



The phytotelmata and foliage macrofauna assemblages of a bromeliad species in different habitats and seasons

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Abstract. 1. The macrofauna living inside the phytotelmata or on the foliage of bromeliads could be directly affected by habitat and seasonality. Habitat may also have indirect effects by affecting plant morphology.

2. In Chaco forests, a facultative epiphytic bromeliad (*Aechmea distichantha*) shows different morphology when growing in sun and shade conditions. Therefore, the abundance and assemblage composition of the macrofauna living on this bromeliad were analysed in different habitats and seasons.

3. Sun plants were shorter, had higher tank water content, but lower litter mass than shade ones. Phytotelmata water temperature and pH were similar between habitats.

4. In the phytotelmata, the macrofauna abundance and richness per plant, as well as total richness, were similar between habitats and among seasons. Detritivores were more abundant than predators in all habitats and seasons. Shade plants had a higher proportion of detritivores than sun plants in spring and summer, but not in winter.

5. On the bromeliad foliage, the macrofauna abundance and richness per plant were lower in winter. There were no differences in abundance between habitats, but shade plants had higher species richness than sun plants. In spring and summer, total richness was higher in shade plants than in sun plants. In spring and summer, detritivores were more abundant for shade, whereas ants were more abundant in sun plants. The proportion of hunting spiders was higher in the shade in spring and summer.

6. Our study showed that habitat mainly affects bromeliad-foliage macrofauna, but not the phytotelmata macrofauna.

Key words. *Aechmea distichantha*, Bromeliaceae, Chaco, phenotypic plasticity, phytotelmata, understory.

Introduction

Phytotelmata are contained aquatic habitats formed naturally by a plant and inhabited by aquatic organisms (Srivastava *et al.*, 2004). They are a common feature of several ecosystems (Kitching, 2000), and range from modified leaves (e.g. Sarrace-

niaceae) to flower parts (e.g. Heliconiaceae), leaf axils (e.g. Bromeliaceae), fruit husks (e.g. Arecaceae) or tree holes (Greeney, 2001). Many different taxa of organisms live in the phytotelmata (Maguire, 1971; Greeney, 2001). While some of them spend their whole life within the phytotelmata, others live only part of their life there, mainly during their juvenile stages. In some phytotelm plant species, such as bromeliads, besides those organisms living inside their aquatic habitats, there are also other species living on their leaf surfaces and on impounded litter (Araújo *et al.*, 2007; Montes de Oca *et al.*, 2007).

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The community structure of the macrofauna living in the aquatic habitat or living on the foliage of a bromeliad plant is known to vary depending on several factors operating at different spatial scales. These factors include regional species pool, resource availability, habitat conditions and probability of predation (Lounibos *et al.*, 1987; Srivastava *et al.*, 2005, 2008; Ngai & Srivastava, 2006; Srivastava, 2006; Yanoviak *et al.*, 2006; Gilbert *et al.*, 2008). At a regional scale, the bromeliad macrofauna varies among different topographic positions (Richardson, 1999; Richardson *et al.*, 2000a; Montes de Oca *et al.*, 2007). At a landscape scale it varies between communities (e.g. forests vs. savannas; Juncá & Borges, 2002), forest types (e.g. primary vs. secondary forests; Srivastava *et al.*, 2005; Ngai *et al.*, 2008), or successional stages (Yanoviak *et al.*, 2006). At a community scale the abundance and structure of the macrofauna community vary between sun vs. shaded sites (Lopez & Iglesias Rios, 2001), but not between different canopy heights (Richardson *et al.*, 2000a; Mestre *et al.*, 2001; Armbruster *et al.*, 2002; Melnychuk & Srivastava, 2002; Pereira *et al.*, 2007; but see Zanin & Tusset, 2007). At a patch scale, the abundance and community structure of arthropods dwelling on bromeliads are affected by differences in architecture among plant species (Armbruster *et al.*, 2002; Jabiol *et al.*, 2009), and even by size differences within a plant species (Richardson, 1999; Armbruster *et al.*, 2002; Juncá & Borges, 2002; Stuntz *et al.*, 2002; Srivastava *et al.*, 2005, 2008; Araújo *et al.*, 2007; Gilbert *et al.*, 2008; Jabiol *et al.*, 2009).

The habitat where the bromeliad species grow may produce direct or indirect effects on the macrofauna communities (Kitching, 2000). Differences in climatic conditions between habitats may have direct effects on macrofauna abundance and species composition by affecting the amount and quality of rainwater and litter mass held inside bromeliad tanks (Lopez & Iglesias Rios, 2001; Melnychuk & Srivastava, 2002). Indeed, local conditions may determine the type of trophic pyramid of the macrofauna community, either 'autotrophic' based on algae or 'heterotrophic' based on accumulated litter (Laessle, 1961), although the former is not common (Srivastava *et al.*, 2008; Haubrich *et al.*, 2009). Habitats may also have indirect effects on macrofauna communities by affecting plant architecture. For instance, bromeliads are highly plastic when exposed to different light environments (Scarano *et al.*, 2002; Cavallero *et al.*, 2009). Bromeliads growing in open areas are shorter, more erect and have a greater sheath area than those from the understorey. This leaf display allows sun exposed plants to hold more water inside their tanks (Cavallero *et al.*, 2009; but see Lopez & Iglesias Rios, 2001), and thus probably affects the habitat structure for the associated macrofauna.

