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Twelve years of Ecological Research on *Nepenthes* in Southeast Asia - Some personal highlights.

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Abstract. I first started performing ecological research on *Nepenthes* in 1989 in Brunei, Borneo. Since then, ecological, biogeographical and taxonomic research on *Nepenthes* have dominated my academic life. The recent publication of my second text, *Nepenthes of Sumatra & Peninsular Malaysia*, marks the end of a major phase of my research career, and this presentation aims to summarise some of the more enjoyable and interesting work I have done. My primary interest in the ecology of *Nepenthes* has always been the structure, assembly and dynamics of the communities of animals which live inside *Nepenthes* pitchers. This work has shown that animal community structure is related to a wide variety of factors, ranging from host-pitcher characteristics to broad-scale geographical processes. The unique interaction between the swimming ant, *Camponotus schmitzi* and its host, *Nepenthes bicalcarata* was described in detail for the first time. Explorations of highland habitats in Borneo yielded much anecdotal information for possible investigation in future years. Recently, my research has focussed on the *Nepenthes* from Sumatra & Peninsular Malaysia. While I was researching this text, no fewer than five new *Nepenthes* taxa were discovered or described from these regions. Further interesting ecological observations were made, in particular, the unusual trapping mechanism of *Nepenthes inermis*, which seems to be part pitfall, part flypaper. Although many of these observations await formal investigation, it is clear that our knowledge of *Nepenthes* in Sumatra and Borneo is much less extensive than we thought, and it is now time to attempt more rigorous field-based experiments in order to better understand the ecology and taxonomy of these wonderful plants.

Introduction

Nepenthes are the famous tropical pitcher plants, producing jug-shaped "pitchers" that are designed to attract, trap and digest small animals. They are common in habitats which are deficient in nutrients (particularly nitrogen), such as swamps, bogs and mountain summits. They make up for the shortfall in soil nutrients by trapping and digesting animals. The nutrients obtained by this process are transported to other parts of the plant to help them to grow and reproduce. This provides them with a competitive advantage over "normal" plants.

Most *Nepenthes* species are found in South-east Asia, particularly in the Sunda region, which includes Borneo, Sumatra, the Malay Peninsula, Java and some of the southern islands of the Philippines. Outlying species occur in Madagascar, the Seychelles, India, Sri Lanka, New Caledonia, Australia and southern China. Secondary centres of diversity include New Guinea, the Philippines and Sulawesi. *Nepenthes mirabilis* has by far the widest geographical distribution of any species, extending from southern China to northern Australia. In contrast, most species have very restricted distributions, and several have only been recorded from single localities.

For convenience, scientists usually divide *Nepenthes* into two major groups, based on the altitudes at which they grow. *Lowland* species are generally confined to altitudes below 1000 m above sea level (a.s.l.), whereas *highland* species are usually found above 1000 m a.s.l. The lowland species are usually found in three major habitat types: tropical heath forest, peat swamp forest and secondary vegetation. *Nepenthes* may be very abundant in secondary habitats which remain moist throughout the year and have poor, acidic soils.

Tropical lowland evergreen rain forests usually occur from sea level up to 1000 or 1500 m a.s.l. Above these altitudes they are replaced by montane forests. The most remarkable montane habitats are the mossy forests, where the trunks and branches of trees are gnarled and festooned with mosses. Highland *Nepenthes* species are particularly abundant in these habitats, especially in sunny areas, such as ridge crests and mountain summits. Many of the highland species are epiphytes, and sometimes the only clue to their presence is a few dead pitchers which have fallen to the ground from the forest canopy.

As well as trapping and digesting insects for nutritional benefit, it has been shown that the pitchers of most *Nepenthes* species also provide habitats for a range of aquatic invertebrates (Beaver 1983, 1985, Clarke and Kitching 1993). The majority of the macrofauna are dipterans, forming discreet communities which have proved useful in food web research. Beaver (1979) classified the organisms found in *Nepenthes* pitchers into three groups. Nepenthebiont species are those which live or develop only within the fluid of *Nepenthes* pitchers: they depend on pitchers for their survival. Nepenthephiles are those species which live or develop primarily in *Nepenthes* pitchers, but are occasionally found in other habitats as well. Nepenthexenes are not usually found in *Nepenthes* pitchers, but occasionally colonise them, for a variety of reasons (see Beaver, 1983).

