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The insects of plant-held waters: a review and bibliography

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ABSTRACT. Phytotelmata habitats have been the focus of much research and are utilized by a wide variety of taxa. In the past 15 years numerous studies in many geographic regions and covering various types of phytotelmata have greatly increased our understanding of these unique habitats. The most recent summary of phytotelmata inhabitants included over 20 families of insects. A review of the literature and extensive work in lowland Ecuador shows the family level diversity is in fact at least twice that reported earlier. A reassessment of previous phytotelmata classification schemes, as well as an extensive bibliography, is provided.

KEY WORDS: aquatic insects, bromeliads, bract, phytotelmata, pitcher-plant, tree-holes

INTRODUCTION

The term 'phytotelmata' was first introduced by Varga (1928) to describe bodies of water impounded by plants, and was later clarified by Kitching (1971). These aquatic habitats are utilized in a variety of ways by a wide range of organisms including insects (Fish 1983), mites (Naeem 1990a), entomostracods (Naeem 1988, Reid & Janetzky 1996, Scourfield 1915), microorganisms (Lackey 1940), annelids (Fragoso & Rojas-Fernández 1996, Sota & Mogi 1996), crabs (Diesel 1989), and anurans (Caldwell 1993, Summers 1992). While phytotelmata (hereafter referred to as PT) may potentially occur everywhere, due in part to the diversity of plant species and the humidity of most tropical regions, these habitats are most prolific in tropical forests. Indeed, the abundance and diversity of PT habitats in a lowland Amazonian rain forest can be quite impressive. The predominantly tropical plant family, Bromeliaceae, is alone thought to include nearly 1000 species that commonly impound water (Fish

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1983). Anyone visiting a tropical forest will undoubtedly encounter copious mosquitoes, most of which will have spent their immature lives in some type of PT. Many creatures such as the magnificent giant tropical damselflies (Pseudostigmatidae, Megapodagrionidae) and most species of poison dart frogs (Dendrobatidae), rely on PT as breeding sites (Caldwell 1993; Fincke 1992a, b; Summers 1992).

While a few specific systems, such as pitcher plants (Sarraceniaceae & Nepenthaceae), have been looked at in detail (Beaver 1983, Fish & Hall 1978; Istock *et al*. 1975, 1983), most studies have focused on the mosquito fauna and little work has been done on other inhabitants. Some attempts to compile literature on the fauna of various PT have been made (Fish & Beaver 1978, Frank 1983, Seifert 1982), but current faunal lists for even the most common types of PT are lacking. The most recent summary of these aquatic habitats and their insect inhabitants (Fish 1983) estimated that over 1500 species of plants form PT of some sort. In that paper, Fish (1983) listed 29 families and over 60 genera of plants reported to impound water. The insect fauna listed by Fish (1983) included representatives from six orders and over 20 families.

Using a literary review and a large data set from Amazonian Ecuador, this study reassesses and amplifies the classification of PT habitats described by Kitching (1971). It reports an additional five orders and over 50 families of insects, summarizes our current understanding of insect use of PT, and points to further directions of research.

THE PLANTS

Kitching (1971) described seven types of PT based on the type of fluid held by the plant (i.e. partially plant-derived or entirely rainwater), the part of the plant used (i.e. stem, leaf, flower, etc.), and whether or not the part is still attached to a live plant. The classification used by Kitching (1971) was taken from Thienemann (1954), and is summarized on the left-hand side of Appendix 1.

Since Kitching's (1971) paper on water-filled tree holes, much work has been conducted on these and other types of PT. After a review of faunal records of all types of PT, they have been re-organized into six separate categories (Appendix 1) using a set of characteristics similar to Kitching (1971). For the purposes of this study, stem rots, such as those seen in columnar cacti or fallen banana stems, are included as an intermediate or peripheral habitat type. These plant parts form largely aqueous habitats of rotting plant matter. Their fauna has not been well described, due in part to the poorly defined parameters of the habitat, but all encountered references are cited. This was done because of the similarities in fauna and because most types of PT include partially or fully decaying plant matter in addition to a truly aquatic habitat.

The major changes to the classification of Thienemann (1954) and Kitching (1971) are as follows. Fallen leaves (here to include fallen bracts or spathes and referred to as fallen plant parts) have been separated out as a distinct type of PT. These habitats are very different in their duration from tree holes, pans and rots. Additionally, they occur almost exclusively at ground-level, and their more fragile structure most likely results in a significantly different nutrient input from the container itself than that of wood-lined treeholes.

