Cambridge University Press
978-0-521-77316-4 - Food Webs and Container Habitats: The Natural History and Ecology of Phytotelmata
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Excerpt
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Introduction

Along the Labi Road in the tiny Sultanate of Brunei lies a series of sandy stream beds. Each is raised above the surrounding forest, presumably by eons of silt deposition during occasional periods of inundation and stream flow. But now, in May, the water flow is a mere trickle, winding around patches of tar seepage; here, not the product of human error and environmental insensitivity, but a natural phenomenon reflecting the oil-bearing strata that underlie this region of northern Borneo. But this is the perhumid tropics and wetness is the order of the day – any day. Treacherous quicksands lie centimetres below the scorched white sand and the peat-swamp forest on each side of the stream bed is permanently inundated with tea-coloured peaty water standing thigh-deep around the tangle of buttress roots, fallen trees, scrambling vines and creepers.

I first came to this nutritionally poor but biologically rich ecosystem in 1989. During the day the biological riches, at least of the more obvious kinds, are largely to be inferred rather than experienced directly. The clean smooth sand is criss-crossed with tracks of mammal and bird, reptile and insect: here the measured marks of a monitor lizard scavenging for carrion, eggs and nestlings; there, the dainty steps of forest rats. A honking flight of bushy-crested hornbills sweeping overhead and the distant exuberance of a gibbon troop call me back to nature immediate rather than nature previous, and direct my attention to the smaller scale concerns of the ecologist and the mundane necessities of field data collection.

For Odoardo Beccari, the egocentric Italian naturalist who visited this region from 1866 to 1868, this was the land of the 'maias' – the orang utans: he describes graphically the shooting, dissecting and killing of any number of the apes, from infants to magnificent old males (Beccari 1904). Alfred Russel Wallace, visiting Borneo in the 1850s in pursuit of beetles, butterflies and birds, noted the faunal contrasts between the Bornean animals and those *of the islands to the east, in particular that of the Celebes (Wallace 1869). The mass of natural historical information accrued by Wallace gelled in a burst of inspiration that came to him, immured by rain, and light-headed with malaria, in a Ternate bungalow. The end result of this concatenation of ideas and observations was Darwin and Wallace's joint presentation to the Linnaean Society of London on July the 1st 1858:* On the Tendency of Varieties to Depart Indefinitely from the Original Type. *The theory of evolution by natural selection had finally seen the light of day and biology would never be the same again!*

For these and many other less tangible reasons, Borneo, for me, was yet another of those ecological destinations that had seemed impossibly distant during my English incubation as a biologist. But by 1989 Borneo had become in my mind the land of pitcher plants, and the opportunity to follow up this impression with my graduate student Charles Clarke, an indomitable pitcher-plant enthusiast and field worker, had been just too much to resist.

We walked gingerly through the quicksands of the Labi stream beds: cascades of the delicate pitchers of Nepenthes gracilis *hanging from their scrambling stems over exposed shrubs, or forming perfect reflections in the mirror-like surfaces of the pitch pools. In the most exposed areas the larger and more robust red and green pitchers of* N. mirabilis *marked out the parent plants, free standing in the stream beds themselves. Scrambling among the branches of the larger trees at the edge of the stream beds the fleshy green leaves of* N. rafflesiana *terminated in dramatic trumpet-shaped upper pitchers hanging like red and yellow decorations on an equatorial Christmas tree. In the peat swamp itself, we waded through the opaque water. Here the squat pitchers of* N. ampullaria *hung in tight wreaths around the stems of their host plants. Last, but by no means least, we stood engrossed by the extraordinary giant pitchers of* Nepenthes bicalcarata, *which diverted even Beccari from his pursuit of the inedible, by its extraordinary combination of features as both an insectivorous pitcher plant, and a mutualistic ant plant.*

I shall return to the details of our pitcher-plant studies in due course: let them now stand as an introduction to all of the so-called phytotelmata – plant-container habitats. Pitchers, of course, act as traps for insects and other arthropods which drown in the fluid contained in the pitchers. They are digested by plant exudates, and the nitrogen-rich nutrients so produced are absorbed by the plant – enabling them, *inter alia*, to live in the nutrient-low substrates of the kerangas forest. But these small perched water bodies offer themselves as habitats for other species of animals which exploit the isolation and protection offered by the pitchers and cream off some of the nutrient base for themselves. A complete food web exists within each of the pitchers and the species of organisms which make up the pitcher fauna are largely restricted to this very special environment, breeding nowhere else.

