malaysia, with Seychelles < Sri Lanka < Madagascar < West Malaysia. As expected (Briand, 1983), there is a corresponding decrease in connectance along the same series, whether potential interference competition is excluded (C_1) or included (C_u).

The differences in food web composition and structure are unlikely to be related to differences in pitcher size and structure (except perhaps within West Malaysia). The pitchers of *N.pervillei*, *N.distillatoria*, *N.madagascariensis* and *N.albomarginata* are of similar size and of the same basic type with the glandular enzyme-secreting tissue confined to the lower 0.3–0.5 of the pitcher. In *N.ampullaria*, the glandular tissue extends to the top of the pitcher. This affects the taxonomic composition of the fauna in *N.ampullaria* (Beaver, 1980) but there is no evidence that it affects the structure of the food web in any important way.

Two theories were put forward by Kitching (1983) to explain the differences between food webs in tree holes in England and Australia. The first suggested that the richer and more complex food web found in tree holes in the warmer climate of Queensland was related to a greater average availability of energy throughout the year. The second hypothesis suggested that the greater complexity was related to greater environmental (climatic and seasonal) predictability. All the systems considered here occur in the tropics between 10°N and 20°S in similar climates in which energy availability in the form of insects falling into the pitchers is likely to be reasonably constant throughout the year on the scale of a patch of pitcher plants (Beaver, 1983).

Differences between countries in Table 1 seem more likely to be related to some complex function of the number of *Nepenthes* species present, the size of the country, its degree of spatial and temporal isolation from the evolutionary centre of the genus, and the size of the local species pool capable of colonizing the pitchers. It has been shown (Beaver, 1983) that colonization of new areas by *Nepenthes* has normally been followed by adaptation to the pitcher plant habitat of elements of the local fauna in the colonized

TABLE 1. Parameters of food webs in *Nepenthes* pitchers in different countries and different species of *Nepenthes*. For further explanation see text.

	Seychelles *N.pervillei*	Sri Lanka *N.distillatoria*	Madagascar *N.madagascariensis*	West Malaysia *N.ampullaria*	West Malaysia *N.albomarginata*
Total no. of trophic types (s)	5	7	8	11	14
No. types of prey (n)	3	4	6	8	9
No. types of predator (m)	3	5	5	8	11
No. types top predator	2	3	2	3	5
No. of basal types	2	2	3	3	3
Prey/predator ratio (n/m)	1.0	0.8	1.2	1.0	0.82
No. predator–prey interactions	6	8	10	18	22
Connectance (C_i)	0.67	0.40	0.40	0.35	0.25
(C_u)	0.78	0.55	0.52	0.50	0.41
Maximum no. connections for each top predator	3,3	3,3,2	4,3	5,3,2	5,4,3,2
Connectance (C_i)×Total no. types (s)	3.35	2.8	3.2	3.8	3.5

TABLE 2. Numbers of genera and species in different guilds of arthropods inhabiting *Nepenthes* pitchers in different areas. (The ubiquitous guild of micro-organisms has been omitted because its taxonomic composition is not reliably known.)

Guild	Seychelles *N.pervillei*	Sri Lanka *N.distillatoria*	Madagascar *N.madagascariensis*	West Malaysia *N.ampullaria*	West Malaysia *N.albomarginata*
Detritus-feeders	1/1•	1/1	1/1	3/4	3/3
Filter-feeders	1/1	2/2	1/4	3/7	2/4
Carrion feeders	0/0	1/1	1/1	1/1	3/4
Aquatic predators	0/0	0/0	0/0	1/1	2/2
Terrestrial predators	0/0	0/0	1/1	1/1	1/1
Pupal parasitoids	0/0	1/1	0/0	0/0	1/1
Totals	2/2	5/5	4/7	9/14	12/15
No. of guilds occupied	2	4	4	5	6

• No. of genera/species present.

area, rather than invasion and colonization by species which were already associated with *Nepenthes* elsewhere. The relative importance of these parameters seems likely to differ between countries. The Seychelles are a small (260 km^2) archipelago, which has been long isolated both spatially and temporally. It has a single species of *Nepenthes* and only a small available pool of potential colonizing species. Madagascar, although even further away from Indomalaysia, is much larger (590 150 km^2), with a much richer pool of potential colonists, and two species of *Nepenthes*. It might therefore be expected to have a richer and more complex food web than the Seychelles. West Malaysia, although smaller (131 300 km^2), has eleven species of *Nepenthes,* is within a relatively short distance of other *Nepenthes*-rich islands, and has a rich local pool of potential colonizers. Near the evolutionary centre of the genus there may also have been a greater time available for speciation among the colonizing species. However, it can be suggested that in West Malaysia the hypotheses suggested by Kitching (1983) are of importance in putting an upper limit on the length of the food chains, even though other factors may also be involved (Pimm, 1982). The highest value of the modal number of connections (a measure of the maximum number of trophic levels) is 5 for the two species of terrestrial predator (a spider and the larva of a mycetophilid fly) in the pitchers of *N.albomarginata* and *N.ampullaria* respectively (Table 1). This is at the upper limit for food chains with small invertebrates as top predators (Pimm, 1982). Most 'top' predators in the *Nepenthes* food webs lie at the end of shorter food chains (Table 1).

