**ORIGINAL ARTICLE**

# Assessing the role of canopy cover on the colonization of phytotelmata by aquatic invertebrates: an experiment with the tank-bromeliad *Aechmea lingulata*

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**ABSTRACT**

The presence of canopy cover may influence the amount of organic detritus and stored water in bromeliad tanks and, consequently, the colonization of these ecosystems by aquatic invertebrates. The aim of this study was to determine the effects of canopy cover on the colonization of the tank-bromeliad *Aechmea lingulata* in the restinga, an ecosystem composed of a variety of plant communities in the sandy coastal plains of Brazil. We hypothesized that the taxonomic composition of invertebrate communities would differ between bromeliads covered and not covered by a dense canopy (shaded and unshaded bromeliads). Prior to the beginning of the experiment, bromeliads of similar size were carefully washed to remove all organisms and organic detritus, and their tanks were filled with 1.0 L of spring water. On days 7, 14, 21, 30, 45, 60 and 90, four bromeliad tanks of each shade treatment were sampled to determine invertebrate communities, stored water and organic detritus. Average daily values of water temperature and light intensity were higher in unshaded than in shaded bromeliads. The amount of fine particulate organic matter (FPOM) and stored water did not differ between treatments, but the amount of coarse particulate organic matter (CPOM) was higher in shaded bromeliads. Ostracoda, Hydracarina and Oligochaeta were the most abundant taxa in bromeliad tanks. Among insects, Culicidae, Chironomidae and Ceratopogonidae were the most representative. Invertebrate colonization occurred quickly and values of abundance were higher in unshaded bromeliads compared to shaded bromeliads. The values for biomass and richness did not differ between treatments or colonization times, and the taxonomic composition of invertebrate communities was similar throughout the experiment. Our results showed that canopy cover had a small influence on the colonization of tanks of *A. lingulata* in restinga, not corroborating the proposed hypothesis. These findings were likely due to the lack of variation in environmental conditions that are relevant to the colonization process, such as stored water and FPOM. However, because the amounts of CPOM were higher in shaded bromeliads, the taxonomic composition of invertebrate communities could have differed if typical shredders were present.

**Key words:** Bromeliaceae; habitat availability; organic detritus; invertebrate biomass; restinga ecosystem.

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## INTRODUCTION

Phytotelmata, temporary water bodies held by terrestrial plants, are useful and valuable models for the study of ecological processes (Srivastava *et al.*, 2004; Brendonck *et al.*, 2010). These ecosystems are easy to handle due to the small size and well-defined physical limits (Kitching, 2000; Srivastava *et al.*, 2004; Srivastava, 2006). Their efficiency was tested by different authors who concluded that natural microcosms are as versatile as artificial ones and, at the same time, exhibit the same biological complexity as other ecosystems (Blaustein and Schwartz, 2001; Srivastava *et al.*, 2004; Jocque and Field, 2014). Several studies have used phytotelm ecosystems to assess insect-plant interactions, processes of colonization (Richardson and Hull, 2000), nutrient cycling (Kitching, 2001), community interactions such as predation (Hammill *et al.*, 2015) and competition (Naeem, 1990b;

Barberis *et al.*, 2013), and patterns of ecological succession (Murrell *et al.*, 2014).

Phytotelm-based ecosystems are important landscape elements that provide habitat for aquatic organisms and contribute to the maintenance of local biodiversity (Naeem, 1990a; Kitching, 2000). Typically, organisms colonizing these ecosystems have a high degree of specificity and endemism (Little and Hebert, 1996; Vieira *et al.*, 2008; Dunthorn *et al.*, 2012) and are mainly represented by immature stages of insects and non-insect invertebrates that find optimal conditions for survival and breeding within phytotelmata (Frank, 1983). Phytotelmata are also important to terrestrial organisms that may use them as foraging sites (Maguire, 1971), refuge against predators (Domingos *et al.*, 2015) and water sources (Frank and Lounibos, 2009). All these characteristics make such ecosystems attractive and suitable for the establishment of complex biological interactions (Richardson, 1999; Richardson and Hull, 2000).