Phytotelmata – defined and described

Pitchers are by no means the only aquatic habitats that occur as plant-based containers and, in 1928, the German biologist Ludwig Varga coined the term *phytotelmata* for the whole class of such ecological situations. Varga carried out extensive work on the flora and fauna associated with the water-filled leaf axils of the European teasel *Dipsacus silvestris* and, in order to put his work into literary context, he drew attention to earlier work on comparable habitats. Varga's work confirmed and established a vigorous interest in the biology of phytotelmata by European, particularly German, ecologists which continued from the very early days of organised limnology and ecology through the 1950s to the present day.

Varga's interest in container habitats appears to have been stimulated by the work of Müller (1879 *et seq*.), Picado (1912, 1913) and van Oye (1921, 1923). These earlier writers focused on the 'tanks' formed by the overlapping leaf-bases of bromeliads which retain water and provide a habitat for a wide range of freshwater and terrestrial organisms. Varga, writing in 1928, was also aware of the existence of an aquatic fauna within the pitchers of the Old World genus *Nepenthes* and the American *Sarracenia* and he quotes the works of Sarasin & Sarasin (1905), Jensen (1910), Günther (1913) and van Oye (1921) as his sources. His designation 'phytotelma' also included water-filled tree holes in branch axils and stumps of the European beech tree *Fagus sylvatica* as well as the water bodies collected in a variety of leaf axils such as those he himself studied in the teasel. Russian work by Alpatoff (1922) on the water bodies collected within the inflated sheathing petioles around the inflorescences of *Angelica sylvestris* had also come to his notice. Varga was not the first author to attempt to draw general attention to this class of habitats but the earlier designations of Müller (1879) ('Miniatür-Gewässern'), Brehm (1925) ('Hängende Aquarien') and Alpatoff (1922) ('Mikrogewässern') were all superseded by Varga's 'phytotelma'.

Of course the mere bestowal of a name on an object does not indicate its first discovery and Frank and Lounibos (1983) have followed long tradition by tracing the earliest record of insects originating from water-filled plant containers to a classical Chinese source. Ch'en Ts'ang-ch'i, writing during the T'ang dynasty sometime between 618 and 905 AD, is quoted by them as follows:

Beyond the Great Wall there is a *wen mu t'sai* (mosquito-producing plant), in the leaves there are living insects which change into mosquitoes.

(Pen T'sao Shih-yi)

Nevertheless Varga (1928) brought this class of habitats into the ken of scientists and, in particular, to the attention of Albrecht Thienemann. Thienemann is deservedly regarded as one of the great organising forces in ecology and limnology in Europe from the early part of the twentieth century until the 1950s. As director of the Max-Planck Institüt in Plön he was influential in directing a large part of German aquatic science throughout much of this period. Thienemann organised a major German research effort in the East Indies, the *Deutsche Limnologische Sunda-expedition*, the Proceedings of which appeared as supplements to the *Archiv für Hydrobiologie*. It was here that Thienemann drew attention to the fauna of *Nepenthes* pitchers in 1932. This work was followed by an equally influential general treatment in 1934, *Die Tierwelt der tropischen Planzengewässer,* which was encyclopaedic in nature and was the basis for the extended treatment he gave the subject in his massive work, *Chironomus*, published in 1954.

Phytotelmata occur in one form or another in a very wide range of ecosystems from subarctic bogs (*Sarracenia* pitchers) to anthropogenic road verges (*Dipsacus* axils, *Angelica* axils, etc.) to deciduous woodlands (tree holes). Container habitats occur on some of the most inhospitable and inaccessible of locations on the face of the Earth. *Heliamphora* pitchers are commonly found only on the remote Venezuelan outcrops known as *tepuyos* (see George 1989). The tiny Australian native pitcher plant *Cephalotus follicularis* shares with other genera of pitchers its predilection for nutrient-poor swamplands. But it is in tropical rainforests that phytotelmata display their full range and ubiquity. To return, by way of example, to the forests and creek beds of the Labi region of Brunei, I found, in addition to six species of *Nepenthes* pitcher plants, water-filled tree holes, water-filled bamboo internodes, a wide range of water bodies in the leaf axils of fleshy plants and the bract axils of inflorescences, together with pools of water in fallen palm leaves, horizontal logs and animal-damaged woody fruits such as coconuts. This range, varying slightly with location, can be found in tropical rainforests around the world.

