



Effects of bromeliad flowering event on the community structuring of aquatic insect larvae associated with phytotelmata of *Aechmea distichantha* Lem. (Bromeliaceae)

Efeito de um evento de floração na estruturação da comunidade de larvas de insetos aquáticos associados aos fitotelmata de *Aechmea distichantha* Lem. (Bromeliaceae)

Felipe Emiliano Amadeo^{1*}, Juliana Déo Dias¹, Bianca Trevizan Segovia¹,
Nadson Ressayé Simões² and Fábio Amodêo Lansac-Tôha¹

¹Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Departamento de Biologia, Universidade Estadual de Maringá – UEM, Avenida Colombo, 5790, Bloco G-90, CEP 87020-900, Maringá, PR, Brazil

²Centro de Ciências Ambientais, Universidade Federal do Sul da Bahia – UFSB, Rodovia BA001, Porto Seguro-Eunápolis, CEP 45810-000, Porto Seguro, BA, Brazil

*e-mail: philamadeo@gmail.com

Cite as: Amadeo, F.E. et al. Effects of bromeliad flowering event on the community structuring of aquatic insect larvae associated with phytotelmata of *Aechmea distichantha* Lem. (Bromeliaceae). *Acta Limnologica Brasiliensia*, 2017, vol. 29, e111.

Abstract: Aim: We aimed to understand how aquatic insect larvae communities associated with bromeliad phytotelmata are affected by plant architecture, predators and resources (local factors), and by geographical distance (regional factors) in two different plant phenological phases. Bromeliad flowering results in plant structural changes, which favours insect dispersal. Considering that local and regional factors may affect the community of aquatic insect larvae, we expected that composition, beta diversity and the importance of those factors would differ in the vegetative growth and flowering phases. **Methods:** We performed six samplings of the bromeliad associated fauna in 2010, three during the first semester - vegetative growth phase - and three during the second semester - flowering phase. In each sampling, we collected 12 plants along the rocky walls with similar location distribution, with a total of 72 bromeliads studied. **Results:** Although beta diversity (PERMDISP) did not differ between vegetative growth and flowering, NMDS followed by ANOSIM showed that composition was significantly different in the distinct phenological phases. IndVal results showed that three Diptera morphospecies were discriminant of the vegetative growth phase. In addition, pRDA revealed differences in the relative contribution of local and regional factors to explain insect larvae community structure. During the flowering phase, local factors predominated, while during vegetative growth, regional factors were more important. **Conclusion:** Differences in dispersal rates between the two phenological phases, likely due to adult insect pollination and further oviposition, influenced community structuring. Therefore, flowering events account for differences not only in the composition, but also in community structuring of aquatic insect larvae inhabiting the phytotelmata of *Aechmea distichantha* Lem. (Bromeliaceae).

Keywords: assembly rules; environmental component; spatial component; inflorescence.



Resumo: Objetivo: Esse estudo teve por objetivo entender como as comunidades de larvas de insetos aquáticas associadas aos fitotelmata são afetadas pela arquitetura da planta, presença de predadores e de recursos (fatores locais) e pela distância geográfica (fator regional) em duas fases fenológicas distintas. A floração de bromélias resulta em alterações estruturais nas plantas, que favorecem o aumento na dispersão de insetos. Considerando que tanto fatores locais quanto regionais podem afetar a comunidade de larvas de insetos aquáticas, nós esperamos que a composição, diversidade Beta e a importância desses fatores sejam diferentes entre as fases de crescimento vegetativo e de floração. **Métodos:** Foram realizadas seis amostragens da fauna associada (insetos adultos e larvas) de bromélias em 2010, três durante o primeiro semestre - fase de crescimento vegetativo - e três durante o segundo semestre - fase de floração. Foram amostradas 12 plantas distribuídas de forma similar nos paredões rochosos por coleta, totalizando 72 bromélias. **Resultados:** Embora a diversidade beta (PERMDISP) não tenha diferido entre as fases de crescimento vegetativo e de floração, a NMDS seguida pela ANOSIM demonstrou que a composição foi significativamente diferente entre as distintas fases fenológicas. Os resultados da IndVal mostraram que três espécies de Diptera foram discriminantes da fase de crescimento vegetativo. A pRDA revelou que diferenças na contribuição relativa dos fatores locais e regionais para explicar a estrutura da comunidade de larvas de insetos aquáticas. Na fase de floração, os fatores locais predominaram, enquanto que durante a fase de crescimento vegetativo, os fatores regionais foram os mais importantes. **Conclusão:** Diferenças nas taxas de dispersão nas duas fases fenológicas, provavelmente em função da polinização e consequente oviposição, influenciaram a estruturação da comunidade. Assim, os eventos de floração não só influenciam na composição, mas também na estruturação da comunidade de larvas aquáticas presentes nos fitotelmata de *Aechmea distichantha* Lem. (Bromeliaceae).

Palavras-chave: regras de montagem de comunidades; componente ambiental; componente espacial; inflorescência.

1. Introduction

Natural communities may be regulated by local factors, such as competition, disturbances, biotic and abiotic variables, and regional factors, such as geographical distance among patches, dispersal capacity among habitats and climate conditions (Hillebrand & Blenckner, 2002; Cottenie et al., 2003; Paradise et al., 2008). These processes, acting in broad temporal and spatial scales, are important in determining diversity patterns and define the aspects of the regional species pool from where local communities are assembled (Caley & Schluter, 1997).

The area in which the species pool is inserted has a fundamental role in the analysis of local and regional factors since it affects richness estimates (species-area relationship) and the scales in which species interact (ecological factors; Hillebrand & Blenckner, 2002). However, area extension is generally difficult to be determined (Srivastava, 1999), thus, most studies use a large randomly chosen area (Caley & Schluter, 1997) or an area that is naturally delimited by landscape geography (Oberdorff et al., 1998). Therefore, the difficulty in manipulating communities reduces the possibility of testing the predictions on the influence of local and regional factors on organismal diversity (Hillebrand & Blenckner, 2002).

Phytotelmata are small aquatic habitats naturally formed in plants (i. e. bromeliads), which can

contain associated organisms (Srivastava et al., 2004; Williams, 2006; Brouard et al., 2012). Those habitats may be considered ideal model systems for the study of ecological processes affecting species diversity in natural communities (Srivastava, 2006), from community assembly rules (Céréghino et al., 2011; Dézerald et al., 2014) to the relationships between diversity and ecosystem functioning (Srivastava & Bell, 2009; Romero & Srivastava, 2010), since each phytotelmata can be considered as a unique small habitat with well-defined frontiers (Schulz et al., 2012), naturally replicated in the environment and composed by taxonomically diverse fauna with multiple trophic levels (Armbruster et al., 2002).