Compared to other aquatic ecosystems, the dynamics of biotic and abiotic factors in phytotelmata occur at short intervals, given that their permanence in the environment depends on the survival of host plants and rates of water collection and evaporation (Cogliatti-Carvalho *et al*., 2010; Dézerald *et al*., 2014). Therefore, small changes in the environmental conditions and characteristics of host plants may result in differences in the structure and composition of phytotelm communities (Ospina-Bautista *et al*., 2008; Dézerald *et al*., 2014; Cardoso *et al*., 2015). Armbruster *et al*. (2002) observed strong correlations among plant morphology and the volume of stored water with the abundance of organisms in bromeliad tanks. Moreover, the availability of nutrients (Richardson and Hull, 2000; Zytynska *et al*., 2012; Petermann *et al*., 2015) and solar radiation (Dézerald *et al*., 2014; Carrias *et al*., 2014) may change water chemical composition and, consequently, influence invertebrate colonization (Richardson, 1999; Gossner *et al*., 2016).

Most of the energy available to heterotrophic organisms in phytotelm ecosystems comes from organic detritus (Moore *et al*., 2004). Among these, leaf litter and fine particulate organic matter (FPOM) constitute the main food resources (Brouard *et al*., 2012). Abiotic (leaching) and biotic processes (microorganisms and invertebrate detritivores) (Graça, 2001) successively decompose this material. As in other aquatic ecosystems (Graça *et al*., 2015), the availability of organic detritus is a relevant factor to phytotelm communities (Walker *et al*., 1997; Brouard *et al*., 2012; Dézerald *et al*., 2013). Thus, both the quantity and quality of organic detritus can influence invertebrate abundance (Armbruster *et al*., 2002) and taxonomic richness (Kitching, 2000, 2001), as well as the biomass for functional feeding groups (Srivastava, 2006; Ptatscheck and Traunspurger, 2015).

Although organic detritus is considered an important energy source to phytotelm communities, the availability of light allows the establishment of primary producers (Marino *et al*., 2012; Leroy *et al*., 2013; Carrias *et al*., 2014). Furthermore, recent studies have found that food resources, *i.e.*, algae and organic detritus, may vary in phytotelmata held by shaded and unshaded bromeliads (Yee and Willig, 2007; Brouard *et al*., 2012; Dézerald *et al*., 2014). According to Kaufman *et al*. (2006), in unshaded bromeliads, algae constitute a high energetic resource to consumers because they provide nutritionally important compounds such as sterols, fatty acids and organic carbon.

*Restinga* is the general name collectively given to a variety of plant communities found in the sandy coastal plains of Brazil (Scarano *et al*., 2002). In this ecosystem, tank-bromeliads occur at the border of clumps that have the central portion occupied by woody species (Scarano, 2002). In this study, we determined the effects of canopy cover on the colonization of tanks of *Aechmea lingulata* (L.) Baker (Bromeliaceae) by aquatic invertebrates. For this, we studied rosettes of *A. lingulata* in two areas of restinga where (i) the bromeliads were covered by a dense clump canopy (shaded bromeliads) and (ii) the bromeliads were not covered due the low height of woody species (unshaded bromeliads). Because differences in the amount of organic detritus and stored water were expected, we hypothesized that the taxonomic composition of invertebrate communities would differ between shaded and unshaded bromeliads.

## METHODS

### Study area

The colonization experiment was developed from June to September 2013 in two areas of restinga at the municipality of Guarapari (Espírito Santo State, SE Brazil). These areas were located at the Paulo César Vinha State Park (20°35'20" S - 40°25'02" W; shaded bromeliads) and the Environmental Protection Area of Setiba (20°34'55" S - 40°25'12" W; unshaded bromeliads). In both sites, the clonal tank-bromeliad *A. lingulata* is commonly found near woody species of the genus *Clusia* L. (Clusiaceae), forming clumps that are interspersed with sand ridges, in a physiognomy determined as non-flooded, open shrubby vegetation (Magnago, 2007). However, clumps in the environmental protection area have lower height and less dense canopies because this area was impacted by sand extraction activities during the 1980s and 1990s (IEMA, 2015).