The structure of the macrofauna community living on bromeliad plants also varies at different temporal scales. In long-lived phytotelm habitats like bromeliads, it is possible to observe processes related to seasonality, invasion and reassembly (Kitching, 2000). Some authors recorded differences in abundance and species richness in bromeliads between dry and wet seasons (Liria, 2007; Montes de Oca *et al.*, 2007; Müller & Marcondes, 2007; Pereira *et al.*, 2007), while others recorded differences between winter and summer (Lopez & Iglesias Rios, 2001; Mestre *et al.*, 2001; but see Lounibos *et al.*, 1987).

We used the long-lived facultative epiphytic bromeliad *Aechmea distichantha* Lem., which shows high phenotypic plasticity (Cavallero *et al.*, 2009), holds phytotelmata (Torales *et al.*, 1972) and diverse macrofauna on its foliage (Theunis *et al.*, 2005) to explore whether there are differences in species richness, species composition and feeding guild structure between sun and shade plants for macrofauna dwelling inside the phytotelmata and for macrofauna living on bromeliad foliage. If so, further explore whether these differences are similar among seasons.

Methods

Study area

The study was carried out in a 400-ha forest of *Schinopsis balansae* Engl. (Barberis *et al.*, 2002) located at Las Gammas, Santa Fe, Argentina (29°28'S-60°28'W, 58 m above sea level). The climate is humid temperate to warm (mean annual precipitation 1000 mm, mean annual temperature 20 °C), with frequent frosts in winter. Rainfall is concentrated in the summer (December–March), while a dry season occurs in winter. Soils have low hydraulic conductivity and high sodium content. The structure and floristic composition of this xerophytic forest change markedly in tens of metres in relation to microtopography and soil moisture. Tree and shrub densities are higher in areas with convex topography (Barberis *et al.*, 2002), where grow populations of two bromeliads: *Bromelia serra* Griseb. and *A. distichantha* (Barberis & Lewis, 2005).

Study species

Aechmea distichantha occurs as a terrestrial or epiphytic plant in deciduous, semideciduous and evergreen forests in southern Brazil, Bolivia, Paraguay, Uruguay and northern Argentina (Smith & Downs, 1979). This tank-forming bromeliad has pungent leaves about 30–100 cm long and reproduces both sexually and asexually. Ramets from one genet exposed to different environmental conditions may show different phenotypes. Shade plants are taller and have larger diameters, whereas sun plants have more leaves and larger sheath mass fraction, and thus higher maximum tank water contents (Cavallero *et al.*, 2009).

Sampling methods

In three different seasons (spring: November 2004, summer: January 2005, winter: June 2005), eight medium to large *A. distichantha* plants were harvested from the understorey (thereafter shade plants) and eight similar plants from forest edges and small open areas (thereafter sun plants). The chosen plants were widely separated (> 5 m) to avoid sampling ramets from the same genet. For each plant, the height from the soil to the top leaf, the largest diameter and the diameter 90° to that were measured. Tank water temperature (Luft digital thermometer) was measured between 1100 and 1400 h to reduce daily temperature variability (Laessle, 1961). Plants were then carefully dislodged

from the soil, and the contained water was poured into buckets, measured in graduated cylinders and placed into plastic bags. The pH (pHTest2® Oakton Instruments) of the whole water tank was measured to reduce pH differences among different water bodies contained within a single plant (Laessle, 1961). Each plant was dismantled leaf by leaf over a large bucket, its number of leaves was recorded and all the captured litter was rinsed off. Then, the water and the litter were filtered through a sieve > 0.045 mm (Twente Metaalgaas BV, Hengelo, The Netherlands), the residue placed on white trays, and carefully searched for macrofauna (i.e. animals that can be seen by naked eye) using forceps. Litter, bromeliad leaf blades, sheaths and stems were oven-dried at 70 °C to constant weight and weighed with a precision scale (SCALTEC SBA 52, Heiligenstadt, Germany). All individuals were separated and preserved in alcohol (70%) until their identification to 'morphospecies'.

Morphospecies were classified according to the place where they spend most of their life as macrofauna dwelling inside the phytotelmata or as macrofauna living on bromeliad foliage (Araújo *et al.*, 2007). Morphospecies were assigned to six feeding guilds (detritivores, herbivores, parasitoids, predators, ants and tourists); spiders were classified as hunting spiders and web-building spiders (Stuntz *et al.*, 2002). For taxonomic identification and species allocation to each feeding guild we followed Stehr (1991), Borror *et al.* (1992), Morrone and Coscarón (1998) and Pastrana (2004).

Data analyses

Despite variation among taxa in the taxonomic resolution of identification, all morphospecies were treated equally in the analyses to maximise sample information. Two data sets were defined: one for species recorded inside the phytotelmata and the other for species recorded on bromeliad foliage. All analyses were carried out separately for each data set. For each macrofauna set, habitat and season combination we estimated species richness, evenness (Pielou index), and diversity (Shannon index) per plant (McCune & Mefford, 1999).