Some of the organisms that have been found living in *Nepenthes* pitchers include spiders, tadpoles, mites, and larvae of mosquitoes, midges and flies. Most pitchers are colonised 4-5 species of different organisms, but in some cases, the communities can be remarkably diverse. For example, in *Nepenthes bicalcarata* pitchers in Brunei, I found a total of 33 species of infaunal organisms (Clarke, 1998a; Clarke and Kitching, 1993).

These communities are of interest to ecologists who study food web dynamics, as these simple communities are highly replicated in space and time, and the host plants are found in a variety of different habitats. This makes it comparatively easy to design and perform experiments on animals communities that would be difficult, if not impossible, to perform elsewhere.

The taxonomy of *Nepenthes* has often been confused and controversial. Although I am an ecologist rather than a taxonomist, a knowledge of the taxonomy of *Nepenthes* has proved very useful in my ecological research, and has recently developed into a strong secondary interest. An important point to bear in mind about current taxonomic trends in *Nepenthes* is that several different scientists hold different and competing views on a number of taxa. These will not be discussed in detail here, but various references are available to those who wish to delve into these issues in greater detail. Suffice to say that the interpretations followed here are my own (see Clarke 1997, 2001).

Brunei I spent most of 1989 and 1990 in Brunei performing ecological research on the animal communities of several lowland *Nepenthes* species. My primary interest was in the dynamics of insect communities found in the pitchers. I investigated whether the structure of these communities was in any way related to external habitat factors, such as geographical location, host pitcher structure and longevity, of habitat. In a preliminary survey, the communities of six lowland species were examined; *N. albomarginata*, *N. ampullaria*, *N. bicalcarata*, *N. gracilis*, *N. mirabilis* and *N. rafflesiana* (Clarke and Kitching, 1993). The food webs for two of these communities are shown in Fig. 1.

We concluded that the structure and dynamics of the food webs is related to the structure and longevity of the host pitcher species (see also Clarke, 1997), the number of sympatric *Nepenthes* species and various biogreographical factors. This views were largely in accordance with the findings of Beaver (1979, 1983, 1985), who studied *Nepenthes* communities in Peninsular Malaysia. However, recent research in Singapore, Malaysia and Sumatra (Kato *et al.*, 1993; Mogi and Chan, 1996, 1997; Sota *et al.*, 1998) contradicts our findings, and suggests that random colonisation processes and interspecific competition among the infaunal species are the primary determinants of community structure in *Nepenthes*. More recent studies (e.g., Clarke, 1998b; Cresswell, 2000) suggest that both views are tenable, and it seems apparent that a more holistic approach to future surveys is needed to decide which factors are the most important determinants of food web structure in the infaunal communities of *Nepenthes* pitchers.

My research into food web dynamics was sidetracked for a considerable period while I investigated the relationship between *N. bicalcarata* and a remarkable species of ant – *Camponotus schmitzi* (Clarke and Kitching, 1995). The ants bore holes into the hollow tendrils of *N. bicalcarata* pitchers, in which they nest. To feed, the ants move into the pitchers themselves, swimming in the fluid and removing large items of prey caught by the pitchers. This behaviour seems to be beneficial to the plants, as the contents of *N. bicalacarata* pitchers frequently become putrid if excess prey is caught. This often kills the infauna, which seems to be an important component of the pitcher's digestive system. In pitchers which contain very little prey, the ants sometimes feed directly upon the infauna. The infauna is of little use to the plant if the pitchers contain no prey, so again, the ants behaviour does not appear to have detrimental effects on the plant. It therefore appears that the ants represent the top predator in the *N. bicalcarata* food chain, and that the food web for this species is the most complex of any *Nepenthes* species studied to date (Clarke, 1998a, c)(Fig. 1).

In return for the benefits provided by the ants to the plant, they receive a food source and domicile, so the association can be considered to be a mutualistic one. Whether the relationship is obligate or facultative for either species is difficult to determine at present. Recenet research by Merbach et al. (2000, pers. comm.) has also shown that the thorns of *N. bicalcarata* pitchers contain giant nectaries, and that these are located in such a position that it is very difficult for most organisms to reach them. However, *C. schmitzi* ants are readily able to reach this nectar source, so it seems that in addition to feeding on the prey caught by the pitchers, the ants obtain nectar from the glands at the tips of the pitcher thorns.

***Nepenthes* of Borneo** At the conclusion of my field studies in Brunei, I commenced work on a more ambitious project – a textbook designed to cover all of the *Nepenthes* species of Borneo. This was based mainly on expeditions made during my time in Brunei, supplemented by extra trips to observe species in other parts of the island.