Several species occupying phytotelmata are endemic, dominated by aquatic insect larvae which emerge from bromeliad tanks as terrestrial winged adults (Romero & Srivastava, 2010). Rainfall water accumulated in bromeliad tanks throughout the year, together with leaf litter and other organic detritus, provide nutrients and spatial refuge to the associated community (Armbruster et al., 2002; Torreias & Ferreira-Kepler, 2011).

In this way, communities inhabiting bromeliad tanks may be affected by several factors, such as resource availability and predation within those environments, geographical distance among plants and habitat conditions (Montero et al., 2010). Habitat conditions are directly affected by plant development, since different ontogenetic

phases (i. e. vegetative growth, flowering, and fruiting) leads to structural and physiological changes throughout bromeliad growth (Cavallero et al., 2009).

Flowering events are accompanied by structural modifications in the three-dimensional architecture of bromeliad leaf rosette, which fold back their leaves allowing pollinators a better access to the inflorescence (Romero & Vasconcellos-Neto, 2005b). Those modifications affect various characteristics of those microhabitats, such as the amount of water and organic matter accumulated and evapotranspiration rates (Zotz & Thomas, 1999). Therefore, bromeliads become less suitable to some of the associated organisms (i.e. predators: spiders - Romero & Vasconcellos-Neto, 2005a), consequently altering community structure (Srivastava, 2006; Gonçalves-Souza, et al., 2010, 2011).

In addition, flowering events enhances insect visitation, which are pollinators or feed on floral nectar (Frank & Lounibos, 2009). The presence of floral stimuli produced by the plants (floral volatiles) reach long distances attracting pollinators (Reisenman et al., 2010) increasing dispersal rates and colonization among plants (Kneitel & Miller, 2003). During the flowering phase, these stimuli (i. e. floral volatiles and nectar) are critical for insects to choose suitable oviposition sites, leading to higher rates of oviposition in the plants (Reisenman et al., 2010) and decreasing the influence of spatial distance on the structure of the aquatic larvae associated to phytotelmata (Paradise et al., 2008).

Beta diversity (Whittaker, 1960; 1972) can be defined as the variation in species composition among sampling units within a region (Anderson et al., 2006; Hill et al., 2017). Several factors such as the habitat structure, degree of isolation, and the dispersal capacity of the organisms may affect beta diversity (Gering & Crist, 2002). In bromeliads, habitat structure influences the available niche space and offers a wide range of essential elements for the animals, such as reproduction, shelter, and foraging sites (Romero & Vasconcellos-Neto, 2005a; Romero, 2006). Although the three-dimensional vegetation structure is recognized for altering the patterns of beta diversity, how this influence occurs remains poorly understood (Zellweger et al., 2017). Dispersal among habitats may affect species composition and diversity in different manners, at both local and regional scales (Kneitel & Miller, 2003). High dispersal rates assure a constant input of new colonizers in new areas

(Winegardner et al., 2012; Heino et al., 2015), leading to the homogenization of community structure at a local scale, and consequently, to a decrease in beta diversity (Cadotte & Fukami, 2005). On the other hand, low dispersal rates prevent species to reach all habitats, even the ones suitable for their development (Winegardner et al., 2012; Heino et al., 2015), increasing beta diversity.

Considering that plant architecture, the presence of predators and resources (local factors) and geographical distance (regional factors) may affect the community structure of aquatic insect larvae in bromeliads, we expect that composition, β -diversity and the relative importance of local and regional factors would be different between vegetative growth and flowering phases. We tested the hypotheses that I) insect larvae composition is different between vegetative growth and flowering phases; II) β -diversity (dissimilarity) is lower during flowering, since this event increases dispersal of insects among plants and consequently enhances oviposition, leading to more homogeneous larvae communities; III) during flowering, local factors would be more important for the community structuring of aquatic insect larvae, since dispersal rates would be sufficient to allow an environmental control based on niche differentiation, while in the vegetative growth phase regional factors would be more influential, considering that dispersal limitation would result in spatially structured communities within the bromeliad phytotelmata.

2. Methods

2.1. Study area

The study area is located in the Paran river basin, between the mouths of Paranapanema and Baia rivers. Sampling was performed at the left bank of the Paran river (Porto Rico, PR, Brazil - 2245'53.5"S 5315'27.2"W and 2243'11.5"S 5310'46"W; Figure 1). The region is characterized by the asymmetry of both sides of the valley, with an elevated left bank marked by rocky walls and sparse flooded areas (Souza Filho & Stevaux, 2004). These rocky walls provide a suitable habitat for the development of several epiphytic plants, such as the bromeliads.

Vegetation of the Upper Paran river basin is inserted in the Atlantic Forest biome in fragments of semideciduous forests forming strings of riparian vegetation near the border of the Paran river (Campos & Souza, 1997; Souza & Kita, 2002). Precipitation varies from 1400 to 1600 mm/year (maximum rainfall during summer), relative annual