Tree holes formed in trunks of fallen trees have been lumped with those formed in standing trees. Although Mattingley (1969) suggests that these may have a different fauna from tree holes in upright trees, the faunal lists of Snow (1958) from a rotting tree stump, as well as personal observations in tropical forests, suggest that these habitats in fact present a rather indefinable continuum of stem hole types. This is readily apparent when one begins to try and separate these two types in the field and finds tree holes of the 'pan' and 'rot' type (Kitching 1971) in standing or fallen trees, either living or dead. Fallen fruit husks also have been separated from other types of fallen plant parts as these habitats almost invariably include a large nutrient input from the rotting flesh of the fruit and husk.

The inflorescence of *Commelina* (Zingiberaceae) described by Kolumbe (1931) and those of *Lobelia* (Zingiberaceae) examined by Coe (1969) have been placed under flower PT. This was done because they both describe rather specialized habitats, and the presence of plant-secreted substances has since turned up in other PT such as bromeliad leaf axils (Fish 1976) and *Heliconia* (Musaceae) flower bracts (Bronstein 1986, Seifert 1982). This distinction of having plant-secreted material, therefore, is possibly underestimated in other types of PT and its effect is not well documented for most. The division of calyx waters delineated by Thienemann (1954) has also been lumped with flower parts, as it refers to an isolated case found in the East Indies.

Therefore, for the purposes of this review, PT have been divided into the six types outlined on the right hand side of Appendix 1. They are as follows: (1) tree holes, (2) leaf axils, (3) flowers, (4) modified leaves, (5) fallen vegetative parts such as leaves or bracts and (6) fallen fruit husks. In addition, the presence of various insect groups in a seventh habitat type, stem rots, has been noted where applicable. These seven habitat types are defined as follows.

(1) Tree holes (TH): Trees that impound water in buttress roots, trunk holes, and lateral pans have been reported from every continent except Antarctica (Fish 1983). Recent studies in Panama have significantly increased understanding of these communities (Finke *et al*. 1997; Yanoviak 1999a, b, c, 2000). In addition, because of similarities in morphology of the habitat, the internodal pools that form in many species of bamboo (Graminae) are included here. These bamboo habitats are formed when shoots break or sustain insect feeding damage that allows water to enter. As bamboo stem holes obviously occur within a taxonomically limited group of plants, and because they are usually morphologically dissimilar to other tree holes, they may represent a separate division within PT. For this review they have been placed in this category.

(2) Leaf axils (LA): Water impounded by inflated leaf axils are the most common type of PT, with the Bromeliaceae alone estimated to have over 1000 species that impound water (Frank 1983). Members of over 26 families of plants including the Agavaceae, Amaryllidaceae, Araceae, Dipsacaceae, Musaceae, Palmae, Pandanaceae (Fish 1983) and Graminae (Soria *et al*. 1978) have been reported to impound water in a similar fashion.

(3) Flower parts (FP): Often flower parts such as the large waxy bracts seen in *Heliconia* (Machado-Allison *et al*. 1983) and *Calathea* (Marantaceae) (Fish & Soria 1978, Wirth & Soria 1981) will impound water. *Heliconi* bracts in particular have been well studied (Seifert 1982), and are known to contain plant derived liquids (Bronstein 1986).

(4) Modified leaves (ML): Pitcher plants (Nepenthaceae and Sarraceniaceae) provide one of the most dramatic types of PT (Beaver 1983). Individual leaves are modified to impound water and plant fluids in which many insects complete their development. The main distinction between these habitats and water impounded by leaf axils is the presence of secreted plant fluids that digest organic material falling into the plant.

(5) Fallen plant parts (FPP): Very little work has been conducted on this type of PT. Occasionally, fallen leaves of large plants may collect enough water to attract insect inhabitants. These PT occur in the large leaves of families such as Musaceae, Marantaceae, Sterculiaceae (Heinemann & Belkin 1977), Palmae and Araceae (H. F. Greeney, *pers. obs.*). In addition, the fallen woody bracts of several genera of palms (especially *Iriartea*) will often fall so as to allow water to collect (Greeney 1999, Hutchings 1994). These bract habitats can remain for over 90 days, and represent a more permanent habitat than fallen leaves (Greeney 1999). For this reason alone, and because the woody structure of the bracts most likely provides a higher nutrient input to the system, bracts should possibly be separated from this category. Because of the lack of faunistic and abiotic data on these habitats, however, they are placed together for this review.