The highlight of this project was a series of expeditions to Kinabalu Park in Sabah during 1996. In addition to exploring Mount Kinabalu, I was able to visit Marai Parai and Mount Tambuyukon, home to *N. edwardsiana* – still the most spectacular of all *Nepenthes* as far as I am concerned. Several interesting observations were made on this expedition. We confirmed that *N. villosa* and *N.* ×*kinabaluensis* found on Mt. Tambuyukon in addition to Mt. Kinabalu (Clarke, 1998d). We found an immature plant of a new natural hybrid: *N. burbidgeae* × *N. edwardsiana*. Unfortunately, the plant was too small to photograph, but from the parentage it is clear that a mature plant of this cross could produce outstanding pitchers. Perhaps the most common species of *Nepenthes* on the summit of Mt. Tambuyukon is *N. rajah*. Here it grows in stunted, windswept health-like vegetation. The climate is extremely harsh and it appears that this species can tolerate much more severe conditions that those it is usually associated with.

The completion of *Nepenthes of Borneo* was a personal milestone and the fact that the book was generally well-received was very gratifying, but I soon came to the realisation that I wanted to do more. Taxonomic disputes relating to several Bornean taxa can only be resolved by undertaking field studies that lie beyond the limits of my enthusiasm, while further progress in ecological research requires additional long periods of field work, which I no longer have sufficient time for. I was approached to write a new text on the entire genus of *Nepenthes*, but I declined, as I do not think that I could do the project justice – it would take at least a decade to do the basic field work, and the financial resources required would be enormous. Instead, I made a counter-proposal to write a second book on the species from Sumatra and Peninsular Malaysia, and this kept me busy from 1997 to 2001.

Nepenthes benstonei In the course of researching *Nepenthes of Sumatra & Peninsular Malaysia* my attention was brought to a taxon from Kelantan that had not been described. Jebb & Cheek (1997) discussed it under *N. sanguinea*, but noted that it could belong to an undescribed species. B. Salmon (pers. comm.) observed the plant in the wild, and sent me several photos. Like Jebb & Cheek, I felt that this taxon could represent a new species, so while attending a Flora Malesiana conference in Kuala Lumpur in 1998, arranged for permission to collect specimens for the herbarium in

Kuala Lumpur. My investigations of this material led me to conclude that it was a distinct species, and I named it *N. benstonei*, after the late Benjamin Stone, who was the first to collect it (Clarke, 1999). This was the first species of *Nepenthes* that I described, and while I had never thought this would be very important, I was actually quite excited by it all!

***Nepenthes* of Sumatra and Peninsular Malaysia** This book was by far the most ambitious project I have every undertaken. Fortunately, unlike Borneo, it is possible to observe most of Sumatra's *Nepenthes* species in the wild with relative ease. Moreover, the taxonomic controversies relating to the Sumatran species are nowhere near as problematic as the Bornean ones. Therefore, with the kind assistance of several friends and colleagues, I was able to obtain photographs of every Sumatran *Nepenthes* species described to date. Of the 29 species I discussed, I was able to observe 27 of them in the field myself.

Many field sites were observed, and this time I devoted much more time to the study of herbarium collections. This was necessary because the emphasis of this text was on taxonomy as much as ecology. The highlight was the discovery of two new taxa of *Nepenthes*. One of these was described in the book as *N. jacquelineae*.

The completion of this project brought to an end all of my current research projects involving *Nepenthes*. It is now my intention to withdraw from active research on *Nepenthes* until I return to Australia, after which time I intend to resume ecological studies on food web dynamics, with the focus on *N. mirabilis* in Australia, and perhaps the species from New Guinea. The objective of listing these research highlights is, more than anything, intended to illustrate how enjoyable my work has been, and how privileged I feel to have been able to work in so many wonderful places, with such amazing plants and animals.

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Table 1. List of metazoan taxa collected from *N. bicalcarata* pitchers in Brunei by Clarke (1998a).

The ecological groupings are based on those of Beaver (1983), where B = nepenthebionts, P = nepenthephiles and X = nepenthexenes.