The climate in the study area is classified as tropical wet and dry (*Aw*), with hot and rainy summers and dry winters. The average annual values of temperature and precipitation are 27.9°C and 1388 mm, and the relative humidity is 80% (INMET, 2013). During the experiment, temperatures of stored water were higher in unshaded bromeliads (23.9±0.6 to 28.2±0.5°C), while levels of dissolved oxygen were higher in shaded bromeliads (1.3±0.1 to 5.5±0.4 mg L$^{-1}$). Electrical conductivity measurements had a wide variation and were initially higher in shaded bromeliads (30.8±16.8 µS cm$^{-1}$ at day 7). However, after the first week of the experiment, higher conductivity values were observed in unshaded bromeliads. The physical and chemical properties of stored water in the tanks of studied bromeliads and values of accumulated rainfall during the experiment are presented in Tab. 1.

### Phytotelm characterization

Prior to the beginning of the experiment, the average daily values of water temperature and light intensity and the percentage of canopy coverage were determined in 20 bromeliads (10 shaded and 10 unshaded). The values of

water temperature and light intensity were measured for 10 days at regular intervals (every 15 min) by data loggers (HOBO Pendant UA-002-64, Onset Computer Corporation, Bourne, Massachusetts, USA) submerged close to the water surface. The percentages of canopy coverage were determined by the analysis of photographs, taken with a digital camera (SONY Steady-Shot DSC-W610) positioned parallel to the ground and immediately above the tanks, using ImageJ Software (US National Institutes of Health, Bethesda, Maryland, USA).

**Experimental design**

In total, 72 rosettes of *A. lingulata* (36 shaded and 36 unshaded) were used in the experiment. In both study areas (625 m² each), the bromeliads were distributed in 4-5 clumps, which were approximately 5 m distant from each other. These bromeliads were chosen because they presented similar values of external diameter (difference between means: 0.11 cm [95% CI: -0.247, 0.466]) and maximum volume of water storage (difference between means: 0.05 L [95% CI: -0.003, 0.100]). At the beginning of the experiment, the bromeliads were carefully washed and rubbed to remove all organisms and organic detritus. After washing, the tank of each bromeliad was filled with 1.0 L of spring water for invertebrate colonization. Eight bromeliads of each shading treatment, which had not been washed, were used as controls to determine invertebrate communities, volumes of stored water and the amount of organic detritus in the tanks at the beginning and the end of the experiment (4 initial and 4 final controls per treatment).

On days 7, 14, 21, 30, 45, 60 and 90, four tanks of each treatment (one per clump) were sampled by turning the rosettes upside down, which is a non-destructive sampling method (Liria, 2007; Jabiol *et al.*, 2009). The water trapped among leaves was removed with a pipette. The samples were individually placed in plastic containers and transported on the same day to the laboratory, where they were washed over a 250 µm mesh. The material retained was preserved in 70% ethanol and posteriorly sorted under a stereomicroscope (Belphotonics STM-pro, Osasco, Brazil; 32x). Except for non-insect taxa, invertebrates found were identified to family level using specific identification keys (Merritt and Cummins, 1996; Costa *et al.*, 2006; Mugnai *et al.*, 2010; Triplehorn and Johnson, 2011). The presence of typical shredders of the tropical region, such as caddisflies of the genus *Phylloicus* Müller, 1880 and chironomids of the genera *Stenochironomus* Kieffer, 1919 and *Chironomus* Meigen, 1803 (Callisto *et al.*, 2007), was evaluated in all samples. All individuals were then separated by taxon, counted, dried (60°C, 72 h) and weighed by an analytical balance (±0.01 mg) for biomass determination. The initial (day 0) and final controls (day 90) of each treatment were sampled following the same procedures.

