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**PHYTOTELMATA: SWAMPS OR ISLANDS?**

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**ABSTRACT**

For phylogenetically lower organisms, phytotelmata resemble islands, and colonization of phytotelmata resembles colonization of artificial containers; colonizers are not selective, and some are eliminated by interaction with specialist members of phytotelm communities. For phylogenetically higher organisms, phytotelmata resemble swamps; colonization occurs by phoresy and by flight, and for the commonly occurring species colonization is highly selective. Phytotelm-inhabiting mosquitoes use plant height, size, color, and water chemistry as ovipositional cues to maintain habitat fidelity.

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**Resumen**

Para organismos bajos en la escala filogenética, las fitotelmatas son parecidas a islas, y la colonización de fitotelmatas es parecida a la colonización de recipientes artificiales; los colonizadores no son selectivos, y algunos son eliminados a través de interacciones con miembros especialistas de las comunidades de fitotelmatas. Para organismos más altos en la escala filogenética, las fitotelmatas se parecen a pantanos; la colonización ocurre a través de foresia y al vuelo, y para las especies más comunes, la colonización es muy selectiva. Mosquitos que habitan fitotelmata utilizan la altura de las plantas, el tamaño, color, y química del agua como señales para la oviposición para mantener la fidelidad al hábitat.
Picado (1913) was an early student of the fauna of bromeliad phytotelmata. Impressed with the number of species and individuals of water-holding bromeliads in Costa Rica, he likened them to:

Un grand marécage fractionné, étendu dans toute
l'Amérique intortropiale (Picado 1911).

Thus phytotelmata may have some of the characteristics of swamps, yet Seifert (1981) considered some phytotelmata from the point of view of island biogeographic theory (MacArthur and Wilson 1967). We could not reconcile these ideas because we supposed that colonization of swamps should contrast with that of islands. Colonization of phytotelmata-swamps should display rapid arrival of the full complement of hinta of other phytotelmata-swamps (which would be specialists to the habitat), negligible species turnover, and high species richness. Colonization of phytotelmata-islands should display a more or less sequential arrival of progressively less vagile species (which would not be specialists to the habitat), high species turnover due to community interactions, and resultant low species richness. Our objective here is to determine, from the existing literature, how colonization of phytotelmata occurs, and whether it suggests that phytotelmata are more similar to islands or to swamps.

Phytotelmata are small bodies of water held by living plants, and ranging from the scarcely perceptible to at least 45 liters. Phytotelmata include treeholes, hollow stems and fallen pods and leaves, modified leaves, leaf axils and flower bracts of plants of at least 29 families (Fish 1983). Here we consider only aquatic organisms using these habitats, though terrestrial organisms, e.g., Staphylinidae, exist there (Seifert 1981, Frank 1983).

Artificial containers of water provide analogs of phytotelmata. They have been used experimentally to examine colonization processes because various factors involved can be separated and thereby simplified (Maguire 1963 a,b, Frank 1980).

Colonization by Non-Phytotelm-Specialists

Maguire (1963b) elucidated 3 mechanisms of colonization of jars placed at various distances from ponds in Texas and Colorado, and arranged at various heights from the ground. He discriminated colonization by considerable numbers of species of algae, unicellular animals, and insects, into 3 modes.

1. Wind and rain. Air currents were very effective in transporting large numbers of dissemnules of some species of small aquatic organisms. Some organisms were splashed by rain from the ground into the lower jars, and large numbers of some algae and protozoa were found in cultures of rain. Small aquatic organisms thus can and do fall from the sky, and sometimes even large organisms such as fish and amphibians are likewise distributed (McAtee 1917, Bajkov 1949, Maguire 1963b).

2. Flight. Mosquito larvae (Culex) appeared in some of the jars, presumably having hatched from eggs deposited there by adults.

3. Assistance from animals (phoresy). Algae, protozoa, and a rotifer were carried by insects, especially dragonflies and wasps. In Texas, raccoons stuck their muddy paws in many of the jars, far as well as close to the ponds, and dispersed some organisms.