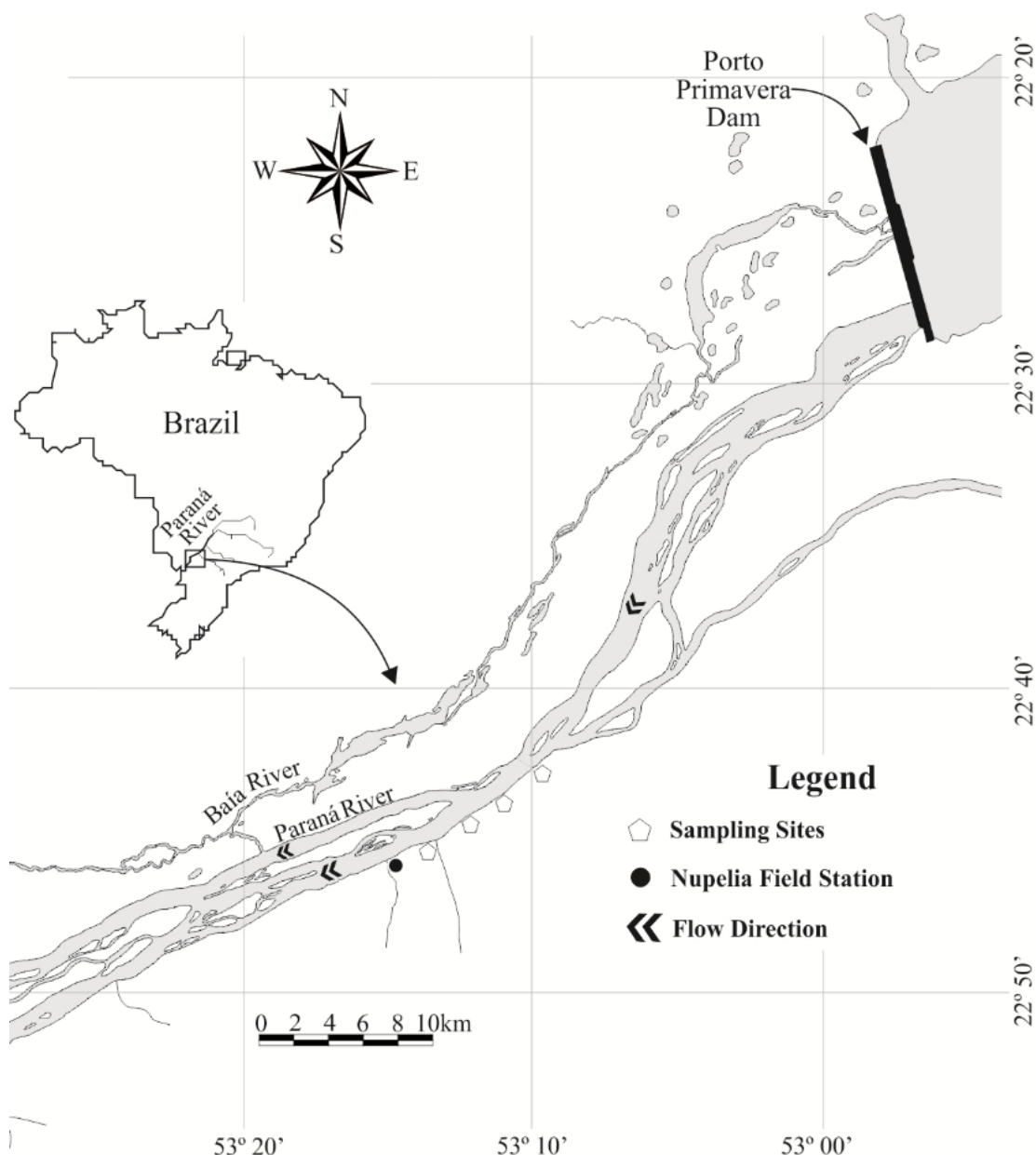


Figure 1. Map showing the sampling sites at the left bank of the Paraná River.

humidity is approximately 70% and the average temperature is 24 °C (IBGE, 1990; IAPAR, 2000).

2.2. Sampling

Aechmea distichantha Lem. (Bromeliaceae) was chosen because of the high density of this plant in the region. This facultative epiphytic bromeliad is widely distributed in South America, occurring from the sea level to 2,400 m altitude (Smith & Downs, 1979). According to Reitz (1983), this Bromeliaceae is 40-100 cm height with few leaves (15 to 25) which grow in a rosette, forming water-collecting cisterns. The foliage has margins covered with thorns, with an acute ending. Water

volume contained in the bromeliad tanks are on average 200 cm³. Flowering usually occurs between June and September, a period in which the plant exhibits a densely flowered inflorescence (70 to 330 flowers), lasting for 20 to 30 days (Srok & Varassin, 2011).

We performed six samplings in 2010, three during the first semester - vegetative growth phase - and three during the second semester - flowering phase. In each sampling, we took 12 plants along the rocky walls with similar location distribution, with a total of 72 bromeliads studied. For each plant, geographical coordinates were taken. Using these data, a distance matrix was constructed, considering

the distance (meters) from each plant in relation to the others (Spatial component). Measurements were taken using Google Earth.

Plants were manually removed from the rocky walls, wrapped in plastic bags and taken to Nupelia/University of Maringá Field Station, where the following measurements of the morphometric parameters were taken: height and width of the plant, perimeter, and height of the bromeliad tank and leaf number. Assuming that bromeliads approximated a geometric shape of a cone, we calculated the plant total volume (V_{plant}) and bromeliad tank total volume (V_{tank}) as cone volume, according to Armbruster et al. (2002) (Equation 1):

$$V = 1/3\pi r^2 h \quad (1)$$

where to calculate the total volume of the plant (V_{plant}), the radius of the plant (r_{plant}) was obtained by dividing plant width by two, and h_{plant} is the height from the base to the top of the central leaf. To calculate bromeliad tank total volume (V_{tank}), bromeliad tank height (h_{tank}) was measured from the plant base to the interlocking of the more internal leaves. Bromeliad tank radius (r_{tank}) was calculated using the perimeter (plant perimeter/2 \times π) (Figure 2).

Leaf number in each plant was considered a proxy of its complexity, since each leaf axil constitutes a discrete water body, compartmentalizing the internal space inside the bromeliad (Armbruster et al., 2002). Water contained within each plant was carefully removed and inspected for macroinvertebrates (including aquatic insect larvae, spiders, ants,

among others). Water volume from each bromeliad was further measured with graduated cylinder.

Sampling of the associated bromeliad fauna followed the protocol described by Armbruster et al. (2002): leaves were cut near the base of the plant, removed, individually checked for more macroinvertebrates and then washed with distilled water inside a white tray. Associated fauna was fixed with 70% alcohol. Insects were sorted, counted and identified to larval and adult morphospecies in the zoology laboratory at Maringá State University. Diagnostic features used for assigning morphospecies were wing venation, structure of mouth parts, chaetotaxy, antennal segmentation and structure, tarsal structure and overall body form, according to Armbruster et al. (2002). The classification of insect morphospecies into each order was based on Borror et al. (1989). Although the identification to morphospecies is common in studies on macroinvertebrate fauna associated with phytotelmata, there are some problems related to its use. For example, the adult and larvae of the same species are usually classified as different morphospecies. However, these different development stages may have different ecological niche, which justifies the identification of different development stages as different morphospecies to better comprehend the functional role of these organisms within phytotelmata (Armbruster et al., 2002; Araújo et al., 2007; Jabiol et al., 2009; Montero et al., 2010).

