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PHYTOTELMATA FAUNAL COMMUNITIES IN SUN-EXPOSED VERSUS SHADED TERRESTRIAL BROMELIADS FROM SOUTHEASTERN BRAZIL

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ABSTRACT. The aquatic communities occurring in terrestrial tank bromeliads under conditions of sun and shade were analyzed in relation to their richness and faunal composition. Three species of bromeliads were studied: *Aechmea bromeliifolia, A. nudicaulis,* and *Neoregelia cruenta.* The study area consisted of two sand dune formations ("restinga") on the southeast Brazil seashore. Ostracods (*Elpidium*) were the most common organisms. The species richness of shaded tanks was significantly higher than that of sun-exposed tanks. Community composition was more often similar between bromeliads growing under the same conditions of exposure than between bromeliads of the same species. Larvae of *Dasyhelea* ceratopogonids were associated with higher water temperature tanks, while *Microculex* culicids and copepods were more frequent at lower temperatures. These results suggest that invertebrate aquatic organisms do not display strong host specificity in choosing bromeliad tanks, but rather that microhabitat conditions are more important. Exposure to sun played a key role in determining richness and composition, probably by affecting water temperatures and by increasing the probability of desiccation.

Key words: Phytotelmata, bromeliad, ostracod, *Dasyhelea, Elpidium, Microculex*

INTRODUCTION

The way organisms recognize and use distinct habitats influences population and community structures, representing therefore an important ecological issue (Rosenweig 1991, Loxdale & Lushai 1999). Depending on the taxon, the scale applied should vary from centimeters to kilometers. Plants that are able to impound rainwater create microhabitats for small aquatic organisms within an otherwise hostile terrestrial ambient. This is the case for the aquatic organisms found in tanks of bromeliads.

The family Bromeliaceae includes many species that develop tanks by the dispositions of their leaves, which accumulate water and detritus (called "phytotelmata"; Smith & Downs 1979, Benzing 1990). In these water collections, communities of invertebrates, characterized by a high diversity of species, are commonly found (Picado 1913). In tanks of shaded bromeliads, insect larvae, micro-crustaceans, and annelids constitute a trophic web sustained by the decomposition of organic matter from the decayed leaves of trees and other overhanging vegetation. In bromeliads grown under sunny conditions, however, the trophic web appears to be sustained, mainly by the primary productivity of microalgae (Laessle 1961, Fish 1983).

These microecosystems are important not only because they are an excellent model for the study of larger systems but also because of their high biodiversity, which includes even endemism (Little & Hebert 1996). Although known since the 19th century (Müller 1878), the ecology of bromeliad phytotelmata is still poorly understood. Almost no information is available on ecological factors that influence the structure and composition of phytotelmata (Lopez et al. 1999, Richardson 1999). In this article, we describe the influence of light and water temperature, on the biodiversity and composition of aquatic communities found in bromeliad tanks.

MATERIALS AND METHODS

We took two sets of samples to determine both the impact of exposure to sun and its effect on tank water temperature on aquatic communities living inside tank bromeliads.

Sun/Shade Conditions

Samples were collected to study sun/shade conditions affecting diversity and community composition in water impounded by three species of tank bromeliads: *Aechmea nudicaulis* (L.) Griseb., *A. bromeliifolia* (Rudge) Baker, and *Neoregelia cruenta* (R. Graham) L.B. Sm., All were growing in a restinga ecosystem of Rio de Janeiro state (southeastern Brazil). The restinga comprises coastal vegetation formations that grow over sandy plains and are characterized by a zonation pattern from shoreline landward (Reinert et al. 1997).

Individuals of the *Aechmea nudicaulis* and

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TABLE 1. Number of samples (N), mean richness, and standard deviations of the faunal aquatic communities found in the tanks of three bromeliad species under sun-exposed and shade conditions.