Leaf litter and small twigs found in the tanks were placed in plastic bags and posteriorly dried (60°C, 72 h) and weighed (± 0.01 g) to determine the amount of coarse particulate organic matter (CPOM > 1 mm). After the removal of invertebrates and CPOM, the water of each sample was filtered over pre-weighed glass fiber GF/F filters (Sartorius Stedim Biotech) and the filters were dried (60°C, 72 h) and calcined (500°C, 4 h) for ash free dry mass (AFDM) determination of accumulated FPOM.

**Data analysis**

The values of water temperature, light intensity and percentage of canopy coverage of shaded and unshaded bromeliads were tested for normality and compared by *t*-tests. Because the total number of invertebrates found in bromeliads showed great variation (2 to 699 individuals), the rarefaction method was used to calculate the expected values of taxonomic richness in samples with standard-

**Tab. 1.** Abiotic water parameters in the phytotelmata of *A. lingulata* shaded and unshaded by the canopy cover during the colonization experiment. Rainfall accumulation during the study period is also shown.

| | Temperature (°C) | | Dissolved O$_2$ (mg L$^{-1}$) | | Conductivity (µS cm$^{-1}$) | | Rainfall (mm) |
|---|---|---|---|---|---|---|---|
| | Shaded | Unshaded | Shaded | Unshaded | Shaded | Unshaded | |
| Initial | 21.9±0.2 | 25.3±0.5 | 4.4±0.5 | 4.5±0.3 | 38.0±7.9 | 25.8±10.9 | - |
| 7 | 22.1±0.6 | 24.1±0.5 | 5.5±0.4 | 5.4±0.2 | 30.8±16.8 | 6.5±5.0 | 5 |
| 14 | 20.6±0.7 | 23.9±0.6 | 5.0±0.5 | 2.1±0.5 | 30.5±15.8 | 42.6±16.8 | 9 |
| 21 | 26.0±0.5 | 28.2±0.5 | 3.5±0.5 | 2.4±0.4 | 16.5±5.4 | 27.1±4.4 | 25 |
| 30 | 25.0±0.3 | 25.8±0.1 | 3.3±0.1 | 3.6±0.1 | 19.5±0.1 | 21.0±0.1 | 25 |
| 45 | – | – | – | – | – | – | 25 |
| 60 | 25.9±0.4 | 27.3±0.5 | 1.3±0.1 | 1.3±0.1 | 17.7±0.7 | 23.9±4.9 | 51 |
| 90 | 22.0±0.2 | 26.4±2.7 | 5.2±0.2 | 2.8±1.5 | 10.6±0.1 | 11.4±0.7 | 73 |
| Final | 23.8±1.6 | 27.2±2.1 | 4.6±0.3 | 2.2±1.3 | 47.0±0.1 | 8.1±2.3 | - |

*−, not measured because of the low volume of water.*

ized sizes E $(S_n)$ (Gotelli and Colwell, 2011). Analyses of Variance (ANOVA) were used to compare the values of abundance, rarefied richness and biomass of invertebrate communities across shade treatments and colonization times (factors). The volumes of stored water and the amount of CPOM and FPOM were also compared by ANOVA. The normality and homogeneity of variance were tested for all data. Additionally, we tested normality on the residuals from the ANOVAs for each response variable. When a model was significant, Tukey tests were used for post hoc comparisons (Zar, 2010). To evaluate the structure of invertebrate communities in shaded and unshaded bromeliads at different colonization times, a non-metric multidimensional scaling (NMDS) test was performed on the log-transformed abundance data followed by determining the Bray-Curtis distance (McCune and Grace, 2002). Analyses of similarities (ANOSIM, 999 permutations) were used to test for significant differences between the communities found in each shade treatment and colonization times (Clarke and Green, 1988). All statistical analyzes were performed using SPSS (version 23.0 for Macintosh, SPSS, Chicago, Illinois, USA) and Primer (version 6, Primer-E Ltd., Lutton, United Kingdom).
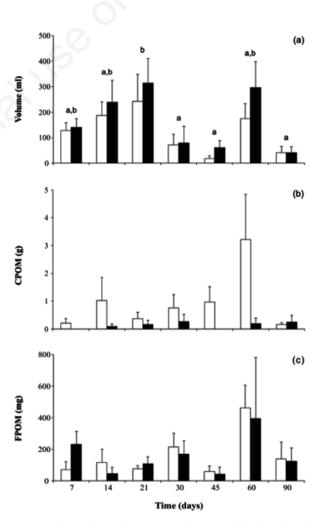
## RESULTS