(6) Fruit husks (FH): The fallen remains of many tropical fruits will often create small pockets of collected water and rotting plant matter. A striking example of this is water collected in broken coconut shells, but husks from the families Apocynaceae, Loganiaceae, Bombacaceae (Lounibos 1978), Lecythidaceae (Caldwell 1993, Heinemann & Belkin 1977), Bignoniaceae (Belkin & Heinemann 1976), and Sterculiaceae (Paine 1943) are all known to hold sufficient amounts of water.

(7) Stem rots (SR): This category has traditionally been left out of discussions of PT. By the original definition (Varga 1928), this is not considered a PT habitat. I include it here, as it represents an example of the transition zone between PT and other similar habitats such as dung, carrion and rotting fruit, and many of the traditional PT inhabitants are represented. After serious trauma or death, some types of plants collapse and begin to rot. Cacti

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(Ryckman & Ames 1953) (Cactaceae), bananas (Winder 1977a) (Musaceae), and other fleshy plants often form a rancid, aqueous pile of rot when dead. Many aquatic insects take advantage of this unique, ephemeral habitat. Included in this category are only those habitats that present a more aqueous habitat and such things as rotten wood and decomposing leaf material are omitted.

THE INSECTS

A total of over 70 families from 11 orders have been reported from PT (See Tables 1–5). The Diptera, Coleoptera and Odonata are best represented, but Hemipterans have also been found and more should be expected to turn up. Trichoptera and Plecoptera have few records. For many of the following families, there are numerous references from each type of PT habitat. Those provided represent examples from a variety of situations and geographic locations.

The following records are broken into three parts. Part 1 includes all families recorded or assumed to be truly aquatic in their use of PT (Tables 1 and 2). Part 2 summarizes those families that, for the most part, probably include semi-aquatic members or species that inhabit the rotting plant or animal matter in or around PT (Table 3). Part 3 contains records of species reported on few occasions or those that likely include terrestrial species foraging in or around PT habitats (Tables 4 and 5).

Truly aquatic insects

Thirteen families of Diptera with truly aquatic species, most species in the suborder Nematocera, have been recorded from almost all conceivable PT habitats. They are by far the most numerous members of most PT communities, and are often the sole macroinvertebrates found there. Mosquitoes are among the most studied and prolific of the dipterans, but flies in the families Ceratopogonidae, Chironomidae and Tipulidae have been found to breed in a variety of PT.

Only 16 families of beetles have been recorded from PT. Of these, only three are found recurrently and are truly aquatic. Many of those normally inhabiting lentic habitats such as gyrinids and haliplids are noticeably lacking. Those that are common, sciritids, hydrophilids and dytiscids, are often known to breed in plant-held waters, but are more commonly found as adults.

A few terrestrial odonates are known from Hawaii (Williams 1936), but the vast majority are aquatic predators as larvae. Six families of Odonata are known to breed regularly in PT, and some of these are known only from such habitats. They represent some of the top predators in many PT communities, and are often the largest invertebrates present.

Of the four main orders of PT inhabitants, Hemiptera are the least common. This is surprising given their powers of dispersal and ability to inhabit other types of temporary habits (Fernando 1959). The most commonly found family

Table 1. Truly aquatic insects. Part 1: Diptera. Numbers represent reference numbers. Families of Diptera thought to be associated with the water held by various phytotelmata. TH, tree holes; LA, leaf axils; FP, flower parts; ML, modified leaves; FPP, fallen plant parts; FH, fruit husks; SR, stem rots.