Spiders (predators) were counted and identified at the family level in the Arachnology laboratory of

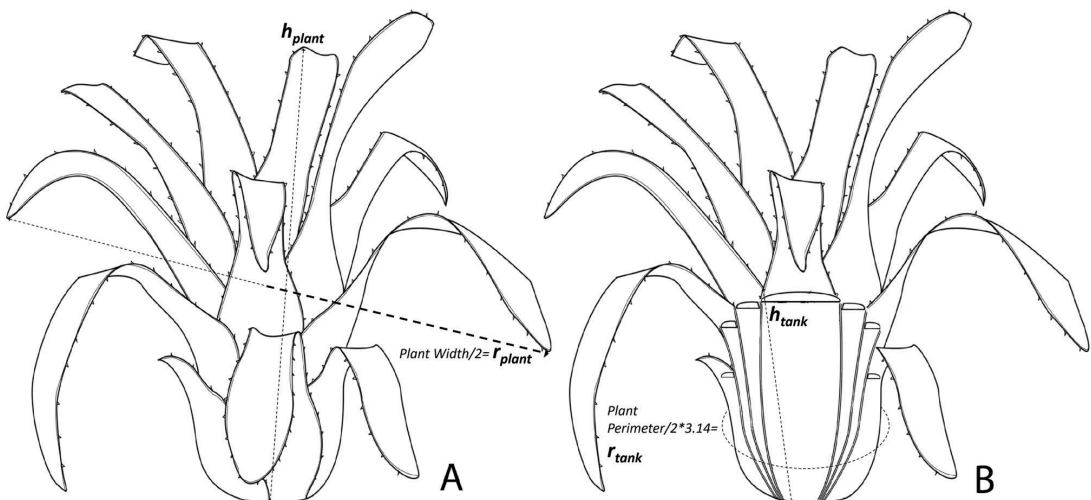


Figure 2. Morphometric parameters measured in the plants (A) and bromeliad tank (B). Dashed lines represent plant measures used in our study.

Museu Paraense Emilio Goeldi (Belém, PA). Spiders were identified to morphospecies and identification was primarily based on the shape of adult female reproductive organs - epigyne. When spider families were composed only by juveniles, we considered those families to be composed of at least one taxon, and this criterion was used in all statistical analyses. Based on ecological characteristics of each family, spiders were grouped in “web weavers” and “hunters”.

To estimate ciliate density, water samples from each plant were analysed *in vivo* using an optic microscope (for more details, see Buosi et al., 2015).

2.3. Study system

Spiders and ants are among the most commonly arthropods found foraging on Bromeliaceae leaves (Montero et al., 2010; Hénaut et al., 2014) and may play an important role in structuring phytotelmata communities (Romero & Srivastava, 2010; Céréghino et al., 2011). Considered as predators in these microhabitats (Romero & Srivastava, 2010; Gonçalves et al., 2017), spiders and ants may affect communities associated with bromeliad leaves and tanks, through the direct reduction in the abundance of prey (consumptive effects), or by altering the behaviour and use of these habitats by these organisms (non-consumptive effects) (Werner & Peacor, 2003; Hill & Weissburg, 2013).

Associations between spiders and bromeliads are common in Neotropical regions (Romero, 2006) and the presence of these predators on the plants may repel pollinators, reducing bromeliad fitness (Gonçalves-Souza et al., 2008). The presence of spiders in bromeliads could lead to a reduction in invertebrate diversity and abundance, changing the composition of the associated fauna, from a community dominated by aquatic insect larvae to a community dominated by other aquatic invertebrates (i.e. ostracods and oligochaete; Romero & Srivastava, 2010). Therefore, the presence of these predators may affect not only aquatic organisms with complex life cycles (i. e. insects), but also those spending their whole life inside phytotelmata (Romero & Srivastava, 2010).

Several ant species use bromeliads as shelter and sites for nest construction, and the interaction between the ants and these plants may be species-specific (Céréghino et al., 2011; Leroy et al., 2012; Talaga et al., 2015; Gonçalves et al., 2017). Although the presence of these organisms in bromeliads may result in some advantage for these plants, such as protection against herbivory or

seed dispersal (Leroy et al., 2012), the predatory behaviour that ants exert on potential pollinators and colonizers may alter the structure of the associated aquatic and terrestrial communities (Gonçalves et al., 2017).

Ciliates have a key role in the flow of energy and matter within bromeliad phytotelmata, being more efficient than metazoans in the nutrient remineralization in the water column (Carrias et al., 2001). In this environment, ciliates can be considered as a proxy of organic matter (Carrias et al., 2001; Petermann et al., 2015b), due to their efficiency in decomposing detritus (Kneitel & Miller, 2002, 2003). Moreover, ciliates are in the intermediate trophic levels of phytotelmata food webs, being grazed by aquatic insect larvae (Kneitel & Miller, 2002).

Considering the importance of the several factors above mentioned for the community structuring of aquatic insect larvae in phytotelmata, spider and ant abundances (predators), ciliate density (resources) and plant morphometric parameters (plant height, plant total volume, leaf number, bromeliad tank height, bromeliad tank total volume and water volume) were considered as local factors (Environmental component) in this study.

2.4. Data analysis

To observe the effect of flowering events on the composition of insect larvae associated with *A. distichantha* (hypothesis I), we performed non-metric multi-dimensional scaling (NMDS; Clarke, 1993) using Jaccard distance (presence/absence data). NMDS rearranges objects in a space with a particular number of dimensions, reproducing the observed distances. Distortion of the two-dimension resolution is expressed by *S* value (stress): the nearer this value is to zero, the better is the adjustment among original distances and the configuration obtained by the analysis (Legendre & Legendre, 1998). Analysis of similarities (ANOSIM; Clarke, 1993) with 9,999 permutations was performed to verify statistical differences in the composition patterns observed in NMDS. ANOSIM is a procedure of non-parametric permutations based on the ranking of the dissimilarity matrix generated by NMDS, comparing the degree of separation within and between sample groups using *R* statistics. If *R*=0 there are no differences in community composition between groups, while *R*=1 indicates complete distinction between communities (Quinn & Keough, 2002). These analyses were performed

using PAST 2.17 (Paleontological Statistics Software Package for Education and Data Analysis - Hammer et al., 2001).