Plant, habitat and phytotelmata variables were analysed with generalised linear models using a factorial design with habitat and season as categorical factors. For count data (i.e. leaf number, abundance and richness) a Poisson distribution was assumed and thus a log-link function was used, whereas for the others a normal distribution was assumed. The latter variables were log₁₀-transformed to improve normality and homoscedasticity. To correct for overdispersion of the data, the models were fitted by quasi-maximum likelihood. All analyses were performed using proc GENMOD from the SAS 8.0 package (SAS Institute Inc., Cary, NC, USA).

For each macrofauna data set, total species richness between habitats and among seasons was compared by rarefaction curves. Curves were built by calculating mean species richness values from random samples of increasing abundance, with 1000 iterations for each abundance level, using the EcoSim program (Gotelli & Entsminger, 2002).

A multivariate analysis of variance with randomisation testing (MULTIV program; Pillar, 2004) was used to evaluate

whether there were differences in species composition between habitats and seasons for each macrofauna set. The Bray-Curtis index was used as a measure of dissimilarity and the pseudo-*F* value = (Q_b/Q_w) as a test criterion where Q_b = sum of squares between groups and Q_w = sum of squares within k groups. In our study, the habitat × season interaction was significant ($P < 0.001$) in both data sets, thus the data of each set were split according to the levels of one factor and then tested for effects of the other factor. For these one-factor designs, the sum of squares (Q_b) was used as the test criterion (Pillar, 2004).

For each season, the species association with either sun or shade habitat was analysed using the Indicator Value Analysis from the PC-ORD program (McCune & Mefford, 1999). This method combines information on the concentration of species abundance in a particular habitat and the faithfulness of occurrence of a species in it. Then it calculates indicator values for each species in each habitat, which are tested for statistical significance using a Monte Carlo technique.

Results

In the 48 bromeliads, 5507 individuals from 96 morphospecies were recorded, belonging to 61 families (14 unknown), 18 orders and six classes (Appendices 1 and 2). Dwelling in the phytotelmata there were 3053 individuals from 13 morphospecies, belonging to 11 families (1 unknown) from two orders (Diptera and Coleoptera) and just one class (Insecta) (Appendix 1). Coleoptera was the most abundant order (69% of individuals) with only two families (Scirtidae and Hydrophilidae), followed by Diptera (31% of individuals) with nine families (Appendix 1). The most abundant families were Scirtidae and Tipulidae (69% and 9% of the individuals respectively). Only one morphospecies was a singleton (i.e. only one individual recorded).

Living on bromeliad foliage there were 2454 individuals from 83 morphospecies, belonging to 50 families (13 unknown), 18 orders and six classes (Appendix 2). Hymenoptera was the most abundant order (48% of the individuals from four families), followed by Haplotaenidia (16% from one family) and Araneae (13% from eight families) (Appendix 2). The most abundant families were Formicidae and Lumbricidae (48% and 16% of the individuals respectively), followed by Lycosidae and Araneidae (4% each). The families with higher morphospecies richness were Lycosidae, Salticidae, Carabidae and Formicidae (five species each) (Appendix 2). Fifteen morphospecies were singletons, while for five morphospecies only two individuals were recorded and in different plants.

Plant and phytotelmata characteristics in different habitats and seasons

Shade plants were taller, had larger diameters, but fewer leaves and lower sheath mass fraction despite having similar biomass than sun plants (Table 1, Fig. 1). There were seasonal differences in leaf number per plant (higher in winter) and sheath

Table 1. ANOVA results for the effects of habitat, season and their interactions on variables related with plant, tank and phytotelmata and bromeliad-foilage macrofauna characteristics.

Source	Variable	Habitat		Season		Habitat × Season		
		$F_{1,42}$	P	$F_{2,42}$	P	$F_{2,42}$	P	
Plant	Biomass	0.46	0.503	0.87	0.425	1.06	0.357	
Characteristics	Height	17.00	< 0.001	0.40	0.675	0.49	0.614	
	Diameter	56.26	< 0.001	0.84	0.440	4.05	0.025	
	Leaf number	7.02	0.011	9.73	< 0.001	0.54	0.589	
	Sheath mass fraction	37.41	< 0.001	5.09	0.011	3.15	0.053	
	Tank	Actual water content	33.51	< 0.001	19.82	< 0.001	4.03	0.025
Characteristics	Maximum water content	48.10	< 0.001	0.16	0.850	1.84	0.171	
	Water pH	8.18	0.007	3.58	0.037	0.95	0.395	
	Water temperature	0.03	0.867	98.61	< 0.001	0.01	0.986	
	Litter mass	16.84	< 0.001	3.38	0.044	2.41	0.103	
Phytotelmata	Abundance	0.28	0.570	11.76	< 0.001	0.20	0.820	
	Macrofauna	Richness	0.32	0.567	2.36	0.107	0.79	0.462
		Evenness	0.23	0.637	5.08	0.011	4.77	0.014
Diversity		0.11	0.744	3.13	0.054	4.24	0.021	
Foliage	Abundance	0.16	0.693	6.18	0.004	2.26	0.117	
	Macrofauna	Richness	14.00	< 0.001	13.46	< 0.001	1.34	0.273
		Evenness	1.97	0.168	4.17	0.022	0.90	0.416
		Diversity	7.40	0.009	3.06	0.057	1.24	0.301

Bold fonts denote significant results.
 Evenness = Pielou index; Diversity = Shannon index.