	Taxon	Family	Feeding strategy	Ecological Group
	Diptera			
1	*Polypedilum* (*Pentapedilum*) *convexum* Johannsen	Chironomidae	Detritivore	P
2	*Dasyhelea nepenthicola* Wirth & Beaver	Ceratopogonidae	Detritivore	B
3	*Aedes* (*Alanstonea*) *brevitibia* Edwards*	Culicidae	Detritivore	B?
4	*Armigeres* (*Armigeres*) sp.	Culicidae	Detritivore?	B?
5	*Culex* (*Lophocearomyia*) *coerulescens* Edwards	Culicidae	Detritivore	B
6	*Culex* (*L.*) *navalis* Edwards	Culicidae	Detritivore	B
7	*Culex* (*L.*) *hewetti* Edwards	Culicidae	Detritivore	B
8	*Culex* (*L.*) *eminentia* Leicester*	Culicidae	Detritivore	B
9	*Toxorhynchites* (*Toxorhynchites*) sp. 1	Culicidae	Predator	B?
10	*Toxorhynchites* (*Toxorhynchites*) sp. 2	Culicidae	Predator	B?
11	*Toxorhynchites* (*Toxorhynchites*) sp. 3	Culicidae	Predator	B?
12	*Tripteroides* (*Rachionotomyia*) *nepenthis* Edwards	Culicidae	Detritivore	B
13	*Tripteroides* (*R.*) *nepenthesimilis* Mattingly*	Culicidae	Detritivore	B
14	*Tripterioides* (*R.*) *tenax* Meijere*	Culicidae	Detritivore	B
15	*Uranotaenia* (*Pseudoficalbia*) *moultoni* Edwards	Culicidae	Detritivore	B
16	*Corethrella calathicola* Edwards	Chaoboridae	Predator	B
17	*Corethrella* sp. 1	Chaoboridae	Predator	X?
18	*Lestodiplosis* sp.	Cecidomyiidae	Predator	B
19	*Xenoplatyura* sp.	Mycetophilidae	Predator	B

20	*Megaselia campylonympha* Schmitz	Phoridae	Detritivore	B
21	*Nepenthosyrphus oudemansi* Meijere*	Syrphidae	Detritivore	B
22	*Wilhelmina nepenthicola* Villeneuve	Calliphoridae	Detritivore & predator	B
23	*Nepenthomyia malayana* Kurahashi & Beaver	Calliphoridae	Detritovore & predator	B
24	Calliphorid sp. 1	Calliphoridae	Detritovore & predator	B?
	Lepidoptera			
25	*Eublemma radda* Swinhoe†	Noctuidae	Herbivore	B
26	Lepidopteran sp.	?	Herbivore	B
	Hymenoptera			
27	*Camponotus* (*Colobopsis*) *schmitzi* Schuitemaker & Stärke	Formicidae	Detritivore & predator	B
28	Encyrtid sp.	Encyrtidae	Pupal parasitoid	B
	Aranae			
29	*Misumenops nepenthicola* Pocock	Thomisidae	Predator	B
	Acari			
30	*Zwickea nepenthesiana* Hirst	Anoetidae	Detritivore	B
	Brachyura			
31	*Geosesarma* sp.	Grapsidae	Detritivore	P?
	Anura			
32	*Philautus* sp.	?	N/A	P?
33	? sp.	?	Detritivore	P?