Taxon	TH	LA	FP	ML	FPP	FH	SR
Culicidae	36, 164, 177, 181, 198	62, 174, 177, 186	121, 125, 126, 155, 174	9, 32, 117, 118, 119, 128	10, 65, 67, 72, 73, 78, 131, 178	22, 104, 174, 177, 178	
Ceratopogonidae	166, 193, 198	62, 99, 163, 171, 186	62, 121, 180, 186, 195	15, 32, 118, 176		163, 180	84, 107, 163, 190
Chironomidae	87, 88, 165, 166, 180	79, 115, 141, 171	62, 125, 126, 127, 180	20, 32, 82, 92	67	191	
Tipulidae	4, 39, 165, 166, 173	2, 3, 62, 99, 185	90, 121			191	
Chaoboridae		62, 192		32, 118			
Cecidiomyiidae	166	120, 168, 190		32, 118		191	190
Psychodidae	39, 49, 165, 166, 198	94, 99, 109, 115, 171	62, 90, 121			191	
Syrphidae	35, 39, 165	99, 115, 160, 168	90, 109, 125, 127, 157	32, 75, 118	67	Greeney unpubl. data	144
Stratiomyiidae	49, 165	24, 28, 99, 111, 161	121, 126, 127, 155, 157			191	
Phoridae	35, 165, 166		90	13, 14, 32, 118		191	
Tabanidae	49, 66, 162	116					
Muscidae	165	58, 168	62, 121	15			
Calliphoridae	90			13, 32, 118			
Richardiidae			155,158, 159				
Anthomyiidae	85, 167, 172						
Dolichopodidae		168, 171		122		191	
Sarcophagidae				1, 118			

is the Veliidae, and there are many taxa known only from tropical bromeliad waters.

Two species of Trichoptera and one species of Plecoptera have been reported from PT. At least one species of calamoceratid has been reported from the leaf axils of bromeliads (McLachlan 1879, Müller 1879), one limnophilid was found in a tree hole (Barnard 1978), and perlid stoneflies have been documented living in tropical *Heliconia* flowers and bromeliads.

Semi-aquatic insects

The families included here have all been reported at least once from PT habitats. For the most part they represent true inhabitants of PT, but may not be associated strictly with the waters contained within. Seven families of flies are included in this category, most of which are well known inhabitants of

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Table 2. Truly aquatic insects. Part 2: Insects other than Diptera. Numbers represent reference numbers. Families of non-dipterous insects thought to be associated with the water held by various phytotelmata. TH, tree holes; LA, leaf axils; FP, flower parts; ML, modified leaves; FPP, fallen plant parts; FH, fruit husks; SR, stem rots.

Taxon	TH	LA	FP	ML	FPP	FH	SR
Coleoptera Sciritidae	91, 132, 169, 182	95, 160					
Hydrophilidae	Greeney unpubl. data	63, 99, 129, 191	127, 155, 158		67		
Dytiscidae		7, 26, 63, 99, 142, 153			67		
Odonata Pseudostigmatidae	54, 55, 57	23, 24				22, 184	
Protoneuridae		108, 146					
Coenagrionidae	130	99, 102, 145, 147, 148, 149, 150, 151, 183					
Megapodagrionidae	90, 105, 182						
Aeshnidae	18, 54, 130, 57	99					
Libellulidae	37, 39, 102, 103, 130			19			
Heteroptera Veliidae	77	44, 45, 46, 47			67		
Trichoptera Calamnoceratidae		113, 132					
Limnophilidae	8						
Plecoptera Perlidae		139	155				

rotting plant matter and other organic substrates. Examples of other orders such as the semi-aquatic leaf beetles (Chrysomelidae) which inhabit *Heliconia* flower bracts are frequently found as larvae which feed below the surface of bract liquids, but on the structure of the bract itself (Naeem 1990b; Seifert & Seifert 1976a, b). Another, the nymphs of a spittlebug (Cercopidae), a member of a family where most nymphs are arguably semi-aquatic in their habits, are reported as the first known aquatic homopterans (Thompson 1997) and live inside the water-filled floral bracts of *Heliconia* as well.

Collembolans inhabit many types of habitats both aquatic and terrestrial. They have been reported from such diverse locations as dung (Mohr 1943) and intertidal zones (Christiansen 1964, Christiansen & Bellinger 1988). From PT they have only been casually mentioned in several situations, but they were found in abundance in bird-made holes in large columnar cacti in Arizona (Soule 1964) and in water-filled stem holes (Park *et al*. 1950, Snow 1958). Park *et al*. (1950) reported podurids, entomobryids and smithurids from tree holes and Mogi & Yamamura (1988) found collembolans in flower bracts. They have been found in bromeliads on several occasions (Cotgreave *et al*. 1993, Dejean &

Table 3. Semi-aquatic Insects. Numbers represent reference numbers. Families of insects thought to be associated with the water held by various phytotelmata, but not necessarily fully aquatic. TH, tree holes; LA, leaf axils; FP, flower parts; ML, modified leaves; FPP, fallen plant parts; FH, fruit husks; SR, stem rots.