Phytotelmata within modern ecology

There is little doubt that the early interest of naturalists in these habitats was fuelled by the fascination with the unusual that drives most natural historians. The range of plants which host phytotelmata, the range of animals which occur within them, and the sometimes curious and always interesting ecological interactions and other processes which occur within them form a legitimate base for their continued study.

But with the extension of community ecology from the descriptive to the predictive stage that has occurred in recent years, phytotelm studies have come to play a much more central role (Pimm 1982, Young 1997). The multitude of ideas on how natural communities have developed through evolutionary time, how they change through ecological time, and how and why they vary geographically call upon theoretical concepts relating to competition, predation and dispersal, as well as more holistic ideas which address structural limitations inherent (or otherwise) in the complex objects we know as food webs. It turns out that the communities which occur in phytotelmata are pre-eminent and predisposed to provide field tests of many of these ideas.

The reasons for this are fourfold:

- Phytotelm communities are aquatic but are located within terrestrial or semi-terrestrial ecosystems such as forests, woodlands, or swamps. Accordingly the aquatic organisms which occur within them encounter distinct edges which impose upon the community a discreteness not readily found in other more complex ecosystems.
- The communities of metazoan animals which occur in phytotelmata are relatively simple with the numbers of species ranging from one or two up to twenty or thirty. This relative simplicity allows the feeding links and hence the food web within them to be defined readily. This is in marked contrast to larger and more diffuse habitats such as lake beds or forest canopies in which species richness may be measured in hundreds of species and the number of potential feeding links is much larger.
- Most phytotelmata occur within larger ecosystems as a series of units scattered spatially within the forest, woodland, road verge or swamp. They are, to all intents and purposes, replicated across the ecological landscape. Of course, this is not a feature unique to phytotelmata and is comparable to the discrete habitat units provided by dung pats, macrofungus fruiting bodies, fallen logs and so forth.
- The replicated, faunistically simple and (usually) accessible units provided by phytotelmata together with their structural simplicity allows them to be manipulated and/or imitated in the field so that experiments can be designed and carried out on manageable scales of space and time.

Drawing upon these features and the rich base of natural historical information available to us, a number of workers including myself have been using phytotelm communities to test ideas within community ecology.

This book, then, is devoted, first, to describing the natural history and basic biology of phytotelm communities and the excitement this engenders. Building on this I go on to describe recent and on-going work which uses these communities to test a range of ideas within community ecology. Most of the investigations have generated at least as many questions as they have answered. But this is not unusual.

The information base

Since the early 1960s my students and I have maintained an interest in phytotelm ecology. This received a major boost in the early eighties when Howard Frank, Phil Lounibos and Durland Fish called a Symposium which was held during the 16th International Congress of Entomology held in Kyoto in 1980 (Frank & Lounibos 1983). During this time I renewed contact with Stuart Pimm who added a critical theoretical dimension to my thinking and field work. This has resulted in a number of collaborative efforts and has underpinned the field research of two of my most recent students, Bertram Jenkins and Charles Clarke.

The observations that are used repeatedly to illustrate points within this book result from our field work in various parts of the world. In general the results have been published in the primary literature and details of study sites and circumstances are to be found in these works. These field investigations were carried out on different occasions during a period of nearly thirty years. Naturally my experience with and appreciation of phytotelmata and what I now see as the key questions to be addressed grew during this period. I summarise here the circumstances surrounding crucial phases in this development so that particular results can be placed in context.

Tree holes in Wytham Woods

During the period 1966 to 1969 I studied a set of tree holes located within beech trees in deciduous woodland at Wytham Woods near Oxford in the United Kingdom. This work formed the basis of a doctoral dissertation, an overview of the results of which is provided by Kitching (1971). Details of population fluctuations in two of the commonest species of Diptera from these sites are presented in Kitching (1972a,b).

Tree holes in Lamington National Park

In 1978 I began examination of the community found within water-filled tree holes in the subtropical rainforest of Lamington National Park in south-east

Queensland. This has remained a research site from that time but was studied intensively from 1978 to about 1984. Student collaborators at the time included Catherine Callaghan, Rosemary Lott, Bertram Jenkins and Stewart Jackson. Stuart Pimm also participated in elements of this work. The basic food web involved is described by Kitching & Callaghan (1982) and comparative analyses presented in Kitching (1983), Kitching & Pimm (1985) and Kitching & Beaver (1990). The process of community reassembly following complete disruption is described by Jenkins & Kitching (1990). Basic work on spatial and temporal variability in food-web structure was also based on Lamington data and is described in Kitching (1987a) and Kitching & Beaver (1990). Results of our earliest manipulative experiments, carried out here, are in Pimm & Kitching (1987).