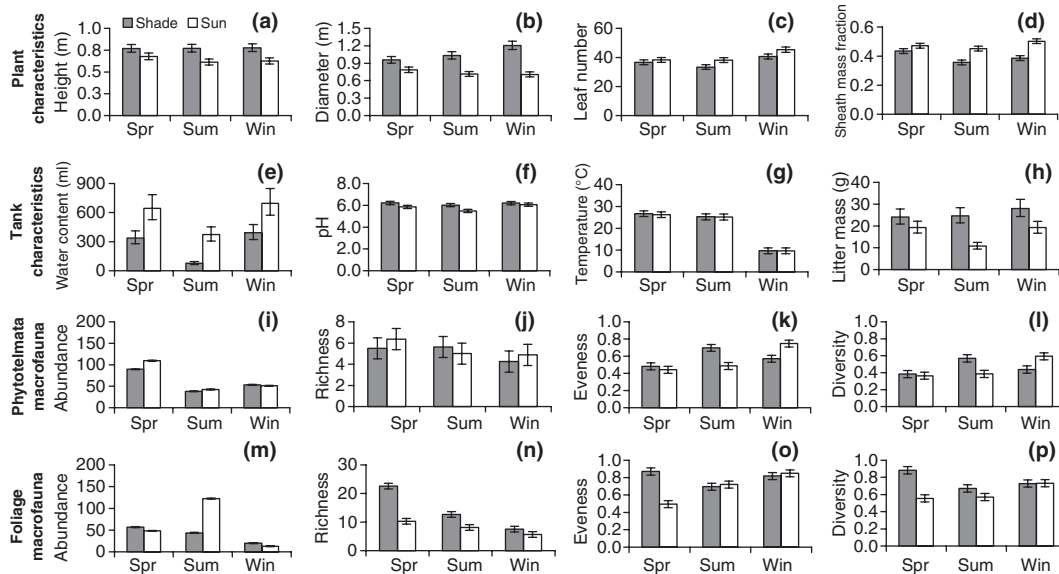


Fig. 1. Plant architecture (a–d), bromeliad-tank characteristics (e–h), phytotelmata-macrofauna characteristics (i–l) and foliage-macrofauna characteristics (m–p) for *Aechmea distichantha* plants grown in sun- and shade-habitats in different seasons. Water contents = Actual water content. Evenness = Pielou index. Diversity = Shannon index. Error bars indicate ± SE.

mass fraction (lower in summer). Shade plants had lower maximum and actual tank water content, higher litter mass and pH, but similar water temperature than sun plants. Actual tank water content, pH and litter mass were lower in summer, whereas temperature was lower in winter.

Phytotelmata-macrofauna characteristics in different habitats and seasons

In the phytotelmata, 1571 individuals were recorded in spring, 645 in summer, and 837 in winter from 9, 13 and 9

morphospecies respectively. Most individuals were larvae. There were 1424 individuals from 12 taxa in shade plants and 1629 individuals from 12 taxa in sun plants.

There were no significant differences in animal community parameters of abundance, species richness, evenness and diversity, between sun and shade plants (Table 1, Fig. 1). There were, however, seasonal differences in abundance and evenness, with abundance per plant being higher in spring than in other seasons (Fig. 1) and with an interactions between evenness and diversity and season (Table 1).

Beta diversity values were lower in spring than in summer or winter, but there were no differences between habitats (i.e. spring: shade = 1.45, sun = 1.41; summer: shade = 2.31, sun =

2.40; winter: shade = 2.12, sun = 1.85). Total richness was similar in shade and sun plants, but contrary to the richness per plant, it was higher in summer than in the other seasons (Fig. 2).

Differences in morphospecies composition between habitats were smaller than among seasons (Table 2). There were differences between habitats in winter, but not in spring or summer. Detritivores were more abundant than predators for all seasons and habitats (Fig. 3). However, there were differences between habitats in relative abundance of each trophic group among seasons. In spring and summer, the proportion of detritivores was higher in sun plants than in shade plants, whereas in winter the proportion of detritivores was higher in shade than in sun plants (Fig. 3).