Taxon	TH	LA	FP	ML	FPP	FH	SR
Diptera	165, 166			83		191	
Sciaridae							
Mycetophilidae				32, 118		191	
Anisopodidae		93, 139					
Aulacigastridae		58, 62					
Asteiidae		186					
Chloropidae				82			
Coleoptera			127, 157,				
Chrysomelidae			158				
Heteroptera			175				
Cercopidae							
Collembola	134	40, 42	121		65		167

Olmstead 1997), and they were often seen in fallen palm bracts in Ecuador (Greeney 1999). The latter record most likely represents individuals landing there after being disturbed from the surrounding leaf litter, but their importance and relation to the PT has not been thoroughly examined in any situation. Because of their small size, and ability to jump rapidly, collembolans are most likely overlooked in many studies, and will probably turn up more frequently with rigorous sampling.

Rarely reported or terrestrial insects

Four families of dipterans representing poorly known or normally terrestrial families have been found in one of the seven habitat types discussed. Again, most of these are likely associated with the decaying organic matter in and around PT rather than strictly with the water inside. Many species of beetles have been collected from various PT, in particular bromeliads. Most of these such as elaterids, cerambycids and tenebrionids are most likely associated with the plant rather than the water held within, but 12 families are included here that may be more closely associated with the damp, rotting areas surrounding PT. Some, such as the pselaphid beetles studied by Park *et al*. (1950), are known only from such habitats. Others, such as the staphylinids, histerids and carabids are probably terrestrial predators taking advantage of the concentrations of prey species often found in PT.

Two families of odonates have been reported once each, and may represent oviposition mistakes in these cases. Three hemipteran families and three homopteran families have also been found, but most of these appear to be rare, terrestrial or possibly accidental.

The only hymenopterans represented in published PT literature are ants (Formicidae). Those reported are not aquatic, but some are amphibious and known to enter pitcher plant waters to extract dead insects (Clarke & Kitching 1993). The most well documented examples are the hanging 'ant gardens'

Table 4. Rarely reported or terrestrial insects. Part 1: Diptera and Coleoptera. Numbers represent reference numbers. Families of insects thought recorded from various phytotelmata, but presumed to be terrestrial in their association, as well as those aquatic families that have been reported on very few occasions. TH, tree holes; LA, leaf axils; FP, flower parts; ML, modified leaves; FPP, fallen plant parts; FH, fruit husks; SR, stem rots.

Taxon	TH	LA	FP	ML	FPP	FH	SR
Diptera				15			
Lauxaniidae							
Lonchopteridae		168					
Sphaeroceridae		96					144
Drosophilidae			121				144
Chloropidae				135			
Scatopsidae							192
Lonchaeidae							144
Milichiidae							144
Coleoptera Staphylinidae	134, 166	28	158		67	Greeney unpubl. data	
scarabaeidae		28, 34, 76, 138			67	Greeney unpubl. data	
Histeridae		Greeney unpubl. data	62				144
Carabidae		99, 139			67	Greeney unpubl. data	
Nitidulidae	134, 166	191					
Pselaphidae	133, 134						
Ptiliidae	134						
Curculiionidae		191			67		192
Dermestidae							167
Hydraenidae		171					
Tenebrionidae							144

(Dejean & Olmstead 1997, Yu 1994). These are formed when carton nest building species of canopy ants have species of bromeliads associated with their aerial nests. Most records are likely species which enter PT to prey on dead and dying inhabitants during periods of drought or as the habitat dries. Besides ants, parasitic hymenopterans have been reared from a syprhid pupa found in a tree hole in eastern Ecuador (H. F. Greeney, unpubl. data) and found in tree holes in northern USA (Park *et al*. 1950). These examples clearly illustrate cases where non-aquatic insects have a definite affect on the aquatic inhabitants, but the foraging by ants in all types of PT most certainly affects their inhabitants to some degree.

While some species of pyralids and other moths are known to have aquatic larvae (Berg 1950), most are not. From PT, pyralids are reported in leaf axils of bromeliads (Winder 1977b), but it was not noted if they were associated with the water therein.