Indicator morphospecies of vegetative growth and flowering phases were identified using Indicator Species Analysis (IndVal; Dufrêne & Legendre, 1997). This analysis combines relative abundance and frequency occurrence of each species, generating an indicator value varying between zero and one. The value is near one when all individuals of a species occur in all plants in a certain phenological phase. Significance ($P < 0.05$) was tested by 1,000 random permutations.

Beta diversity of insect larvae associated with phytotelmata was measured through permutation test of multivariate homogeneity of groups dispersions (PERMIDISP; Anderson et al., 2006). The biological matrix with presence/absence data of insect larvae was transformed into a distance matrix based on Jaccard distance. In this analysis, beta diversity is measured as the mean dissimilarity of a sample in relation to the group centroid (Anderson et al., 2006), in our case, flowering and vegetative growth phases of *A. distichantha* (hypothesis II).

The relative importance of local and regional factors in the diversity of aquatic insect larvae associated with *A. distichantha* (hypothesis III) was evaluated through Partial Redundancy Analysis (pRDA; Legendre & Legendre, 1998; Legendre et al., 2005). RDA is an extension of multiple regression analysis, with a dependent variable (insect larvae composition) and different explanatory matrices: local factors (environmental component using morphometric parameters, ciliate density and the abundances of ants, hunter spiders and web weaver spiders) and regional factors (spatial component using geographical distances). A Principal Coordinates of Neighbour Matrices (PCNM - Borcard & Legendre, 2002; Borcard et al., 2004; Diniz-Filho & Bini, 2005; Dray et al., 2006; Griffith & Peres-Neto, 2006) was applied to a distance matrix (meters) and scores were used as explanatory variables of the spatial component. Abundance data was Hellinger transformed (Legendre & Gallagher, 2001). The significance of the components was tested through 9,999 Monte Carlo randomizations (Borcard et al., 1992) and R^2 adjusted values were considered. IndVal analysis, PERMIDISP, PCNM and pRDA were performed in R software (R Development Core Team, 2013).

3. Results

Considering both phenological phases, we collected 3,481 insect larvae associated with *A. distichantha*, distributed in four orders and 16 morphospecies (Table 1). Diptera and Lepidoptera were the most representative orders, with seven morphospecies each. Coleoptera and Neuroptera showed only one morphospecies. Out of all the morphospecies registered, we verified that nine were common to both phenological phases (vegetative growth and flowering). Flowering showed the highest number of morphospecies ($n=13$), out of which four were exclusive. During vegetative growth, three morphospecies were exclusive, with a total of 12 morphospecies in this phase.

Regarding the contribution of each order to total abundance, Coleoptera was the most representative, with around 96% total abundance registered (3,349 individuals), consisting of the Scirtidae family (vegetative growth: 1,446 ind.; flowering: 1,903 ind.). Highest values of abundance of the aquatic larvae community were registered in the flowering phase, with 1,959 individuals (56% of abundance). In the vegetative growth phase, 1,522 individuals were collected (44% of abundance).

Table 1. Morphospecies occurrence of aquatic insect larvae found in *A. distichantha* of the rocky walls at the left bank of the Paraná River (PR, Brazil) during both phenological phases.

Order	Morphospecies	Phenological Phase	
		Vegetative Growth	Flowering
Coleoptera			
	Scirtidae	+	+
Diptera			
	Diptera01	+	+
	Diptera02	+	+
	Diptera03	+	+
	Diptera04	+	+
	Diptera05	+	+
	Diptera06	+	
	Diptera07	+	
Lepidoptera			
	Lepidoptera01	+	+
	Lepidoptera02	+	+
	Lepidoptera03	+	+
	Lepidoptera04	+	
	Lepidoptera05		+
	Lepidoptera06		+
	Lepidoptera07		+
Neuroptera			
	Neuroptera01		+

NMDS results indicated a separation of morphospecies of aquatic insect larvae between vegetative growth and flowering phases (Figure 3; NMDS stress: 0.25). ANOSIM results confirmed significant differences in community composition between the phenological phases ($R=0.12$; $p<0.001$).

According to IndVal results, only three morphospecies were considered discriminant and only in the vegetative growth phase: Diptera01 (IndVal: 0.49; $p<0.01$), Diptera02 (IndVal: 0.31 $p=0.01$) and Diptera05 (IndVal: 0.22; $p=0.01$).

PERMDISP results showed no significant differences in beta diversity of insect larvae between the phenological phases (Figure 4), indicating that the variation in taxa composition is similar between flowering and vegetative growth phases.

pRDA revealed that different components affected insect larvae diversity in phytotelmata during vegetative growth and flowering phases (Table 2). As expected, local factors (environmental

component) were more important for larvae community during flowering (19%), with the contribution of plant morphometric parameters (plant height and total volume) together with ciliate density as the main responsible for community structuring in this phenological phase (Table 3), whereas regional factors (spatial component) were not significant.

During vegetative growth, abundance of web weaver spiders and bromeliad tank total volume (environmental component), together with PCNMs 6 and 9 (spatial component) were selected to explain community variation (Table 3). However, only the spatial component (regional factors; 6%) was significant and explained community structuring of aquatic insect larvae during this phenological phase (Table 2).

4. Discussion

Throughout the study, we found 3,481 aquatic insect larvae in the phytotelmata, distributed in four orders and 16 morphospecies. Species composition was significant different between vegetative growth and flowering (hypothesis I), whereas beta diversity was not significant different between the two phenological phases (hypothesis II). The relative contribution of local and regional

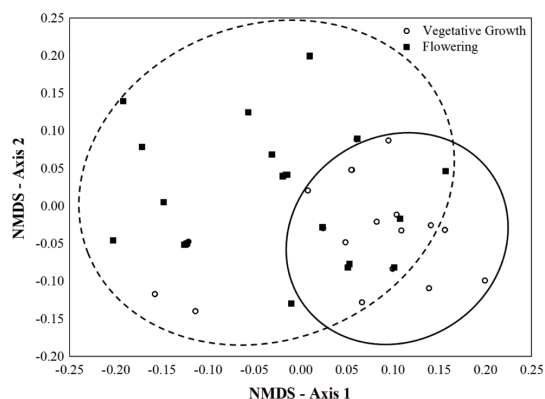


Figure 3. Non-metric multi-dimensional scaling (NMDS) ordination for phenological phases (vegetative growth and flowering), based on composition of insect larvae associated with *A. distichantha* in rocky walls.