Shaded bromeliads showed higher percentages of canopy coverage than unshaded, by 66.5% on average (95% CI: 59.284, 73.611). Consequently, average daily values of water temperature and light intensity were higher in unshaded than shaded bromeliads (temperature: 1.5°C on average [95% CI: 0.657, 2.323]; light intensity: 8943.8 Lux on average [95% CI: 6315.2, 11572.1]).

During the experiment, the volume of stored water in bromeliads ranged from 18.7±10.9 to 315.0±192.3 ml (Fig. 1a). These values did not differ between treatments. However, values observed at day 21 were higher than those observed at days 30 (202.50 ml on average [95% CI: 17.378, 387.622]), 45 (238.37 ml on average [95% CI: 53.253, 423.497]) and 90 (236.50 ml on average [95% CI: 51.378, 421.622]) (treatment: $F_{1,56}$=0.140, P=0.711; time: $F_{6,56}$=4.335, P=0.002; interaction: $F_{6,56}$=0.203, P=0.974; $R^2$=0.395). Regarding the amount of organic detritus, the dry mass of CPOM and FPOM ranged from 0 to 3.22±1.62 g and 44.2±33.2 to 463.5±141.7 mg, respectively (Fig. 1b,1c). The amount of CPOM was higher in the shaded bromeliads than in unshaded bromeliads, by 0.82 g on average (95% CI: 0.186, 1.460) and did not differ among colonization times (treatment: $F_{1,56}$=10.916, P=0.002; time: $F_{6,56}$=1.514, P=0.197; interaction: $F_{6,56}$=1.396, P=0.239; $R^2$=0.403). The amount of FPOM did not differ between treatments or colonization times (treatment: $F_{1,56}$=1.353, P=0.251; time: $F_{6,56}$=0.954, P=0.468; interaction: $F_{6,56}$=0.973, P=0.455; $R^2$=0.235).

In total, 5206 (23 taxa) and 8714 (20 taxa) organisms were sampled in the shaded and unshaded bromeliads, respectively (Tab. 2). Ostracoda (Crustacea) was the most abundant taxon, accounting for approximately 46% of all sampled organisms. Hydracarina (Acari) and Oligochaeta (Annelida) were also abundant (16 and 15%, respectively). Among insects, larvae of the dipteran families Culicidae (11%), Chironomidae (6%) and Ceratopogonidae (3%) were the most representative.

The abundance of invertebrate communities ranged from 49.5±16.5 to 269.0±81.3 ind. (Fig. 2a). Invertebrate colonization occurred quickly in both shaded and unshaded bromeliads, and after day 14, the values of abundance in experimental bromeliads were similar to those observed in the initial controls. However, the abundance



**Fig. 1.** Volume of stored water (a) and amount of CPOM (b) and FPOM (c, mean±EP) observed in the phytotelmata of *A. lingulata* shaded (open bars) and unshaded (solid bars) by the canopy cover during the colonization experiment. Values with different superscript letters were significantly different.

values for treatment bromeliads observed at the end of the experiment (day 90) were lower than those values observed in the final controls. During the experiment, values of abundance were higher in unshaded bromeliads, by 80.8 ind. on average (95% CI: 5.177, 156.484), and did not differ among colonization times (Tab. 3). Values of taxonomic richness ranged from 4.0±0.5 to 6.0±0.4 taxa (Fig. 2b). In both treatments, these values were higher in experimental bromeliads than in controls. Values of total invertebrate biomass showed high variation in unshaded bromeliads (3.8±1.0 to 13.4±9.6 mg); these values were similar to controls in shaded bromeliads (3.0±0.8 to 8.4±3.5 mg, Fig. 2c). The richness and biomass of invertebrate communities did not differ between treatments or colonization times (Tab. 3).