Bromeliad	Habitat	N	Mean richness	SD
Aechmea bromeliifolia	Sun	20	1.95	1.00
	Shade	20	3.70	1.38
Aechmea nudicaulis	Sun	36	3.08	1.08
	Shade	25	3.72	1.24
Neoregelia cruenta	Sun	27	3.19	1.11
	Shade	10	3.70	1.70
	Total	158	3.15	1.29

Neoregelia cruenta studied were growing on the restinga of Barra de Maricá (42°49–54′W, 22°55–59′S). Plants of *A. bromeliifolia* were sampled in the restinga of Jacarepiá (42°20–43′W, 22°47–57′S). Both areas are characterized by vegetation islands consisting of pioneer shrubs and associated herbaceous plants, alternated with open sandy areas.

Water, detritus, and organisms were collected from the central tanks of the bromeliads with the aid of a siphon. Samples were collected during the summer of 1994. Plants were chosen depending on their extreme light conditions; i.e., only well-shaded or sun-exposed individuals from each species were analyzed. The central tanks of 158 individuals (83 sun-exposed plants and 75 shaded plants) distributed among the three species were studied (TABLE 1).

Animal taxa were identified through a Bausch & Lomb stereomicroscope, and the species richness in each tank was evaluated. Through the analysis of variance (Zar 1984), the effects of microhabitats (sun vs. shade) and plant species over richness were compared.

From the number of tanks where a determined taxon occurred, the frequency of occurrence for each group of data was calculated (TABLE 2). Frequencies were used to calculate the Sorensen coefficient of similarity between the groups. From the coefficient of similarity, a cladogram was constructed using the method of linking groups from the nearest neighbor (Greig-Smith 1983).

Water Temperature Effects

Samples were collected to study water temperature effects on aquatic fauna of exposed

TABLE 2. Frequency of tank aquatic fauna occurring among three bromeliads species under sun-exposed or shaded conditions. *Dasyhelea* ceratopogonid larvae showed strong association with sun-exposed bromeliads whereas harpacticoid copepods are mostly found in shaded tanks. *Elpidium* ostracods showed high frequencies in all sets of samples.

Class	Family	Taxa	Average frequency	*A. nudicaulis* Sun N = 36	*N. cruenta* Sun N = 27
Crustacea	Limnocytheridae	*Elpidium* spp.	89.75%	93.33%	89.12%
Insecta	Culicidae	Culicidae spp.	35.78%	45.09%	37.35%
Crustacea	—	Harpacticoidea spp.	34.72%	0.00%	5.00%
Oligochaeta	Naididae	*Dero* sp.	32.68%	27.02%	18.82%
Insecta	Ceratopogonidae	*Dasyhelea* sp. 1	26.86%	47.02%	74.12%
Insecta	Scirtidae	Scirtidae sp.	22.18%	13.16%	15.00%
Nematoda	—	Nematoda spp.	18.40%	5.97%	41.47%
Insecta	Chaoboridae	*Corethrella* sp.	10.61%	23.16%	5.00%
Insecta	Psychodidae	Psychodidae sp.	9.75%	0.00%	0.00%
Crustacea	—	Cyclopoidea sp.	7.91%	0.00%	5.00%
Insecta	Chironomidae	Tanypodinae sp.	5.64%	0.00%	0.00%
Insecta	Phoridae	Phoridae sp.	5.19%	2.63%	0.00%
Turbellaria	—	Turbellaria sp.	3.43%	0.00%	0.00%
Insecta	Tipulidae	Tipulidae sp.	3.18%	0.00%	0.00%
Acarina	—	Acarina spp.	3.14%	0.00%	13.82%
Insecta	Chironomidae	Chironominae sp.	2.83%	0.00%	0.00%
Insecta	Ceratopogonidae	*Forcipomyia* sp.	2.57%	0.00%	7.94%
Insecta	Coenegridae	*Leptagrion* sp.	2.38%	9.30%	0.00%
Insecta	Ceratopogonidae	*Culicoides* sp.	2.16%	0.00%	0.00%
Insecta	Veliidae	Veliidae spp.	0.44%	2.63%	0.00%

TABLE 3. Analysis of variance of the microhabitats (sun/shade) and effects of bromeliad species on the aquatic fauna richness of their tanks.