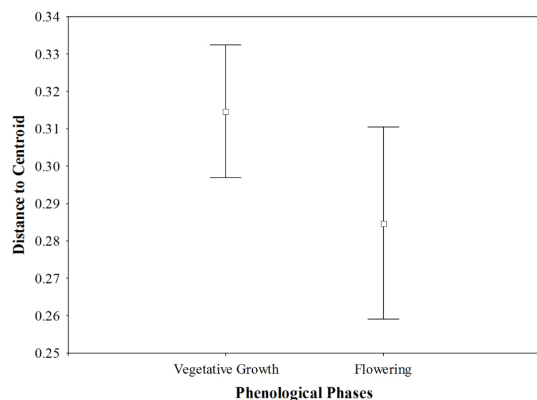


Figure 4. Distances to centroid in vegetative growth and flowering phases.

Table 2. Variance partitioning showing the relative contribution of [a] pure spatial component, [b] shared component, and [c] pure environmental component. Residuals: non explained variation. X1= Spatial model and X2= Environmental model.

	Phenological phases			
	Vegetative Growth		Flowering	
	R² Adj	P	R² Adj	P
[a] = X1 X2	0.06197	0.031	0.00233	0.384
[b]	0.03792		-0.02366	
[c] = X2 X1	0.04186	0.066	0.19755	0.004
Residual	0.85824		0.82378	

Significance $P<0.05$; R^2 Adj, coefficient of determination, statistically significant results shown in bold font.

Table 3. Environmental and spatial variables selected in pRDA analysis during each phenological phase (vegetative growth and flowering) of *A. distichantha*.

Phenological Phase	Environmental Variables	Spatial Variables
Vegetative Growth	bromeliad tank total volume, "web weaver" spiders	PCNM 6, 9
Flowering	plant height, plant total volume, ciliate density	PCNM 6, 9

Statistically significant results shown in bold font.

factors in structuring the insect larvae community (hypothesis III) was different between vegetative growth and flowering phases. During flowering, local factors predominated, whereas during vegetative growth, regional factors were more important.

Significant differences regarding insect larvae composition between vegetative growth and flowering phases may be explained by the differences in plant architecture and insect dispersal among bromeliads in the two phenological phases. During flowering, the structure of leaf rosette in bromeliads is modified to offer better access to pollinators (Romero & Vasconcellos-Neto, 2005a, b). These modifications alter several plant morphological parameters (Zotz & Thomas, 1999), influencing the attributes of the insect larvae community and their predators in phytotelmata (Armbruster et al., 2002). In addition, insect dispersal enhanced by pollination during flowering, which leads to an increase in oviposition rates (Reisenman et al., 2010), counteracts the limited dispersal during vegetative growth, constituting another factor responsible for differences in species composition between phases. However, those factors do not seem to influence beta diversity patterns which, contrary to expected, were not different between the phenological phases.

Although phytotelmata may harbour many of the main aquatic insect orders, Diptera is considered the most common, with over 20 families present (Williams, 2006). Indeed, we found that three Diptera morphospecies were discriminant in the vegetative growth phase. Several morphological and behavioural traits of this insect order suggest long term association with phytotelmata (Williams, 2006). Diptera larvae are very abundant in bromeliads (Araújo et al., 2007), pitcher plants (Baiser et al., 2011) and tree-holes (Blakely et al., 2012), and are considered the main predators in the phytotelmata of several bromeliad species, where they exert a great influence on microorganisms (Walker et al., 2010; Baiser et al., 2011). Although several studies show that zygoptera larvae are the main aquatic predators within phytotelmata (Petermann et al., 2015a; Romero et al., 2016), in the bromeliads used in our study no larval forms of these organisms were observed. Paradise (2000) suggest that alterations in pH due to the decomposition of organic matter by Scirtidae larvae (Coleoptera) within phytotelmata may lead to a reduction in the mortality and an increase in the abundance of Diptera larvae in this habitat. In fact,

we found very high abundances of Scirtidae larvae in *A. distichantha* phytotelmata.

Insect larvae community structuring was influenced by different factors in the two phenological phases. During flowering, ciliate density (proxy of resource availability) and the morphometric parameters plant height and plant total volume were the most important local factors. Plant parameters are directly related to plant architecture and habitat complexity - the main predictor of arthropod distribution in vegetation (Gonçalves-Souza et al., 2011). According to Lawton (1983), seasonal changes may considerably affect plant architecture. In bromeliads, flowering events cause profound alterations in the three-dimensional leaf rosette structure, which opens to guarantee better access of pollinators to plant inflorescence (Romero & Vasconcellos-Neto, 2005a, b). These modifications alter habitat conditions, such as water availability, resource capture (Zotz & Thomas, 1999) and the presence of predators (Romero & Vasconcellos-Neto, 2005b).

By actively participating in nutrient cycling and bacterial population control in aquatic environments, ciliates are considered important components within food webs in those ecosystems (Sherr & Sherr, 2002; Durán-Ramírez et al., 2015). Carrias et al. (2001) point out that these organisms are key components to phytotelmata metabolism, since they are more efficient than metazoan in nutrient remineralization, that are released in the water column of this microhabitat and may be absorbed by the plants during development. This efficiency in organic matter degradation leads to an increase in the abundance of those microorganisms with the large amount of detritus input in phytotelmata (Kneitel & Miller, 2002; 2003), thus they are considered as a proxy of organic matter in this habitat (Carrias et al., 2001; Petermann et al., 2015b). Furthermore, since they are in the intermediate level of food webs in those ecosystems, ciliates serve as a resource to insect larvae in phytotelmata (Kneitel & Miller, 2002).

Therefore, insect larvae community structuring during flowering may be explained by the alterations in plant structure in response to the flowering event itself, which changes the physical characteristics of the plants, besides enhancing the capture of organic matter by the bromeliad, increasing ciliate abundance. Thus, the combined effects of those factors lead to modifications in the community of insect larvae in this phenological phase.

In contrast to the flowering phase, aquatic insect larvae during the vegetative growth phase were structured by regional factors (spatial component). Spatial distribution of plants in the environment may affect the community attributes of associated arthropods (i. e. species richness: Gonçalves-Souza et al., 2011; and abundance: Hanski, 1982), since this distribution directly influences plant exposure to organisms, consequently enhancing colonization (Neuvonen & Niemelä, 1983) and dispersal of associated fauna.