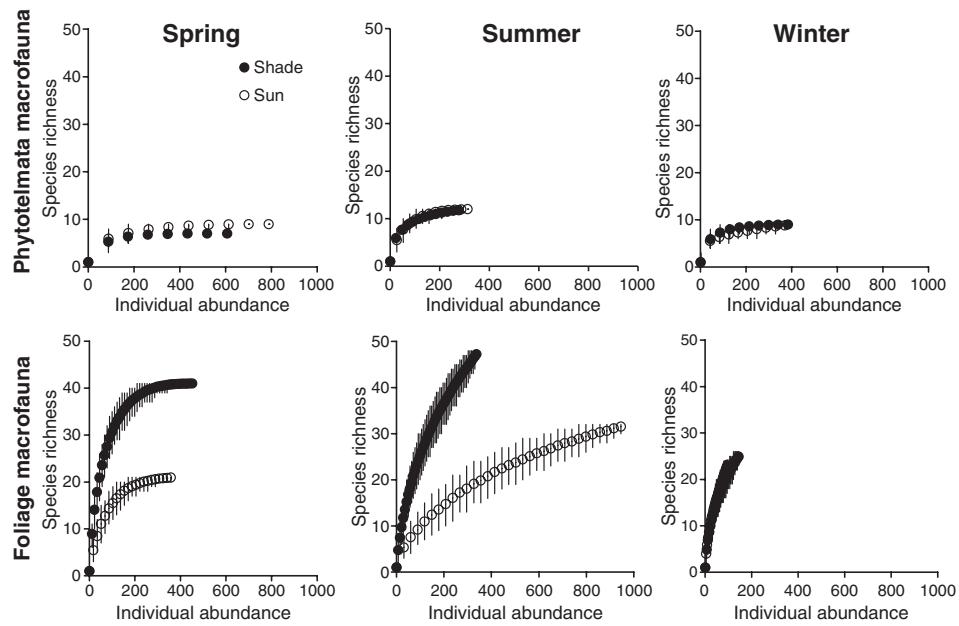


Fig. 2. Sample-based rarefaction curves for phytotelmata and foliage macrofauna from sun and shade plants in the three sampled seasons. Vertical bars are 95% confidence intervals.

Table 2. MANOVA results for the effects of habitat within each season and for seasons within each habitat on species composition of the phytotelmata and bromeliad-foliage macrofauna assemblages.

Source of variation	Comparison between habitats						Comparison among seasons			
	Spring		Summer		Winter		Shade		Sun	
	SS (Q)	P	SS (Q)	P	SS (Q)	P	SS (Q)	P	SS (Q)	P
Phytotelmata										
Between groups	0.16	0.199	0.27	0.092	0.25	0.048	0.97	0.001	1.05	0.001
Within groups	1.48		2.23		1.49		3.27		1.93	
Total	1.64		2.50		1.74		4.24		2.98	
On foliage										
Between groups	0.85	0.001	0.82	0.006	0.20	0.701	2.36	0.001	2.03	0.001
Within groups	3.55		4.71		3.66		4.92		7.00	
Total	4.40		5.53		3.85		7.28		9.03	

As a test criterion the sum of squares between groups (Q) was used. Bold fonts denote significant P-values (<0.05).

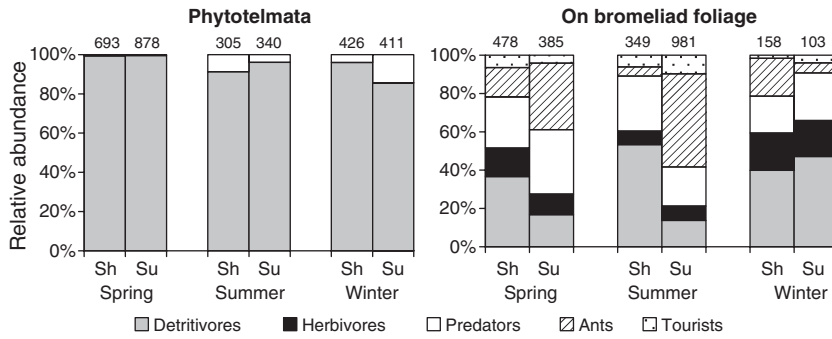


Fig. 3. Relative abundance of detritivores and predators dwelling in the phytotelmata and of detritivores, herbivores, predators, ants and tourists on the foliage of *Aechmea distichantha* plants harvested from shade (Sh) and sun (Su) conditions in spring, summer and winter. The number above each bar denotes the total individuals found in each habitat × season interaction. Parasites and unknown species were not considered.

Foliage macrofauna characteristics in different habitats and seasons

We recorded 863 individuals in spring, 1330 in summer, and 261 in winter from 48, 52 and 32 morphospecies respectively. Most individuals were adults. There were 985 individuals from 71 taxa in shade plants and 1469 individuals from 55 taxa in sun plants. Twenty-eight morphospecies were recorded only in shade plants and 12 morphospecies only in sun plants (Appendix 2).

The foliage macrofauna abundance per plant was similar between habitats, but there were more individuals in summer (Table 1, Fig. 1). Species richness per plant was higher in the shade than in the sun and higher in spring than in summer or winter. Likewise, species diversity per plant was higher in spring than in summer or winter (Table 1, Fig. 1).

Beta diversity values were lower in spring than in summer or winter, but there were no differences between habitats (spring: shade = 1.77, sun = 2.05; summer: shade = 3.72, sun = 2.94; winter: shade = 3.47, sun = 4.27). Total richness was also higher in shade plants than in sun plants in spring and summer, but there were no differences in total richness in winter. Total richness was higher in spring and summer than in winter (Fig. 2).

Differences in morphospecies composition between habitats were smaller than among seasons (Table 2). There were differences between habitats in spring and summer, but not in winter (Table 2). Detritivores and predators were more abundant than

herbivores for all seasons and habitats (Fig. 3). However, the proportion of different trophic groups varied according to habitat and seasonality. In summer and spring, plants in the sun had proportionally more ants, whereas plants in the shade had proportionally more detritivores. In winter, plants from both habitats had proportionally more detritivores than any other trophic groups (Fig. 3). In spring, eight morphospecies (four detritivores, one predator, two herbivores and one ant) were more represented in shade plants (Table 3). In summer there was one detritivore morphospecies better represented in shade plants and one ant morphospecies in sun plants.