Phytotelmata in Sulawesi

In January and February 1985 I participated in the Royal Entomological Society's centenary expedition ('Project Wallace') to northern Sulawesi, Indonesia. Field work on tree holes and bamboo containers was carried out in the tropical rainforest of the Dumoga-Bone National Park and work on the fauna of *Nepenthes maxima* at nearby Lake Mooat. Basic descriptions of the food webs encountered are in Kitching (1987b), a specific account of a tree-hole dragonfly that was encountered is Kitching (1986a), and Kitching & Schofield (1986) provide a semi-popular account of the pitcher-plant work.

Tree holes in New England

The northern Tablelands of New South Wales provide ready access to a variety of rainforest ecosystems and during the period 1986 to 1991 we studied water-filled tree holes in subtropical and, so-called, warm temperate rainforest in Dorrigo National Park, and cool temperate *Nothofagus*-dominated rainforest at New England and Werrikimbe National Parks. The basic results are incorporated in the comparative analyses presented later in this work. Experimental manipulations of energy supply patterns to analogues of these tree holes were made by Bertram Jenkins and are described in his thesis (Jenkins 1991) and in Jenkins *et al.* (1992).

Phytotelmata in the northern New Guinea

In January and February 1988 I received a research fellowship to work at the Christensen Institute just north of Madang in New Guinea. I was able to identify food webs from water-filled tree holes, bamboo containers and the bract axils of the zingiber, *Curcuma australasica*. These are described in Kitching (1990). Further results from this work appear for the first time in this volume.

Tree holes in northern Florida

In mid-1988, under the aegis of the US/Australia Cooperative Science Scheme, I spent an extended period working in northern Florida. Studies of the food web occurring in tree holes on the Tall Timbers Reserve of the University of Florida, Tallahassee, intended to build on the earlier work of Bradshaw and his colleagues, were only partly successful due to the extended drought being experienced at the time! Some of these results are presented here.

Phytotelmata in the Daintree

In January and February of both 1989 and 1990 the University of New England mounted expeditions to the Daintree region of far north Queensland based at Cape Tribulation. During this period Jenkins and I carried out the most extensive study of tree-hole communities that I am aware of, sampling and analysing the contents of over eighty sites. In addition we examined the water bodies in the leaf axils of an undescribed species of *Freycinetia* (Pandanaceae) and the bract axils of the inflorescences of the so-called 'backscratcher ginger', *Tapeinocheilus ananassae*. A few observations of animals occurring in fallen rat-opened coconuts were made, along with observations on the fauna of water-filled leaf bases of fallen palm fronds. Some of these results are presented in this volume for the first time.

Nepenthes *pitcher plants in northern Borneo*

As indicated in the opening paragraphs of this chapter, in May and June 1989, I assisted Charles Clarke in his studies of *Nepenthes* pitcher plants in northern Borneo. The results of these studies are presented in Clarke & Kitching (1993). A full account of the work comprises Clarke's doctoral dissertation (1992).

Tree holes in tropical Queensland

In the wet season of 1993, in preparation for writing this book, we undertook studies of the faunas of water-filled tree holes at a number of rainforest sites in Queensland selected to fill gaps in our knowledge, hitherto restricted to sites in the subtropical extreme south-east, and the lowland tropical North. Additional studies were carried out in higher altitude forests at Eungella National Park, on the Atherton Tablelands, and at Paluma; more southerly tropical lowland forests at Bellenden Ker National Park and in the subtropical forests of the Conondale Ranges north of Brisbane. This work was done with the assistance of Beverley Kitching, Charles Clarke, Peter Juniper and Heather Mitchell and the results appear for the first time in the present work.

Other studies

Of course the extensive work of other writers also forms a vital part of the information on which the present analyses are based. In particular the work of the following researchers form an indispensable part of the foundation for this work: Beaver on *Nepenthes* pitcher plants in West Malaysia; Bradshaw, Frank, Lounibos and many others on phytotelm mosquitoes in North, Central and South America; Seifert on the axil waters of *Heliconia* species in Central America; Kurihara, Mogi and other Japanese colleagues on phytotelm mosquitoes in Japan and south-east Asia; and, Machado-Alison and his students on Venezuelan phytotelms.