The structure of invertebrate communities varied more in shaded than unshaded bromeliads (Fig. 3). In both treatments, the communities observed in the experimental bromeliads were spatially distant from those observed in initial controls. However, invertebrate communities did not differ between treatments or colonization times (ANOSIM; treatment: R=0.020, P=0.295; time: R=0.018, P=0.368). Typical invertebrate shredders were absent in all samples from both treatments.

## DISCUSSION

The colonization of tanks of *A. lingulata* by aquatic invertebrates was little influenced by the presence of
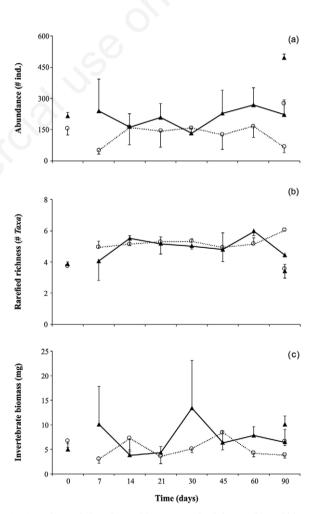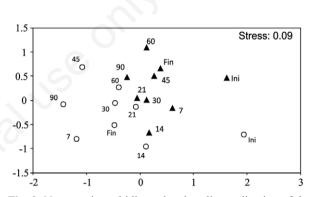
**Tab. 2.** Relative abundance (%) of the invertebrate taxa found in the phytotelmata of *A. lingulata* shaded and unshaded by the canopy cover during the colonization experiment.

|  | Shaded | Unshaded |
|---|---|---|
| Diptera |  |  |
| Culicidae | 13.66 | 9.89 |
| Chironomidae | 8.86 | 3.87 |
| Ceratopogonidae | 3.75 | 2.31 |
| Tipulidae | – | 0.05 |
| Psychodidae | 0.08 | 0.16 |
| Tabanidae | 0.27 | 0.20 |
| Stratiomyidae | 0.02 | 0.02 |
| Muscidae | 0.02 | – |
| Empididae | 0.17 | 0.13 |
| Coleoptera |  |  |
| Elmidae | 0.10 | 0.05 |
| Scirtidae | 0.56 | 0.76 |
| Staphylinidae | 0.04 | 0.05 |
| Psephenidae | 0.02 | – |
| Ephemeroptera |  |  |
| Baetidae | 0.02 | – |
| Odonata |  |  |
| Gomphidae | – | 0.01 |
| Libellulidae | 0.02 | – |
| Coenagrionidae | 0.02 | – |
| Blattodea |  |  |
| Blattidae | 0.04 | 0.02 |
| Collembola | 1.42 | 0.71 |
| Crustacea |  |  |
| Ostracoda | 46.16 | 47.13 |
| Harpacticoida | 0.19 | 0.14 |
| Cyclopoida | 0.21 | 0.50 |
| Acari |  |  |
| Hydracarina | 6.05 | 20.60 |
| Annelida |  |  |
| Oligochaeta | 17.75 | 13.31 |
| Nematoda | 0.60 | 0.10 |
| Number of individuals | 5206 | 8714 |
| Number of taxa | 23 | 20 |



**Fig. 2.** Values of abundance (a), taxonomic richness (b) and biomass (c, mean±EP) of invertebrate communities found in the phytotelmata of *A. lingulata* shaded (open circles, dotted line) and unshaded (solid triangles, solid line) by the canopy cover during the colonization experiment. Values not connected by lines represent the initial and final controls.

canopy cover. Beyond values of light intensity and temperature of stored water, canopy cover influenced only the amount of CPOM in bromeliads. However, the volume of water and the amount of FPOM, which are important variables for the colonization process (Kitching, 2000; Armbruster *et al.*, 2002; Dézerald *et al.*, 2015b), did not differ between treatments and contributed to the high similarity of the communities sampled throughout the experiment. These results differ from those found in studies developed in tropical forest ecosystems (Montero *et al.*, 2010; González *et al.*, 2014) and are probably related to the characteristics of restinga (*i.e.*, less dense vegetation composed of species adapted to low water availability and high temperatures and solar radiation) (Zaluar and Scarano, 2000; Scarano, 2002).