Dermapterans, orthopterans, thysanapterans, psocopterans, and cockroaches are all occasionally found in PT. Some such as the orthopterans and cockroaches are most likely using the conveniently dark microhabitats provided by

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Table 5. Rarely reported or terrestrial insects. Part 2: Insects other than Diptera and Coleoptera. Numbers represent reference numbers. Families of insects thought recorded from various phytotelmata, but presumed to be terrestrial in their association, as well as those aquatic families that have been reported on very few occasions. TH, tree holes; LA, leaf axils; FP, flower parts; ML, modified leaves; FPP, fallen plant parts; FH, fruit husks; SR, stem rots.

Taxon	TH	LA	FP	ML	FPP	FH	SR
Odonata					67		
Gomphidae							
Calopterigidae	100						
Heteroptera					67		
Corixidae							
Hydrometridae					67		
Gesastocoridae					67		
Cicadellidae	134						
Lygaeidae			121				
Aphididae			121	143			
Hymenoptera Formicidae	134	42, 196		32	67	Greeney unpubl. data	
Lepidoptera		191					
Pyralidae							
Dermaptera	Greeney unpubl. data	24, 139	157		67	Greeney unpubl. data	144
Orthoptera		40, 42	121		67		
Thysanoptera		40	121				
Blatoedea		40, 42	121, 159		67	Greeney unpubl. data	
Psocoptera		40					

many PT, as diurnal refuges. Others, such as various species of dermapterans are probably foraging there in a similar fashion as predatory beetles and ants.

DISCUSSION

PT present biologists and community ecologists with an interesting and unique set of questions. For many aquatic insects they are refuges from terrestrial existence in areas where there is little ground water available. For others they are foraging arenas or a convenient refugia from the elements. The plants themselves offer a long continuum of habitats ranging from water-filled bromeliad leaf axils to semi-aqueous cactus rots or the moist walls of tree holes. While reviewing the literature for this manuscript and during fieldwork in Ecuador, it became apparent that the distinction between true PT inhabitants and those simply opportunistically associating with the plant is often difficult to determine. During many surveys, all insects found in or near the various PT flora were listed (Laessle 1961, Picado 1913). Many of these are at first glance discounted from the truly aquatic members of the fauna. It is prudent to point out, however, that there are aquatic cockroaches (R. L. Smith, *pers. comm.*), lepidoptera (Berg 1950), and other chiefly terrestrial insects. The importance of these non-aquatic inhabitants is generally poorly understood, but some, such as predatory spiders (Mogi & Chan 1997) and ants (Clarke & Kitching 1993) are at least thought to have an effect on the aquatic inhabitants. The effects of other non-aquatic insects such as ants and termites which eat or nest in some PT (Dejean & Olmstead 1997, Yu 1994) may also have unknown effects on these communities. Other terrestrial species such as *Bdelyrus* (Scarabaeidae) dung beetles, often found feeding inside bromeliad leaf axils (Cook 1998, Huijbregts 1984, Pereira *et al*. 1960), are most likely not part of the aquatic fauna but compete directly for detrital resources. It is therefore prudent to include these non-aquatic inhabitants in the faunal lists.

The great diversity of life histories associated with insect families also requires that species listed as aquatic PT inhabitants are examined carefully before inclusion. Good examples of this can be found in the Tipulidae and Anthomyiidae. Records of tipulids from PT such as those by Alexander (1912, 1915), Fish & Soria (1978) and Williams (1939) most likely represent truly aquatic examples. Dudley (1982) reports tipulids reared from water-soaked wood, and tree hole records such as Keilin (1927) and Snow (1958) are examples of tipulids that may be utilizing the rotting walls of this habitat rather than the water held within. Anthomyiids have been reared only from stem hole habitats, and the records of Tate (1935) and Keilin (1917) most likely are truly aquatic species. Soule (1964), however, reported anthomyiids occurring in the water-filled holes of *Cereus* cacti. As these flies are regular inhabitants of rotting materials (Beaver 1969), Soule's (1964) record may be of a species living in damaged cactus tissue. Similarly, Keilin (1927) reported anthomyiids inhabiting the rotten wood inside a chestnut tree hole. Occasionally a species presents an obvious example of a non-aquatic inhabitant of PT such as the aphids inhabiting pitcher plants (Robinson 1972). In most cases, however, the distinction is more difficult to make without detailed ecological and life history data. Other examples of doubtfully aquatic species can be found for cecidiomyiids (Winder & Silva 1972) and sciarids (Sota 1996, Winder & Silva 1972). All records from PT that include water as well as rotting vegetative material, require more detailed observations to confirm the aquatic nature of their inhabitants.