Effects on aquatic fauna richness	Effect		Error			
	df	MS	df	MS	F	p-level
Sun/shade	1	23.54889	152	1.428821	16.48135	0.0000078
Bromeliad species	2	3.965046	152	1.428821	2.775048	0.065507859
Both effects	2	9.204979	152	1.428821	6.442361	0.002062534

Aechmea nudicaulis growing at the south side (more shaded in winter, in southern latitudes) as compared to plants growing at the north side (more sunny in winter) of shrub formations at Barra de Maricá restinga (Rio de Janeiro, Brazil). To understand in more detail the effect of sun exposure and water temperatures on the aquatic fauna, we sampled 44 central tanks of *A. nudicaulis* at Barra de Maricá during the winter (June–September).

The bromeliads were sampled in a small open area (ca. 6 m^2) between shrub formations (ca. 2 m height). Although all the plants were growing in exposed sand, during winter the shrubs project shadows over the bromeliads growing on the south side of the shrub (as expected at 22°S latitude). This shadow protects some bromeliads from the midday sun, whereas bromeliads at the north side of the shrub receive full solar radiation.

Because of the proximity of sun-exposed and shaded plants, we had a natural experiment for testing the influence of sunlight and water temperature on the tank communities. Thus during winter 2001, we collected contents of central tanks of 22 shaded plants and 22 sun-exposed plants. The water temperature was measured before the sampling at about midday on clear days.

The contents of the 44 tanks were analyzed to determine the occurrence of aquatic macroscopic fauna. We compared water temperature of the tanks where each taxon occurred and tested whether the temperatures were significantly different (analysis of variance; Zar 1984).

TABLE 2. Extended.

A. bromeliifolia Sun N = 20	*A. nudicaulis* Shade N = 25	*N. cruenta* Shade N = 10	*A. bromeliifolia* Shade N = 20
82.50%	88.56%	100.00%	85.00%
10.00%	77.24%	40.00%	5.00%
0.00%	68.30%	50.00%	85.00%
25.00%	20.21%	40.00%	65.00%
40.00%	0.00%	0.00%	0.00%
19.50%	45.43%	30.00%	10.00%
40.00%	2.94%	20.00%	0.00%
10.00%	25.49%	0.00%	0.00%
5.00%	8.50%	30.00%	15.00%
0.00%	42.48%	0.00%	0.00%
0.00%	8.82%	20.00%	5.00%
0.00%	8.50%	10.00%	10.00%
0.00%	5.56%	10.00%	5.00%
0.00%	14.05%	0.00%	5.00%
0.00%	0.00%	0.00%	5.00%
0.00%	16.99%	0.00%	0.00%
7.50%	0.00%	0.00%	0.00%
5.00%	0.00%	0.00%	0.00%
0.00%	2.94%	0.00%	10.00%
0.00%	0.00%	0.00%	0.00%

RESULTS

Shade/Sun Conditions

The mean richness value was 3.15 morphospecies per tank (SD 1.29) (TABLE 1). No significant difference was found for the richness values between different bromeliad species ($p > 0.05$). The tanks from shaded bromeliads, however, presented a higher richness ($p < 0.01$) than tanks from sun plants (TABLE 3).

The collected organisms were grouped in 20 taxa (TABLE 2). The most frequent taxon was the ostracod (genus *Elpidium*), occurring in 90% of all the tanks analyzed (SD 6.24%). Ostracods also showed a uniform occurrence in all group of tanks. Other taxa were highly variable, and some appeared strongly associated with shade or sun conditions. Harpaticoid copepods, for example, occurred almost only in shaded bromeliads and were virtually absent in exposed bromeliads. Larvae of *Dasyhelea* ceratopogonids presented a reverse pattern, however, being found only in tanks of exposed bromeliads (whereas larvae of *Culicoides* ceratopogonids appeared to be restricted to shaded bromeliads).