In spring and summer there was a higher proportion of hunting spiders than web-building spiders, whereas in winter there was a higher proportion of web-building spiders (Fig. 4). In spring and summer the proportion of hunting spiders was higher in the shade than in the sun, whereas in winter there were no differences between habitats in the proportion of hunting and web-building spiders.

Discussion

The macrofauna assemblage

The macrofauna associated with *A. distichantha* encompassed a large variety of morphospecies, including aquatic, amphibious and terrestrial organisms. As some of them are more related

Table 3. Abundance (N) and indicator values (IV) of morphospecies recorded on the foliage of *Aechmea distichantha* plants grown in shade and sun conditions in different seasons.

Family	Morphospecies	Feeding guild	Total N	Comparison between habitats								
				Spring			Summer			Winter		
				N	IV	P	N	IV	P	N	IV	P
Anisolabididae	<i>Euborellia annulipes</i> Lucas	DET	23	13	75.0	0.011 Shade	4	25.0	0.512	6	25.0	0.451
Lumbricidae	<i>Oligochaeta</i> sp. 193	DET	374	90	75.0	0.012 Shade	278	51.9	0.231	6	12.5	1.000
Pyrilidae	<i>Aglossa caprealis</i> Hübner	HER	9	8	62.5	0.029 Shade	1	12.5	1.000			
Lumbricidae	<i>Oligochaeta</i> sp. 194	DET	18	11	62.5	0.034 Shade	7	7.1	1.000			
Cicadidae	<i>Cicadidae</i> sp. 231	HER	6	6	62.5	0.034 Shade						
Carabidae	<i>Harpalini</i> sp. 222	PRE	5	5	62.5	0.034 Shade						
Formicidae	<i>Basicerus</i> sp. 227	ANT	18	18	62.5	0.048 Shade						
Blattellidae	<i>Ischnoptera</i> sp. 005	DET	71	50	70.0	0.044 Shade	8	75.0	0.009 Shade	13	38.5	0.566
Formicidae	<i>Myrmicinae</i> sp. 038	ANT	721				721	62.3	0.030 Sun			

Bold fonts denote significant results ($P < 0.05$). Feeding guild codes: ANT: ants, DET: detritivores, HER: herbivores, PRE: predators.

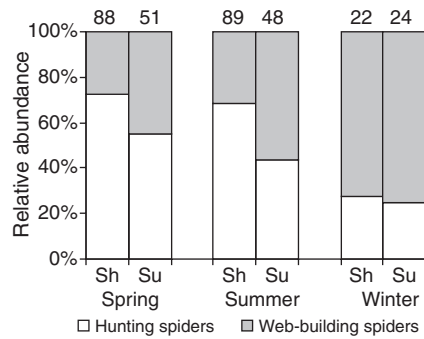


Fig. 4. Relative abundance of hunting and web-building spiders living on *Aechmea distichantha* plants harvested from shade (Sh) and sun (Su) conditions in spring, summer and winter. The number above each bar denotes the total spiders found in each habitat \times season interaction.

than others to the bromeliad microcosm, we could not talk about a true community, but of an assemblage of co-occurring morphospecies (Cotgreave *et al.*, 1993). In our study, seven morphospecies comprised almost 80% of all individuals. Similarly, Juncá and Borges (2002) found that 10 species comprised more than 70% of all individuals, and Jabiol *et al.* (2009) found that five to seven taxa represented at least 80% of the individuals. However, we found very few singletons, which is opposite to other studies that found a long tail with more than 50% of the species with just one individual (Cotgreave *et al.*, 1993; Armbruster *et al.*, 2002; Jabiol *et al.*, 2009). The low number of singletons could be a result of collecting animals from wet sieved litter, and not from free water and thus probably not detecting some small organisms. Although our sampling was consistent throughout all treatments, our data could be an under-estimation and care should be taken when comparing with other studies. In these, leaves and impounded debris have usually been washed and organisms collected under water, where movement aids their visibility.

In the phytotelmata of our study, the most abundant order was Coleoptera (mainly *Scirtidae*) and the richest was Diptera. Similar results were found by Cotgreave *et al.* (1993), Mestre *et al.* (2001) and Ospina-Bautista *et al.* (2004) for epiphytic bromeliads, and by Juncá and Borges (2002) for terrestrial bromeliads. By contrast, almost all organisms captured by Liria (2007) and Jabiol *et al.* (2009) were Diptera. On the other hand, Richardson (1999) found that Coleoptera were more abundant between 600 and 900 m a.s.l., whereas Diptera were dominant below 600 and above 900 m a.s.l. In our study, the more abundant guilds in the phytotelmata were detritivores. Likewise, Stuntz *et al.* (2002) found that detritivores encompassed more than 80% of the individuals. Conversely, Armbruster *et al.* (2002) found a large proportion of herbivores. However, it should be noted that these authors classified all Coleoptera larvae as phytophagous chewer, but some could be detritivores (e.g. *Scirtidae*). Finally, we recorded very few top predators dwelling inside the bromeliads, which match other phytotelmata studies (Yanoviak *et al.*, 2006).

On the bromeliad foliage the most abundant and richest order in our study was Hymenoptera (mainly ants), followed by

Haplotaenidae and Araneae. Similarly, Wittman (2000) and Stuntz *et al.* (2002) reported that Hymenoptera represented a high percentage of their bromeliad samples. In our study we observed a very low damage on bromeliad foliage, which agrees with the very few chewing and sap-sucking herbivores. Similarly, Stuntz *et al.* (2002) recorded very few herbivores, but all of them were sap-suckers.