According to Kneitel & Miller (2003), dispersal among local communities may have a variety of effects on species diversity and composition. For instance, an increase in dispersal rates - as we expected during flowering - may lead to an increase in the richness and abundance of the organisms, while decreasing variation among communities in a certain area (Kneitel & Miller, 2003). On the other hand, during vegetative growth, reduced dispersal may lead to an increase in the importance of the spatial component in community structuring.

Differences in dispersal rates between vegetative growth and flowering phases could be explained by the increase in resource availability for adult insects, due to bromeliad inflorescence. During the reproductive phase, plants produce floral stimuli (floral volatiles - Reisenman et al., 2010) and offer rewards to pollinators (Nicholls & Altieri, 2013), generally nectar or pollen (Labandeira, 2011). Concerning the interactions between bromeliads and insects, other resources may be offered, such as resin and other material for nests, shelter, foraging, mating and oviposition sites (Kevan & Baker, 1983; Labandeira, 2011). Accordingly, this wide range of resources during flowering becomes a decisive factor for insect larvae fitness, in part due to the choice of oviposition sites by adult insects - active dispersers of this community (Basset & Novotny, 1999; Gonçalves-Souza et al., 2014). During vegetative growth, the absence of those rewards results in a decline of insect movement among plants and oviposition. Thus, we suggest that insect behaviour as a function of bromeliad flowering determines aquatic larvae community structuring in both phenological phases. However, since our samplings were performed in distinct seasons, further experimental studies are necessary to disentangle the effects of seasonal fluctuation and the phenological phase of plants on invertebrate fauna.

5. Conclusion

The hypothesis that community composition of aquatic insect larvae is different between the phenological phases was corroborated. Variation in this attribute could be attributed to differences in bromeliad architecture, insect dispersal and higher rates of oviposition among plants in the phenological phases, which is likely the result of rewards offered by the plants during the flowering phase. However, those factors may not seem to affect beta diversity patterns, which were not different between vegetative growth and flowering phases, contrary to expected in hypothesis II. Finally, our third hypothesis regarding the relative importance of local and regional factors in structuring the community of aquatic insect larvae was corroborated. During flowering, local factors were more important in community structuring, whereas during vegetative growth, regional factors predominated in explaining community variation.

Acknowledgements

The authors would like to thank the post-graduate course in Ecology of Continental Aquatic Habitats (PEA, Maringá State University) and NUPELIA for financial support, material, equipment and facilities during the samplings. This study was supported by the Brazilian Research Council (CNPq) and the Brazilian Federal Agency for the Support and Evaluation of Graduate Education (CAPES).

References

- ANDERSON, M.J., ELLINGSEN, K.E. and MCARDLE, B.H. Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 2006, 9(6), 683-693. PMID:16706913. <http://dx.doi.org/10.1111/j.1461-0248.2006.00926.x>.
- ARAÚJO, V.A., MELO, S.K., ARAÚJO, A.P.A., GOMES, M.L.M. and CARNEIRO, M.A.A. Relationship between invertebrate fauna and bromeliad size. *Brazilian Journal of Microbiology*, 2007, 67(4), 611-617. PMID:18278311.
- ARMBRUSTER, P., HUTCHINSON, R.A. and COTGREAVE, P. Factors influencing community structure in a South American tank bromeliad fauna. *Oikos*, 2002, 96(2), 225-234. <http://dx.doi.org/10.1034/j.1600-0706.2002.960204.x>.
- BAISER, B., ARDESHIRI, R.S. and ELLISON, A.M. Species richness and trophic diversity increase decomposition in a co-evolved food Web. *PLoS One*, 2011, 6(5), e20672. PMID:21673992. <http://dx.doi.org/10.1371/journal.pone.0020672>.