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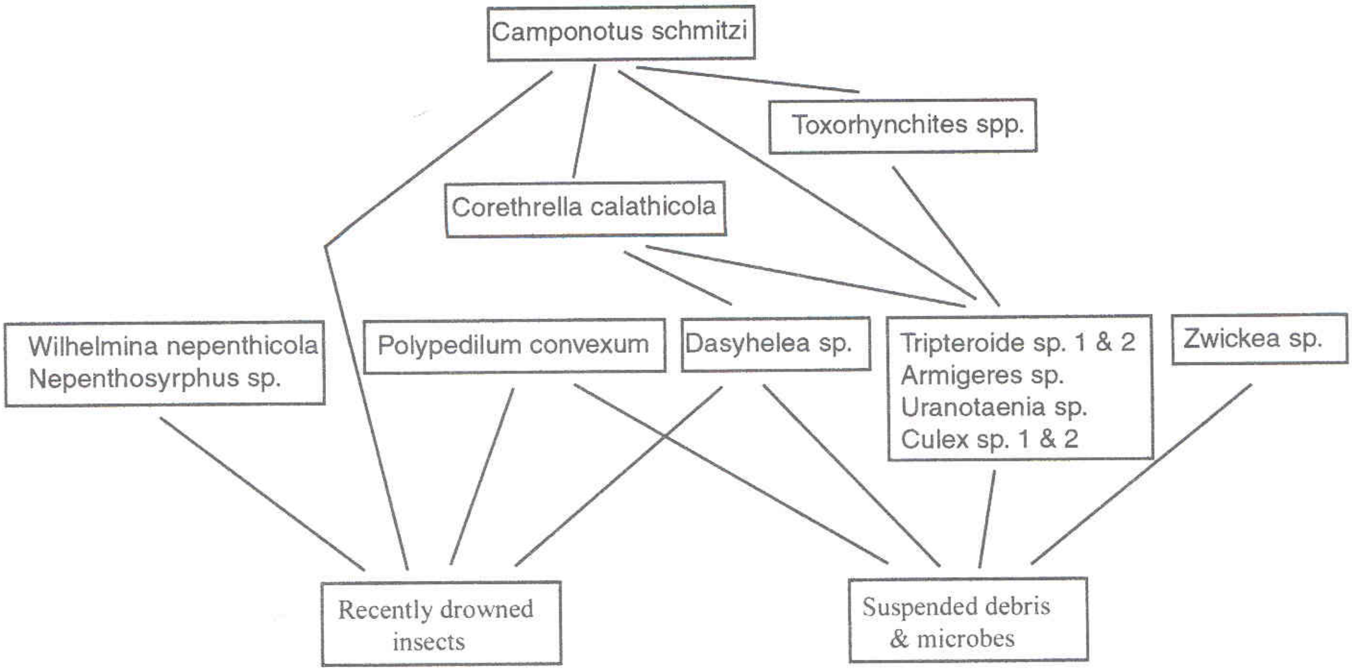
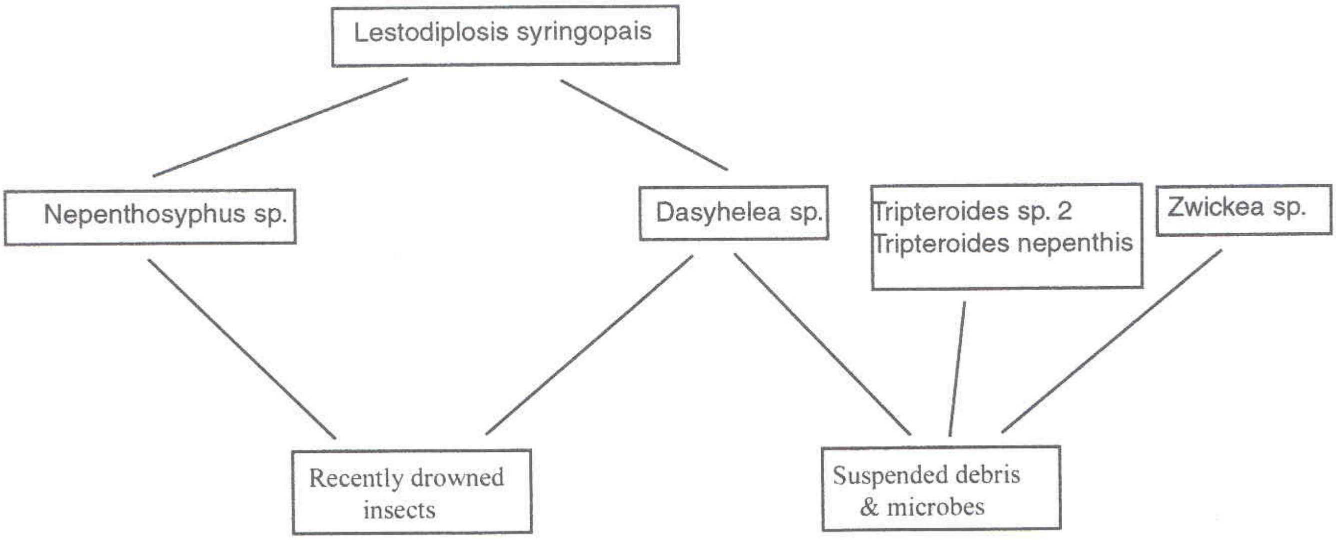
* Denotes species which were not identified with certainty.

† Denotes species attributed to *N. bicalcarata* by Beaver (1983) which were not found in *N. bicalcarata* pitchers in this study.

Figure 1. Food web diagrams for the metazoan communities of two Nepenthes species from Brunei (adapted from Clarke & Kitching (1993)). Arrows between species indicate feeding interactions.



(a) Nepenthes bicalcarata



(b) Nepenthes rafflesiana