The effect of habitat on the phytotelmata and bromeliad-foliage macrofauna assemblages

Aechmea distichantha plants grown on shade conditions were taller, had fewer but longer and narrower leaves with lower sheath mass fraction. These patterns of biomass allocation also affected the tank ability of holding water and litter mass (Guimarães-Souza *et al.*, 2006; Cavallero *et al.*, 2009). In our study, sun plants held more water in their tanks due to their higher sheath mass fraction, whereas shade plant had more litter mass possibly because of their higher projected leaf area (Cavallero *et al.*, 2009) and their location beneath the understorey (Laessle, 1961; Haubrich *et al.*, 2009).

There were no differences in the temperature of the water held inside plants of *A. distichantha* from sun and shade habitats, despite significant differences in air temperature between both habitats (Cavallero *et al.*, 2009). This pattern could be related to the larger amount of water held inside sun plants (Cavallero *et al.*, 2009) that could ameliorate temperature fluctuation. On the other hand, the selected bromeliads were located on forest edges and small open areas and thus they were not fully exposed to sun during the whole length of the day. By contrast, Lopez and Iglesias Rios (2001) and Guimarães-Souza *et al.* (2006) found higher water temperature in exposed than in shaded habitats for bromeliad species in the Brazilian restinga. Similarly, Laessle (1961) reported wide temperature fluctuations between day and night in sun plants, but moderate to little diurnal fluctuations in shade plants. Indeed, inner reservoirs showed the widest temperature fluctuations in sun plants (Laessle, 1961).

Differences in plant architecture may also affect the macrofauna richness and diversity by modifying the habitat within the tanks. In our study, plants grown in the understorey had similar species richness than sun plants, despite having a significantly higher detrital biomass. By contrast, Jabiol *et al.* (2009) found fewer taxa in bromeliads with higher amounts of fine particulate organic matter. Neither of these patterns matches the 'more individuals hypothesis', which states that habitats with higher productivity should have higher species richness (Srivastava & Lawton, 1998; but see Richardson *et al.*, 2000b). However, it is not sure whether the phytotelmata in the understorey were really more productive than the phytotelmata in the sun. Laessle (1961) reported that sun plants were more productive than shade ones, because the former held algae inside their tanks. This pattern could be expected because chlorophyll *a* content varies by several orders of magnitude among bromeliads (Haubrich *et al.*, 2009) and sun plants have higher oxygen concentration and lower ammonium concentration (Guimarães-Souza *et al.*, 2006). On the other hand, sun plants had larger maximum tank water content and also more leaves than shade plants, which

may increase complexity and thus species richness (Srivastava, 2006).

The architecture of the epiphytic plants may influence the feeding guild structure by affecting the amount of water and litter mass held in its interior (Stuntz *et al.*, 2002). In our study, shade and sun plants supported similar proportion of detritivores despite shade plants held a higher amount of litter mass. This pattern was expected because both shade and sun plants are heterotrophic systems (Guimarães-Souza *et al.*, 2006).

We recorded a higher proportion of hunting spiders in shade than in sun plants. It is likely that greater litter depth and complexity in shade plants favour hunting spiders (Stuntz *et al.*, 2002), whereas litterfall may affect web-building spiders. On the other hand, the predominance of web-building spiders on sun plants may be related to the ability of this strategy to capture flying insects and tourists in a more open habitat (Stuntz *et al.*, 2002).

The effect of seasonality on the phytotelmata and bromeliad-foilage macrofauna assemblages

We recorded lower tank water content in summer and lower water temperature in winter. Even though the dry season occurs in winter, there are several drought periods during summer, thus the tank water content may follow higher fluctuations in summer than in winter. It is known that plant size not only affects the amount of water held inside the tank (Armbruster *et al.*, 2002; Cavallero *et al.*, 2009), but also the time elapsed until its desiccation (Zotz & Thomas, 1999).

Environmental differences among seasons are likely to explain the lower abundance and species richness in winter than in summer or spring. For bromeliads in Brazilian forests, Lopez and Iglesias Rios (2001), Mestre *et al.* (2001) and Müller and Marcondes (2007) suggested that seasonal differences in arthropod assemblages were due to low temperature. By contrast, Liria (2007) and Montes de Oca *et al.* (2007) suggested that during the dry season, bromeliads represented the only available wet reservoirs in the Venezuelan and Mexican forests, thus the higher abundance of arthropods during the dry season. In our study site, it is likely that low temperatures in winter set up the lower limit of the carrying capacity for the phytotelmata and bromeliad-foilage macrofaunas, whereas in spring or summer this limit is controlled by other factors such as tank water content or the amount of litter mass. Moreover, low temperature may also explain the lack of differences in abundance or richness or between habitats in winter for the phytotelmata and bromeliad-foilage macrofaunas.