The use of patchily distributed resources such as PT has been thought to play a crucial role in structuring communities (Kitching 1987). PT are similar, with respect to their patchy and ephemeral nature, to other insect habitats. Community level studies on dung (Hanski 1980, Hanski & Koskela 1979, Merritt & Anderson 1977), carrion (Hanski & Kuusela 1980, Payne 1965), fruit (Atkinson 1985), fungi (Hingley 1971, Paviour Smith 1960), and rotting wood (Elbourn 1970, Fager 1968) have all noted the importance of the habitats' discrete nature. Despite the fact that these habitats are placed in a separate 'habitat system type' from PT by Elton & Miller (1953), their communities show striking similarities. PT also share many similarities with other types of temporary waters such as rain puddles (Cantrell & McLachlan 1982, McLachlan 1981) and rock pools (Ranta 1982). This similarity was apparent to Elton &

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Miller (1953) as demonstrated by the fact that PT, ditches, small ponds and 'trickles' are all clustered in the same region of their aquatic habitat classification matrix. Habitats such as dung and carrion have been termed 'non-fleeing' resources (Charnov *et al*. 1976). In other words, their use or consumption has no effect on their production. Many PT habitats such as fallen palm bracts can potentially present a similar situation for their detritivorous inhabitants. The use of these habitats by detritivorous mosquitoes and chironomids has no impact on their production or distribution. The question then from Charnov *et al*. (1976) is: How can these habitats support the large numbers of species that are so often seen (Atkinson & Shorrocks 1984, Beaver 1977, Hanski & Cambefort 1991, Mogi & Yong 1992, Ranta 1982, Williams 1975)? Given these similarities, the large amount of overlap between the types of insects inhabiting PT and these other habitats is not surprising.

The enormous diversity of insects recorded from PT mirrors the diversity of tropical organisms in general. While PT habitats comprise only a small portion of the habitat in most tropical areas, they are without a doubt important systems that house a variety of interesting and often unique species. It is my hope that this review provides a useful summary of the knowledge to date on the entomofauna of these ecologically important habitats, and sparks further research into the biology of all their inhabitants.

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Appendix 1. Divisions of phytotelmata

Criteria for dividing phytotelmata into groups used in Kitching (1971) and those proposed. Examples from each division of phytotelmata.

After Kitching (1971)		Proposed classification	
Criteria	PT type and examples	PT type and examples	Criteria
Liquid derived at least in part from plant, digestive secretions present	Pitcher plants. Serraciniaceae, Nepenthiniaceae	Modified leaves (ML) Serraciniaceae, Nepenthiniaceae	Water held by living tissue, non-woody plant tissue, leaves or leaf axils, modified leaves for prey capture
Liquid derived at least in part from plant, digestive secretions absent	Flower inflorescence. Zingiberaceae	Flower parts (FP), Zingiberaceae, Marantaceae, Heliconiaceae	Water held by living tissue, non-woody plant tissue, held by flower part
Liquid mostly rain water, contained in green plant part, in leaf axils	Leaf axils. Bromeliaceae, Pandanaceae	Leaf axils (LA). Bromeliaceae, Pandanaceae, Palmae	Water held by living tissue, non-woody plant tissue, leaves or leaf axils, collects rain water
Liquid mostly rain water, contained in green plant part, in calyx	Calyx waters. One example from calyx of East Indian plant	Fruit husks (FH). Fallen fruits of Sterculiaceae, Cucurbitaceae, Palmae	Water held by fallen plant part, in fruit, seed pod, or husk
Liquid mostly rain water, contained in non-green plant part, in flowers	Flower bracts. (non-plant derived liquids) Heliconiaceae, Marantaceae	Fallen plant parts (FPP). Fallen leaves, fallen flower bracts	Water held by fallen plant part, not in seed pod or fruit
Liquid mostly rain water, contained in non-green plant part, in woody part, standing stems or trunks	Tree holes. Holes in standing trees, bamboo internodes	Tree holes (TH). holes in tree trunks or roots, fallen or standing, bamboo internodes	Water held by woody plant part, usually stem, trunk, or root, may be dead or living part
Liquid mostly rain water, contained in non-green plant part, in woody part or fallen part	Tree holes and fallen parts. Holes in fallen trees, fallen fruit husks, fallen leaves		

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