Does colonization of phytotelmata differ in character or in degree from these 3 modes? If it does not, then the community composition of organisms inhabiting phytotelmata might be expected to resemble that of artificial containers such as jars.

If colonization of phytotelmata by small aquatic organisms differs from that of artificial containers, then it might be expected that algae inhabiting phytotelmata would be specialists, but the evidence suggests they are not specialists. The diatoms of bromeliad leaf axils in the states of Rio de Janeiro, Guanabara, and Pernambuco (Brazil) were surveyed by Tavares de Lyra (1971, 1976). All of the 36 species (11 genera)
discovered were non-specialists, i.e., all were known from other sorts of habitats, and no new species were found. This seems to be true of other phytotelmata: we are not aware of species of algae or non-parasitic protozoa known only from these habitats.

However, apparent lack of lack of specialization by phytotelm-inhabiting algae is only part of the story. Inside a screened patio at Vero Beach, Florida, washed bromeliads of the species *Billbergia pyramidalis* (Sims) Lindley were planted in pots and set out in a grid design interspersed with green plastic beakers. Bottled drinking water was poured into the beakers and into the central cup of each bromeliad. Water was added from time to time to prevent the containers drying out. Within some weeks, the water in the beakers was green with algae but there was no obvious growth of algae in the bromeliads (Frank, unpublished). This suggested that something had prevented growth of algae in the central cups of the bromeliads. Other instances of exclusion have been studied and are due to biotic interactions.

Exclusion

The experiments with jars carried out by Maguire (1963a, b) showed that dissemineles of the ciliate *Colpoda* were frequently carried to jars at various distances from the ponds. *Paramecium* was also distributed to the jars, but was negatively associated with *Colpoda*. The most attractive explanation was that the highly vagile *Colpoda* quickly reached the jars, but was quickly eliminated, and prevented from reinvasion, when *Paramecium* arrived there (Maguire 1963a, b).

In a study area in Puerto Rico, *Paramecium* was found in some *Heliconia caribaea* Lamark (= *H. bihai* L. forma B) bracts but not in axils of 180 bromeliads (4 species in 3 genera) even though the bromeliads were only a few meters distant (Maguire & Belk 1967). Absence of *Paramecium* from the bromeliad axils and from some of the *Heliconia* bracts was suspected to be due to exclusion or elimination by some biological interaction. Further study showed a negative association between mosquito larvae and protozoa in general in the *Heliconia* bracts (Maguire et al. 1968). In Costa Rica, Vandermeer et al. (1972) renewed this enquiry, and found that mosquito larvae eliminated *Paramecium* from *Heliconia* bracts; *Paramecium* was capable of living in filtered water from bromeliad axils but not in unfiltered water, so interaction with some member of the microcommunity of bromeliad axils was responsible for elimination of the protozoan from that community. In *Sarracenia* pitcher plants too, mosquito larvae limit the community of protozoa (Addicott 1974).

**Colonization by Winged Specialists**

Along the insects occurring in bromeliad leaf axils, Diptera are dominant in numbers of species and usually in numbers of individuals. In contrast to the non-specialist diatoms recorded from bromeliad leaf axils, these Diptera are specialists. Larvae of many of the 214 recorded bromeliad-inhabiting neotropical mosquito species have seldom been found in other habitats, and in such exceptions these other habitats have generally been plant axils (Frank & Curtis 1961).

Specialization of bromeliad-inhabiting mosquitoes is not merely to bromeliads vs. other habitats. Larvae of some mosquitoes are more abundant in axils of some bromeliad species than in others, for reasons which are becoming apparent. At a Venezuelan study site, *Toxorhynchites haemorrhoidalis* (Dyar & Knab) larvae were found in leaf axils of bromeliads of 2 species: *Aechmena aquilega* (Salish.) and *Aechmea nudicaulis* (L.). However, they were more abundant, and their survival was better, in axils of *A. nudicaulis*. Larvae of *Toxorhynchites theobaldi* (Dyar & Knab) occurred sympatriically, but only in
sections of bamboo stems, suggesting an ovipositional discrimination (Lounibos et al. 1987).