Some studies have suggested the volume of water is the main factor that influences the colonization of phytotelm ecosystems because it determines habitat size and susceptibility to colonization (Srivastava *et al.*, 2008; Dézerald *et al.*, 2014; Gossner *et al.*, 2016). Although unshaded bromeliads have higher capacity of water collection (Dézerald *et al.*, 2014), tanks held by these plants are also subject to higher evaporation rates as a result of direct exposure to solar radiation (Dézerald *et al.*, 2015b; Buosi *et al.*, 2015). In this study, the volumes of stored water differed only between colonization times and were related to rainfall values during the experiment. Because rosettes of *A. lingulata* had similar size and capacity of water storage, the absence of differences between treatments suggests that canopy cover provided by the restinga vegetation did not influence the rates of water collection and evaporation or the availability of habitat to aquatic invertebrates.

The accumulation of FPOM in bromeliad tanks oc-

curred quickly and the amounts observed after one week were similar to those observed in initial and final control treatments (data not shown). According to Frank and Lounibos (2009), the amount of FPOM in phytotelmata may have different origins, including the excreta of animals and detritus produced by the decomposition of dead plants and animals. Moreover, these organic particles can be carried by the wind; therefore, FPOM input rates are not necessarily related to the presence of canopy cover (Ngai and Srivastava, 2006; Brouard *et al.*, 2011). The amount of FPOM found in tanks of *A. lingulata* was independent of canopy cover and colonization times, as was observed by Dézerald *et al.* (2013) in tank-bromeliads sampled in different vegetation types.



**Fig. 3.** Non-metric multidimensional scaling ordination of the invertebrate communities found in the phytotelmata of *A. lingulata* shaded (open circles) and unshaded (solid triangles) by the canopy cover. Labels indicate the colonization time (in days) and initial (Ini.) and final (Fin.) controls.

**Tab. 3.** Results of the Analyses of Variance (ANOVA) used to test for differences in the abundance, taxonomic richness and biomass (ln[x+1] transformed data) of the invertebrate communities found in the phytotelmata of *A. lingulata* of different shade treatments and colonization times.

|  | SS | df | F | P |
|---|---|---|---|---|
| **Abundance** | | | | |
| Treatment | 7.656 | 1 | 6.171 | 0.017 |
| Time | 5.463 | 6 | 0.734 | 0.625 |
| Treatment×time | 6.287 | 6 | 0.845 | 0.543 |
| Error | 52.102 | 42 | | |
| **Taxonomic richness** | | | | |
| Treatment | 0.035 | 1 | 1.005 | 0.322 |
| Time | 0.135 | 6 | 0.636 | 0.700 |
| Treatment×time | 0.189 | 6 | 0.893 | 0.509 |
| Error | 1.410 | 40 | | |
| **Biomass** | | | | |
| Treatment | 0.379 | 1 | 0.746 | 0.393 |
| Time | 1.462 | 6 | 0.481 | 0.819 |
| Treatment×time | 1.164 | 6 | 0.383 | 0.886 |
| Error | 20.290 | 40 | | |

*SS, sum of squares; df, degrees of freedom. $R^2$ values= 0.271 (abundance), 0.200 (taxonomic richness), 0.130 (biomass).*