The similarities between the different food webs are now examined. The product of connectance (C_1) and total number of trophic types remains approximately constant in all areas, and the values are near the constant (3.1 based on eighteen food webs) for the hyperbolic function linking the two parameters (Pimm, 1982). This suggests either that the systems differ little in stability, or that variations in the interaction strength compensate for the changes in connectance and species number (Pimm, 1982). These two possibilities cannot be separated at˙ present. The ratio of the number of prey trophic types to predator trophic types is also approximately constant

(Table 1). This relative constancy at a value near unity, if it is not an artefact (Glasser, 1983), suggests that if one prey trophic type is added to a food web, an opportunity is created for the addition of one predator trophic type. The mean value of the ratio (0.94) is very similar to that (0.88) found by Briand & Cohen (1984) for a wide variety of food webs. Thus in both respects the present food webs fit neatly into the body of empirical data on food webs.

Species can be added to communities in two ways: (1) by increasing the number of guilds present; (2) by increasing the size of guilds that are already present. Either method may be of prime importance in a particular community (Wilson, 1974; Cody, 1975; August, 1983). A more detailed analysis of the guilds of arthropods present in the five food webs under consideration is shown in Table 2. Since the microhabitat within the pitcher is essentially the same in each case, it is reasonable to suppose that the potential number of guilds that can occupy the microhabitat is the same in each geographical area. It is clear that not all these guilds are occupied in the outlying areas. Comparing occupied guilds, the numbers of genera and species within several of the guilds also tend to be smaller in the outlying areas. Thus both methods by which species are added to communities are of importance in these systems. The data also suggest that the systems in the outlying species of *Nepenthes* have much unfilled niche space, and that species living in those pitchers are less closely packed within the guilds. We may have here an illustration of how food webs change to become more complex, while at the same time certain properties of the web are kept approximately constant.

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Appendix

Food web matrices

The number at the top of each column indicates the predator trophic types. The number at the left of each row indicates the prey trophic types. An entry of 1 in the matrix indicates a direct feeding relationship between predator and prey types. Rows and columns containing only zeros have been omitted. A key below each matrix identifies the trophic types.

Seychelles (*Nepenthes pervillei* Blume)

	1	2	3
3	1	1	0
4	1	0	1
5	0	1	1

1 *Uranotaenia nepenthes* (Theobald)
2 *Creutzeria seychellensis* Nesbitt
3 Micro-organisms
4 Recently drowned insects
5 Older organic debris

Sri Lanka (*Nepenthes distillatoria* L.)

	1	2	3	4	5
2	1	0	0	0	0
5	0	0	1	1	0
6	0	1	1	0	1
7	0	0	0	1	1

1 *Trybliographa* sp.
2 *Megaselia deningi* Disney
3 *Tripteroides dofleini* (Guenther)/*Uranotaenia nivipleura* Leicester
4 *Zwickia guentheri* Oudemans
5 Micro-organisms
6 Recently drowned insects
7 Older organic debris

Madagascar (*Nepenthes madagascariensis* Poiret)

	1	2	3	4	5
2	1	0	0	0	0
3	1	0	0	0	0
5	0	0	1	1	0
6	1	0	0	0	0
7	0	1	1	0	1
8	0	0	0	1	1

1 *Theridion* sp.
2 Chloropidae sp.
3 *Uranotaenia* spp.
4 *Creutzeria* sp.
5 Micro-organisms
6 Live insects
7 Recently drowned insects
8 Older organic debris

West Malaysia (*Nepenthes ampullaria* Jack)

	1	2	3	4	5	6	7	8
2	1	0	0	0	0	0	0	0
4	1	1	0	0	0	0	0	0
5	1	1	0	0	0	0	0	0
6	1	1	0	0	0	0	0	0
7	0	0	0	1	1	1	0	1
9	1	0	0	0	0	0	0	0
10	0	0	1	1	0	0	1	0
11	0	0	0	0	0	1	1	1

1 *Xenoplatyura beaveri* Matile
2 *Corethrella calathicola* Edwards
3 *Nepenthomyia malayana* Kurahashi & Beaver
4 *Tripteroides* spp./*Uranotaenia moultoni* Edwards

5 *Culex* spp.
6 *Dasyhelea* spp.
7 Micro-organisms
8 Anoetidae spp.
9 Live insects
10 Recently drowned insects
11 Older organic debris

West Malaysia (*Nepenthes albomarginata* Lobb)

	1	2	3	4	5	6	7	8	9	10	11
4	1	0	0	0	0	0	0	0	0	0	0
6	1	1	0	1	0	0	0	0	0	0	0
7	1	0	1	0	0	0	0	0	0	0	0
8	1	0	1	0	0	0	0	0	0	0	0
9	1	0	0	1	0	0	0	0	0	0	0
10	0	0	0	0	0	0	1	1	1	0	1
12	1	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	1	1	1	0	0	1	0
14	0	0	0	0	0	0	0	0	1	1	1

1 *Misumenops nepenthicola* (Pocock)
2 Encyrtidae sp.
3 *Toxorhynchites klossi* Edwards
4 *Lestodiplosis syringopais* (Hering)
5 *Nepenthosyrphus* sp./*Pierretia urceola* Shinonaga & Beaver
6 *Endonepenthia schuitemakeri* Schmitz/ *Megaselia ?nepenthina* Schmitz
7 *Tripteroides* spp.
8 *Culex* spp.
9 *Dasyhelea nepenthicola* Wirth & Beaver
10 Micro-organisms
11 Anoetidae spp.
12 Living insects
13 Recently drowned insects
14 Older organic debris