In Florida, the natural habitat of aquatic stages of *Toxorhynchites rutulus* Coquillett is treeholes. These insects are found also in junk containers and especially scrap tires which probably is a consequence of females preferring to oviposit in dark containers of water. Rarely are they found in bromeliad leaf axils; axils of the indigenous bromeliad *Tillandsia utriculata* L. provide an unfavorable habitat for the larvae because too few prey are available (Frank et al. 1984).

Fourteen species of *Aedes* mosquitoes were found to occur in one or both of two wooded areas of coastal Kenya, and larvae of thirteen of these species were found in treeholes. However, the treehole habitat was partitioned: there was no evidence that height of treeholes above ground was a physical barrier, but it influenced which mosquitoes oviposited there, and treehole volume was also an important determinant (Lounibos 1981).

Aquatic stages of *Wyeomyia vanduzeei* Dyar & Knab and *W. mitchellii* (Theobald) often are abundant in water held in bromeliad leaf axils in south Florida and have various adaptations to existence in that habitat. *Catapsis berteroniana* (Schult.) Mez bromeliads growing exposed on the tops of dwarf red mangrove trees in Everglades National Park harbor aquatic stages of *W. vanduzeei* but not of *W. mitchellii*, even though larvae of the latter species inhabit bromeliad leaf axils in nearby shaded areas. This is at least in part due to a much greater willingness of *W. vanduzeei* adults to fly out from shaded areas (Frank & O’Meara 1985) making them better colonizers. Another behavioral difference between adults of the 2 species is the response of females to color. Whereas *W. vanduzeei* females prefer to oviposit in artificial bromeliads colored dark green (over deep blue, and strongly over deep red), *W. mitchellii* females prefer to oviposit in artificial bromeliads colored deep red (over dark green, and strongly over deep blue). This probably is a response to the quality of light reflected from bromeliads in shaded vs. exposed areas, in the sense that light reflected from bromeliads in the shade of tree canopies will be of longer wavelength (more red, less blue) than light reflected from bromeliads directly exposed to the sky (Frank 1986). Other attributes of these mosquito species suggest not only a high degree of specialization to the bromeliad habitat, but also interspecific differences leading to differing micro- and macrohabitat associations.

Chemical cues to oviposition sites are used by some phytotelm-inhabiting mosquitoes. In Kenya, adult *Eretmapodites subsimplicipes* (Edwards) oviposit preferentially in fruit husks of Apocynaceae and Loganiaceae cast off by monkeys, but the sympatric *Eretmapodites quinquevittatus* (Theobald) does not oviposit in this habitat. The first of these mosquitoes prefers to oviposit in water from such husks, but the second prefers tapwater (Lounibos 1978). In Venezuela, adult *Trichoprosopon digitatum* (Rondani) oviposits in water in cacao husks; given the choice of water from such husks vs. water from arid axils, in artificial containers, they prefer the former (Lounibos 1980).

Winged specialists among the Diptera perhaps have been able to achieve their dominance of phytotelm communities by the mobility of the adult stages. This has enabled them to search for and colonize these temporary habitats, to partition the available resources, and to achieve a high level of species richness.

**Colonization by Wingless Specialists**

*Paramecium* does not form cysts which would provide resistance to unfavorable conditions and aid in dispersal. In Puerto Rico, individuals of *P. multimicronucleatum* Powers & Mitchell are transported between *Heliconia caribaea* bracts by *Caracolus*
snails; the snails may move as far as 6 m in a single night (Maguire & Belk 1967). This species of Paramecium is not a Helifonia specialist, though the form seen in the bracts has not often been found in other habitats.

The hypopus stage of some mites is a form resistant to harsh conditions, and is terminated when conditions alleviate. However, the hypopus of the North American treehole mite Naiadacarus arboricola Fashing is found only in May-June, and is not influenced by harsh conditions such as desiccation and starvation (Fashing 1976). Instead, there is a temporal coincidence with the oviposition period of treehole-inhabiting syrphid flies of the genus Mallota. Hypopi were found on female flies (rarely males) which seem to provide phoretic dispersal of the mite from one treehole to another.