Higher beta diversity in summer than in spring for phytotelmata and bromeliad-foilage macrofaunas could be related to resource availability and habitat conditions, due to higher water content fluctuations as a result of higher water evaporative demand. Nevertheless, other factors (regional pool of morphospecies, resource availability, habitat conditions and probability of predation), which in turn may affect the rates of phytotelmata colonisation and extinction (Srivastava *et al.*, 2005; Ngai & Srivastava, 2006; Srivastava, 2006), cannot be discarded because we only recorded seasonal patterns of mac-

rofauna abundance and species composition, but not their dynamics.

Final comments

The abundance and morphospecies composition of the macrofauna living on terrestrial bromeliads may also depend on the size of the bromeliad population, the degree of overlap between bromeliad species, or the distance between bromeliad populations. These factors are important because human intervention could affect the availability of arthropods dwelling in plant-held waters by modifying the forest landscape (Ngai *et al.*, 2008). For our study site in particular, the area occupied by the *Schinopsis balansae* forests has been markedly reduced in the last years, leading to a higher fragmentation (Carnevale *et al.*, 2007). Forest fragmentation probably reduced the number and sizes of bromeliad populations, the proportion of sun and shade bromeliad plants, and hence affects the diversity of those arthropods living on bromeliad phytotelmata and foliage. Therefore, future studies should include these factors taking into account different spatial and temporal scales.

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Appendix 1

Feeding guild, number of morphospecies and individuals for the phytotelmata macrofauna families recorded from *Aechmea distichantha* plants grown in the sun and in the shade. Stage codes: A: adults, L: larvae. Feeding guild codes: DET: detritivores, PRE: predators.

Class	Order	Family	Stage	No. morphospecies	No. individuals		Feeding guild
					Sun	Shade	
Insecta	Coleoptera	Hydrophilidae	A	1	3	0	PRE
		Scirtidae	L	2	1160	934	DET
	Diptera	Chaoboridae	L	1	73	21	PRE
		Chironomidae	L	1	81	141	DET
		Culicidae	L	1	147	85	DET
		Psychodidae	L	1	15	8	DET
		Stratiomyidae	L	1	12	16	DET
		Syrphidae	L	1	10	24	DET
		Tabanidae	L	1	10	13	PRE
		Tipulidae	L	2	106	171	DET
Unknown	L	1	12	11	DET		

Appendix 2

Feeding guild, number of morphospecies and individuals for the macrofauna families recorded from foliage and impounded litter of *Aechmea distichantha* plants grown in the sun and in the shade. Stage codes: A: adults, L: larvae, N: nymphs. Feeding guild codes: ANT: ants, DET: detritivores, HER: herbivores, PAR: parasitoids, PRE: predators, TOU: tourists.

Class	Order	Family	Stage	No. morphospecies	No. individuals		Feeding guild
					Sun	Shade	
Oligochaeta	Haplotaxida	Lumbricidae	A	2	123	269	DET
Arachnida	Araneae	Araneidae	A	2	53	47	PRE
		Clubionidae	A	1	7	13	PRE
		Ctenidae	A	1	1	2	PRE
		Dictynidae	A	3	12	18	PRE
		Lycosidae	A	5	26	79	PRE
		Pisauridae	A	1	0	1	PRE

Appendix 2. *Continued*

Class	Order	Family	Stage	No. morphospecies	No. individuals		Feeding guild
					Sun	Shade	
		Salticidae	A	5	14	25	PRE
		Sparassidae	A	3	10	14	PRE
	Pseudoscorpionida	Unknown	A	1	0	7	PRE
	Scorpionida	Buthidae	A	1	7	1	PRE
Crustacea	Isopoda	Porcellionidae	A	1	33	68	DET
Diplopoda	Julida	Rhinocricidae	A	1	3	11	DET
	Polydesmida	Oniscodesmidae	A	1	1	0	DET
Insecta	Blattaria	Blaberidae	A	2	3	6	DET
		Blattellidae	N	1	18	53	DET
	Coleoptera	Bruchidae	A	1	1	0	TOU
		Carabidae	A	5	1	16	PRE
		Chrysomelidae	A	1	3	8	TOU
		Coccinellidae	A	1	1	0	PRE
		Curculionidae	A	3	10	10	TOU
		Elateridae	L	2	5	0	TOU
		Nitidulidae	A	1	2	7	DET
		Scarabaeidae	A	2	1	6	DET; HER
		Staphylinidae	A	3	7	18	PRE; DET
		Unknown	L-A	4	3	17	TOU
	Dermaptera	Anisolabididae	A	1	0	23	DET
	Diptera	Therevidae	L	1	0	25	PRE
	Embioptera	Unknown	N-A	2	1	6	TOU
	Hemiptera	Pyrrhocoridae	N	1	0	4	TOU
		Unknown	A	2	3	7	TOU
	Homoptera	Cicadidae	N-A	4	6	24	HER
	Hymenoptera	Evaniidae	A	1	1	0	PAR
		Formicidae	A	5	1062	119	ANT
		Unknown	A	1	0	1	PAR
		Unknown	A	1	1	0	PRE
	Lepidoptera	Acrolophidae	L	1	38	44	DET
		Lycaenidae	L	1	0	6	HER
		Pyralidae	L	1	0	9	HER
		Unknown	L	2	8	14	HER
	Orthoptera	Acrididae	A	2	2	1	HER
		Gryllidae	N	1	1	0	TOU
		Tettigoniidae	N	1	0	1	HER
Amphibia	Anura	Hylidae	A	1	1	5	PRE