As expected, larger amounts of CPOM were found in shaded bromeliads. However, high availability of plant detritus in this treatment did not result in significant differences in the taxonomic composition of invertebrate communities. Although CPOM represents an important energy source in many aquatic ecosystems (Vannote *et al*., 1980), typical invertebrate shredders were not found in the communities sampled. Organisms assigned to this functional feeding group have been observed in bromeliads of forest ecosystems (see Montero *et al*., 2010; Marino *et al*., 2012; González *et al*., 2014). Shredders are important to aquatic food webs because they provide food to other consumers (Graça, 2001). González *et al*. (2014) observed that the growth of the insect shredders *Polypedilum* sp. Kieffer, 1913 (Diptera, Chironomidae) and *Phylloicus bromeliarum* Müller, 1880 (Trichoptera, Calamoceratidae) was higher when exposed to leaf detritus enriched with nutrients (N and P) and suggested that leaf quality is also important to the development of shredders in bromeliad tanks. Possibly, the xeromorphic characteristics of leaf detritus produced in restinga, such as thick cuticles, wax deposition and high tannin content (Rôças *et al*., 1997; Boeger and Wisniewski, 2003; Mantuano *et al*., 2006), are related to the absence of typical shredders in the bromeliads studied. However, even with refractory characteristics, leaf detritus may contribute indirectly to maintenance of phytotelmata in the study area because they can provide nutrients to the host plants (Benzing and Renfrow, 1974; Inselsbacher *et al*., 2007).

Although phytotelmata constitute dynamic ecosystems subject to strong seasonal fluctuations (Cardoso *et al*., 2015; Amundrud and Srivastava, 2015; Ptatscheck and Traunspurger, 2015), values of abundance, taxonomic richness and biomass of the communities sampled in bromeliads did not differ among colonization times. Moreover, the experiment duration was long enough for all taxa present in controls to colonize tanks in both treatments. The absence of differences in most of the ecological parameters evaluated and the dominance of few taxa in shaded and unshaded bromeliads reflect the ecological filters provided by the studied ecosystems (Lopez and Rios, 2001; Lopez *et al*., 2009; Marino *et al*., 2012), which selected the colonizing organisms and resulted in communities with similar structure and taxonomic composition.

The abundances of Ostracoda and Hydracarina in the tanks of *A. lingulata* are likely related to the high resistance of these organisms to stressful environmental conditions, including desiccation (Smith *et al*., 2001; Di Sabatino *et al*., 2008; Rossi *et al*., 2011). The ability of some aquatic invertebrates to produce dormant eggs is an adaptation that favors success in bromeliad tanks (Williams, 1997, 2005). In addition, the passive dispersion presented by ostracods also contributes to the wide range of these organisms in phytotelm communities (Jocque *et*

*al*., 2013). Alternatively, the low abundance of insects, compared to non-insect invertebrates, may be related to the high water temperatures in the bromeliads. Several authors have suggested that temperature is one of the factors that most affects the reproduction, growth and survival of insects, as well as predict their distribution and abundance on small temporal and spatial scales (Chesson and Huntly, 1997; Dixon *et al*., 2009; Dézerald *et al*., 2015a). In this context, the results obtained in this study corroborate the findings of Lopez and Rios (2001) in a restinga area of the State of Rio de Janeiro. The authors observed that Ostracoda was the most abundant taxon in bromeliad tanks, while insects, particularly the family Culicidae, were found in low abundance in unshaded bromeliads.

## CONCLUSIONS

The obtained results showed that the canopy cover had a small influence on the colonization of tanks of *A. lingulata* by aquatic invertebrates. Consequently, the communities sampled in shaded and unshaded bromeliads were similar, not corroborating with the proposed hypothesis. These findings were likely a result of the lack of variation in environmental conditions that are relevant to the colonization process, such as the volume of water and the amount of FPOM. However, because the amount of CPOM was higher in shaded bromeliads, we believe that the taxonomic composition of sampled communities would differ if typical invertebrate shredders were present. The importance of organic detritus and primary production as energy sources to phytotelm ecosystems in the restinga should be better evaluated, given that the canopy cover does not seem to exert a significant influence on most environmental conditions and leaf litter has refractory characteristics that may affect the presence of certain functional groups.

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