Structure and content

This work is designed to be encountered both as a whole and in parts. Accordingly, for the student of phytotelmata, I hope the traditional beginning-to-end read will be educational, profitable and thought-provoking. But, in addition, each chapter presents an essay within areas of natural history and ecology and those with more specialised interests will find value in reading them in at least partial isolation from the remainder of the work.

The basic structure and intended logic of the book are summarised in Figure 1.1. I have grouped the chapters into five parts after this Introduction. I have prefaced each of these parts with a word picture of some of the field experiences involved, deliberately to try to recreate some of the excitement of the naturalist, to offset in part the objectivity of the ecologist.

Part I contains three substantial 'background' chapters describing the plants, animals and physico-chemical environment of phytotelmata in general. These provide information on the underlying biology, natural history and environmental science which are the vital context of later discussions on the ecology of phytotelm communities. An extended annexe at the end of the book is a family-by-family treatment of the phytotelm fauna.

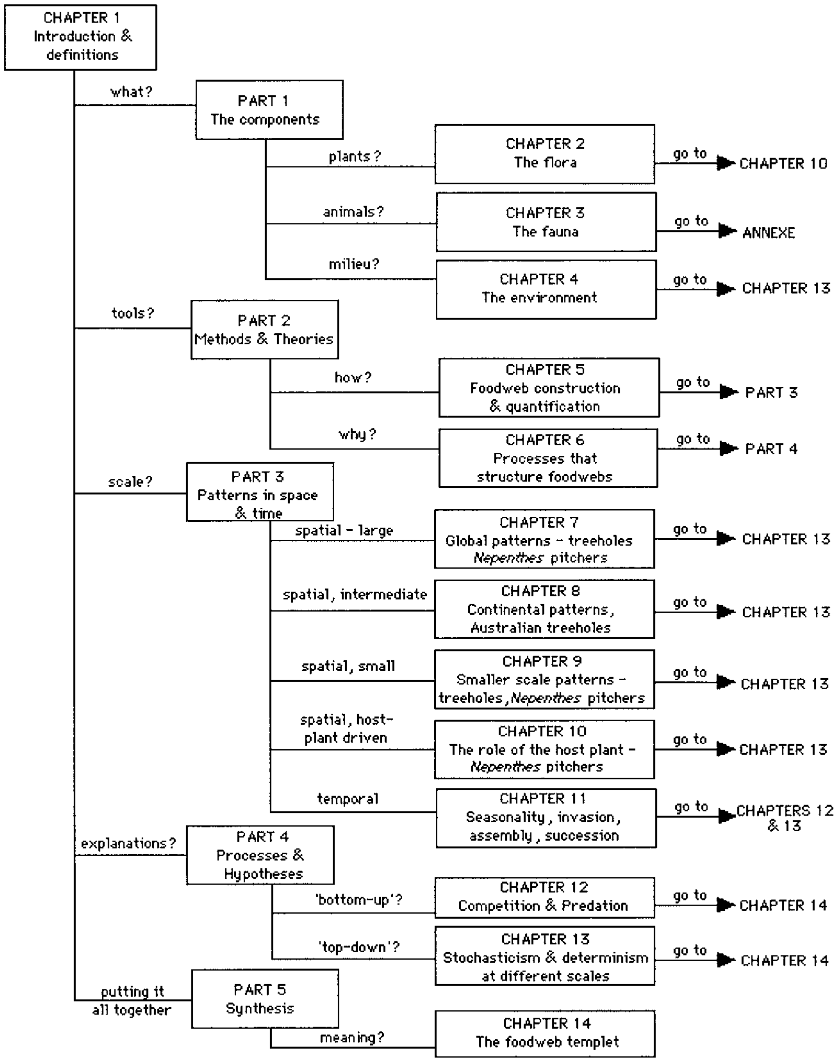

Fig. 1.1. The structure and logic of the book.

Part II of the work contains two important chapters. The first introduces the idea of the food web by presenting examples from each phytotelm type. The chapter defines key formalisms concerning the food-web statistics which will be used without further explanation in later chapters. The second chapter (Chapter 6) in this section reviews segments of the theory of food webs from the recent literature. In addition the chapter explores the biological mech-