The similarity index among tanks sampled in the same habitat (sun or shade) was higher than the similarity between tanks from the same bromeliads (FIGURE 1). Excluding the effects of habitats, tanks of *Aechmea bromeliifolia* were more similar to tanks of *Neoregelia cruenta* than to tanks of *A. nudicaulis.*

Water Temperature Effects

Central tanks from north side plants (receiving sun during winter at southern latitudes)

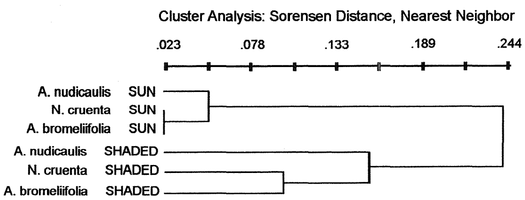

FIGURE 1. Dendrogram of similarity (Sorensen) between the groups of collected data obtained in tanks of bromeliads. Microhabitat (sun/shade) explains the similarity groups better than does association with bromeliad species.

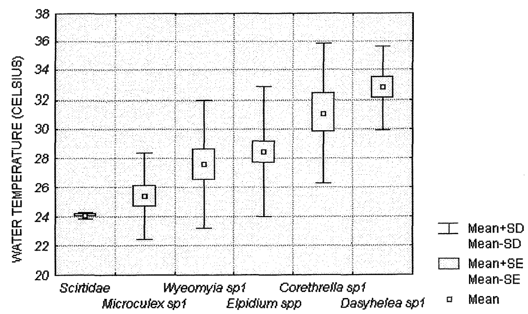

FIGURE 2. Water temperatures box plot of *Aechmea nudicaulis* tanks (N = 44, measured about 12:00 hours on clear sunny days during winter) where faunal taxa were collected. Lower temperatures were associated with bromeliads growing at the south side of shrubs (shaded during winter at southern latitudes), whereas higher temperatures were associated with tanks on the north side of shrubs border (exposed to sun during winter at southern latitudes). *Dasyhelea* ceratopogonids appeared strongly associated with higher temperature tanks, whereas Scirtidae beetles and *Microculex* mosquitoes preferred low temperature conditions.

showed significantly higher water temperatures (mean 33.0°C, SD 2.0°C) than plants at the south side (shaded during winter) of the shrubs (mean 24.5°C, SD 0.5°C; $p < 0.01$, Tukey test). Ceratopogonidae (*Dasyhelea* sp.) and Chaoboridae (*Corethrella* sp.) were found mostly in tanks with higher water temperatures, at the north side ($p < 0.001$, Tukey test; FIGURE 2). Culicidae (genera *Wyeomyia* and *Microculex*) and Scirtidae beetle larvae were more abundant at significantly lower temperatures (south side) ($p < 0.01$, Tukey test; FIGURE 2). *Elpidium* ostracods, found in high frequencies at both sides (north and south), did not present significant association with water tank temperature ($p > 0.05$, Tukey test; FIGURE 3).

DISCUSSION

Although several tank bromeliad organisms have a high degree of endemism (Little & Hebert 1996), others seem to have little selectivity (Fish 1983). The degree of exposure to sunlight may have had a major influence on the distribution of these communities. The sun-exposed bromeliads presented less richness of organisms in their tanks in comparison to those in the shade. This may be the result of the more stressful conditions in exposed tanks that produced higher water temperatures and increased the risk of dehydration.

Water temperature plays an important role in aquatic insect communities, affecting its occurrence and distribution, even in small spatial scale (Ward 1992). Under field conditions, sun-exposed bromeliads presented tank water temperatures almost 13°C above those of shaded plants and reached 40°C during summer. Even in winter, we measured values as high as 36°C on the north side (sun-exposed) tanks.

The results presented here strongly support *Dasyhelea* larval preferences for sun-exposed bromeliads with high water temperature. Hayford et al. (1995) found high densities of *Dasyhelea* larvae living in a thermal spring in Colorado (USA) and concluded that this ceratopogonid is thermophylic (perhaps a pre-adaptation that allows the genus to invade sun-exposed bromeliads).