Aquatic stages of the mosquito Aedes sierrensis (Ludlow) inhabit treeholes in western North America and are parasitized by a protozoon, Lambrornella clarki (Corliss), and a nematode, Octomyospermis troglodytes Poinar & Sanders. Free-living stages of both parasites occur in treehole water, and adult mosquitoes that survive parasitism serve to disperse the parasites between treeholes (Hawley 1985, Washburn et al. 1986).

Tadpoles of poison-arrow frogs of the genus Dendrobates (Anura: Dendrobatidae) are known to inhabit bromeliad leaf axils in the neotropics (Silverstone 1973, Young 1979, Lannoo et al. 1987). In Costa Rica, adult D. pumilio Schmidt were found in leaf litter in a cacao plantation (Young 1979). There, as in other neotropical cacao plantations, tall trees provide shade for the much smaller cacao trees and, coincidentally, provide a substrate for bromeliads. An adult frog was observed to carry a tadpole on its back from 0.5 m above ground level to about 12 m, to a clump of bromeliads (Young 1979).

The aquatic worm Dero (Aulophorus) superterrenus Michaelsen (Oligochaeta: Naididae) was discovered in bromeliad leaf axils in Costa Rica and has been recorded from no other habitat (Picado 1913, Frank 1983). Aquatic oligochaetes abundant in leaf axils of bromeliads in the vicinity of Vero Beach, Florida, were identified as of the same species (Hiltunen in litt.), the first record of this worm from the USA. How did D. superterrenus achieve its present distribution, and how is it able to move from one bromeliad to another? Phoretic dispersal is a strong possibility.

**DISCUSSION**

Attempted equation of colonization of clumps of Helifonia inflorescences by insects with colonization of islands presents 3 major difficulties (Seifert 1975). First, the faunal coefficient (z) is higher than for true islands. Second, mainland effects (nearest neighbor distance) are of little importance in influencing species richness, perhaps because the source of colonists could not be identified. Third, with increasing size of Heliconia clumps, populations of common Heliconia-inhabiting insects increase more rapidly than does invasion by additional species; perhaps this was because the specialist insects invariably reached the clumps and their populations multiplied.

We accept Picado's (1911) comparison of phytotelmata with a fractionated swamp insofar as the phylogenetically higher organisms are concerned. The aquatic insects with winged adults, at least those present in substantial numbers, show directed arrival, site selection, and specialization. Specialization, by partitioning available habitats, has permitted a high level of species richness. Some higher organisms incapable of flight have evolved other methods of colonization, and here we list Naiadacarus and Dendrobates with the possibility that Dero will fall into the same group. Dispersal by Paramecium is not in the same category, because it can be carried by snails to various aquatic habitats, and it is eliminated from phytotelm communities by action of other community members.
For the lower organisms such as algae and non-parasitic protozoans, phytotelmata apparently are islands with the distinction that these islands are living and temporary, and that extinction with phytotelm death is inevitable. These organisms are not specialists, their arrival at phytotelmata is undirected, and some are excluded by interaction with specialist inhabitants. If Seifert (1981) had used dispersion of these organisms instead of insects as the basis of his study with clumps of Heliconia inflorescences, he might have found more similarity to islands.

Organisms inhabiting pitchers of Nepenthes were classified by Thienemann (1932) into 3 groups: nepenthobions (specialists), nepenthophiles (those whose habitat includes *Nepenthes* pitchers *inter alia*), and nepenthexenes (accidentals). Rolfort (1950) adapted corresponding expressions for treehole inhabitants: dendrolimnetobions, dendrolimenphiles, and dendrolimnetoxenes. Such expressions have not been coined for inhabitants of phytotelmata in general (they would be unwieldy), but it is clear that the concepts can be equated with organisms discussed in these pages.

Finally, it is worth recalling that there are fewer species of Heliconia inhabitants in small Caribbean islands than in comparable areas of the neotropical mainland (Seifert 1981). Likewise, the bromeliad fauna in Florida lacks aquatic Odonata, Hemiptera, Coleoptera and Trichoptera, and is depauperate relative to neotropical areas of comparable size (Frank 1983). In these cases “isolation” may be important in determining species richness.

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