In laboratory experiments, *Elpidium* ostracods and *Dasyhelea* larvae showed more resistance to high temperatures than did Culicidae larvae and

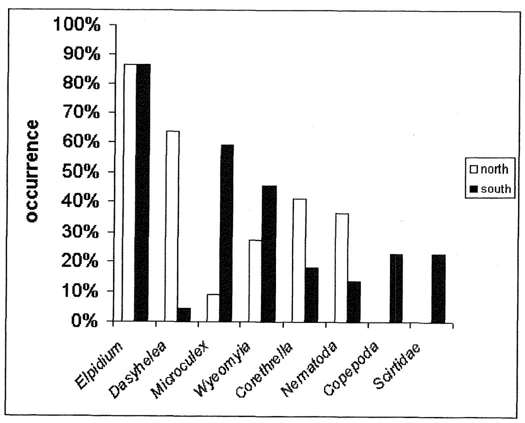

FIGURE 3. Comparative frequency of aquatic fauna between 22 *Aechmea nudicaulis* central tanks growing at the north side of shrub formations (exposed to sun during winter at southern latitudes) with 22 tanks growing on the south side (shaded during winter at southern latitudes). *Elpidium* ostracods showed no preference between north and south, but other groups appeared to be much more frequent at one of the sides during winter (e.g., *Dasyhelea* ceratopogonids at the north, sunny side or *Microculex* culicids at the south, shaded side).

copepods. Additionally, Pennak (1958) reported that some ostracods are extremely tolerant to dehydration, surviving for years without water under dormancy.

During a dry period at Barra de Maricá (summer 1993), we collected *Elpidium* and *Dasyhelea* larvae alive from sun-exposed bromeliads that were completely dry for at least one week. During this period, only shaded bromeliads retained some water. This combination of adaptations, resistance to heat and dehydration, allows both taxa to reach high densities in sun-exposed tanks. *Elpidium* ostracods appeared to be extremely flexible, reaching high densities in all thermal conditions, but we do not know yet whether those we encountered are all conspecific, or whether we are dealing with several, more stenothermic, cryptic species (Little & Hebert 1996).

Phoretic dispersion of *Elpidium* between tank bromeliads, attached to the skins of amphibians and reptiles (Lopez et al. 1999), may be aided by the ostracod's resistance to dehydration. We now have evidence (L.C.S. Lopez & R.I. Rios unpubl. data) that *Elpidium* can even survive ingestion with bromeliad tank water, passing through vertebrate guts unharmed and being expelled alive inside amphibian or mammals feces, which opens a new dispersion route to these ostracods and demonstrates their resistance to harsh conditions.

Sun or shade microhabitats could influence tank aquatic animals in two ways. Organisms can select the tanks to be colonized by the degree of exposure, or alternatively they colonize all bromeliads with no specific distinction in a first step but suffer different rates of extinction in the tanks of different microhabitats.

Dasyhelea ceratopogonids, whose flying adults may choose sun-exposed bromeliads in which to deposit their eggs, could be an example of the first process.

The second process, of colonization followed by extinctions, is represented by the dispersion of harpaticoid copepods. The results obtained here show that these organisms were highly frequent in shaded bromeliads but absent in sun-exposed bromeliads. Madeira et al. (1995) verified, however, that these copepods could be found in the tanks of exposed bromeliads during the winter in the restinga of Maricá. In this way, these animals may invade sun-exposed bromeliads during the winter, when tank water temperature is lower; but they may be excluded by higher temperatures and/or dehydration during the summer. The copepod populations occurring in tanks of bromeliads would have a continuous process of extinction and recolonization, creating a metapopulation system (Hanski 1994).

Our second set of samples, comparing tanks between the south and north sides of shrubs, supports the above hypothesis. We found copepods only at the south (shaded, low temperature) side and *Dasyhelea* larvae strongly concentrated at the north side (sun-exposed).

In the winter, exposed bromeliads at the south side of the shrubs appeared to harbor transitional community structures, between sun-exposed and heavily shaded tanks (as found under the canopy inside the shrubs). The south side tanks lack high densities of *Dasyhelea* (typical of the extreme sun condition), but we did not also find larvae of *Culicoides,* Tipulidae and Tanypodinae (typical of the heavy sun micro-habitat).

Resampling during summer in the same area would test these ideas. We could investigate whether, as a result of the change in the sun position (sunlight will then reach the south side of the shrubs), *Dasyhelea* will increase its densities at the south side, whereas culicid and copepod populations will diminish. We seek to build a more detailed picture, in space and time, of this complex mosaic of "water islands" provided by terrestrial bromeliads and spread over the dry sand dunes.

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