- BASSET, Y. and NOVOTNY, V. Species richness of insect herbivore communities on *Ficus* in Papua New Guinea. *Biological Journal of the Linnean Society*, 1999, 67(4), 477-499. <http://dx.doi.org/10.1111/j.1095-8312.1999.tb01943.x>.
- BLAKELY, T.J., HARDING, J.S. and DIDHAM, R.K. Distinctive aquatic assemblages in water-filled tree holes: a novel component of freshwater biodiversity in New Zealand temperate rainforests. *Insect Conservation and Diversity*, 2012, 5(3), 202-212. <http://dx.doi.org/10.1111/j.1752-4598.2011.00155.x>.
- BORCARD, D. and LEGENDRE, P. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 2002, 153(1-2), 51-68. [http://dx.doi.org/10.1016/S0304-3800\(01\)00501-4](http://dx.doi.org/10.1016/S0304-3800(01)00501-4).
- BORCARD, D., LEGENDRE, P. and DRAPEAU, P. Partialling out the spatial component of ecological variation. *Ecology*, 1992, 73(3), 1045-1055. <http://dx.doi.org/10.2307/1940179>.
- BORCARD, D., LEGENDRE, P., AVOIS-JACQUET, C. and TUOMISTO, H. Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, 2004, 85(7), 1826-1832. <http://dx.doi.org/10.1890/03-3111>.
- BORROR, D.J., TRIPLEHORN, C.A. and JOHNSON, N.F. *An introduction to the study of insects*. New York: Harcourt Brace Jobanovich Colleg Publishers, 1989.
- BROUARD, O., CÉRÉGHINO, R., CORBARA, B., LEROY, C., PELOZUELO, L., DEJEAN, A. and CARRIAS, J.-F. Understorey environments influence functional diversity in tank-bromeliad ecosystems. *Freshwater Biology*, 2012, 57(4), 815-823. <http://dx.doi.org/10.1111/j.1365-2427.2012.02749.x>.
- BUOSI, P.R.B., CABRAL, A.F., UTZ, L.R.P., VIEIRA, L.C.G. and VELHO, L.F.M. Effects of Seasonality and Dispersal on the Ciliate Community Inhabiting Bromeliad Phytotelmata in Riparian Vegetation of a Large Tropical River. *The Journal of Eukaryotic Microbiology*, 2015, 62(6), 737-749. PMID:25963550. <http://dx.doi.org/10.1111/jeu.12232>.
- CADOTTE, M.W. and FUKAMI, T. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. *Ecology Letters*, 2005, 8(5), 548-557. PMID:21352459. <http://dx.doi.org/10.1111/j.1461-0248.2005.00750.x>.
- CALEY, M.J. and SCHLUTER, D. The relationship between local and regional diversity. *Ecology*, 1997, 78(1), 70-80. [http://dx.doi.org/10.1890/0012-9658\(1997\)078\[0070:TRBLAR\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(1997)078[0070:TRBLAR]2.0.CO;2).
- CAMPOS, J.B. and SOUZA, M.C. Vegetação. In: A.E.A.M. VAZZOLER, A.A. AGOSTINHO and N.S. HAHN, eds. *A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos*. Maringá: Eduem, 1997, pp. 331-342.
- CARRIAS, J.F., CUSSAC, M.E. and CORBARA, B. A preliminary study of freshwater protozoa in tank bromeliads. *Journal of Tropical Ecology*, 2001, 17(4), 611-617. <http://dx.doi.org/10.1017/S0266467401001456>.
- CAVALLERO, L., LÓPEZ, D. and BARBERIS, I.M. Morphological variation of *Aechmea distichantha* (Bromeliaceae) in a Chaco forest: habitat and size-related effects. *Plant Biology*, 2009, 11(3), 379-391. PMID:19470109. <http://dx.doi.org/10.1111/j.1438-8677.2008.00123.x>.
- CÉRÉGHINO, R., LEROY, C., CARRIAS, J.F., PELOZUELO, L., SÉGURA, C., BOSCH, C., DEJEAN, A. and CORBARA, B. Ant-plant mutualisms promote functional diversity in phytotelm communities. *Functional Ecology*, 2011, 25(5), 954-963. <http://dx.doi.org/10.1111/j.1365-2435.2011.01863.x>.
- CLARKE, K.R. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 1993, 18(1), 117-143. <http://dx.doi.org/10.1111/j.1442-9993.1993.tb00438.x>.
- COTTENIE, K., MICHELS, E., NUYTEN, N. and DE MEESTER, L. Zooplankton Metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology*, 2003, 84(4), 991-1000. [http://dx.doi.org/10.1890/0012-9658\(2003\)084\[0991:ZMSRVL\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2003)084[0991:ZMSRVL]2.0.CO;2).
- DÉZERALD, O., TALAGA, S., LEROY, C., CARRIAS, J.F., CORBARA, B., DEJEAN, A. and CÉRÉGHINO, R. Environmental determinants of macroinvertebrate diversity in small water bodies: insights from tank-bromeliads. *Hydrobiologia*, 2014, 723(1), 77-86. <http://dx.doi.org/10.1007/s10750-013-1464-2>.
- DINIZ-FILHO, J.A.F. and BINI, L.M. Modelling geographical patterns in species richness using eigenvector based spatial filters. *Global Ecology and Biogeography*, 2005, 14(2), 177-185. <http://dx.doi.org/10.1111/j.1466-822X.2005.00147.x>.
- DRAY, S., LEGENDRE, P. and PERES-NETO, P.R. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, 2006, 196(3-4), 483-493. <http://dx.doi.org/10.1016/j.ecolmodel.2006.02.015>.
- DUFRENE, M. and LEGENDRE, P. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 1997, 67(3), 345-366.
- DURÁN-RAMÍREZ, C.A., GARCÍA-FRANCO, J.G., FOISSNER, W. and MAYÉN-ESTRADA, R. Free-living ciliates from epiphytic tank bromeliads in Mexico. *European Journal of Protistology*, 2015, 51(1), 15-33. PMID:25497463. <http://dx.doi.org/10.1016/j.ejop.2014.09.002>.

- FRANK, J.H. and LOUNIBOS, L.P. Insects and allies associated with bromeliads: a review. *Terrestrial Arthropod Reviews*, 2009, 1(2), 125-153. PMID:20209047. <http://dx.doi.org/10.1163/187498308X414742>.
- GERING, J.C. and CRIST, T.O. The alpha-beta-regional relationship: providing new insights into local–regional patterns of species richness and scale dependence of diversity components. *Ecology Letters*, 2002, 5(3), 433-444. <http://dx.doi.org/10.1046/j.1461-0248.2002.00335.x>.
- GONÇALVES, A.Z., SRIVASTAVA, D.S., OLIVEIRA, P.S. and ROMERO, G.Q. Effects of predatory ants within and across ecosystems in bromeliad food webs. *Journal of Animal Ecology*, 2017, 86(4), 790-799. PMID:28342283. <http://dx.doi.org/10.1111/1365-2656.12671>.
- GONÇALVES-SOUZA, T., ALMEIDA-NETO, M. and ROMERO, G.Q. Bromeliad architectural complexity and vertical distribution predict spider abundance and richness. *Austral Ecology*, 2011, 36(4), 476-484. <http://dx.doi.org/10.1111/j.1442-9993.2010.02177.x>.
- GONÇALVES-SOUZA, T., BRESCOVIT, A.D., ROSSA-FERES, D.C. and ROMERO, G.Q. Bromeliads as biodiversity amplifiers and habitat segregation of spider communities in a Neotropical rainforest. *The Journal of Arachnology*, 2010, 38(2), 270-279. <http://dx.doi.org/10.1636/P09-58.1>.
- GONÇALVES-SOUZA, T., OMENA, P.M., SOUZA, J.C. and ROMERO, G.Q. Trait-mediated effects on flowers: artificial spiders deceive pollinators and decrease plant fitness. *Ecology*, 2008, 89(9), 2407-2413. PMID:18831161. <http://dx.doi.org/10.1890/07-1881.1>.
- GONÇALVES-SOUZA, T., ROMERO, G.Q. and COTTENIE, K. Metacommunity versus Biogeography: A Case Study of Two Groups of Neotropical Vegetation-Dwelling Arthropods. *PLoS One*, 2014, 9(12), e115137. PMID:25549332. <http://dx.doi.org/10.1371/journal.pone.0115137>.
- GRIFFITH, D.A. and PERES-NETO, P.R. 2006 Spatial Modeling in Ecology: The Flexibility of Eigenfunction Spatial Analyses. *Ecology*, 2006, 87(10), 2603-2613. PMID:17089668. [http://dx.doi.org/10.1890/0012-9658\(2006\)87\[2603:SMIETF\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87[2603:SMIETF]2.0.CO;2).
- HAMMER, Ø., HARPER, D.A.T. and RYAN, P.D. *PAST: paleontological statistics software package for education and data analysis* [software]. Palaeontological Association, 2001. 9 p. [viewed 4 July 2016]. Available from: http://palaeo-electronica.org/2001_1/past/issue1_01.htm
- HANSKI, I. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, 1982, 38(2), 210-221. <http://dx.doi.org/10.2307/3544021>.
- HEINO, J., MELO, A.S. and BINI, L.M. Reconceptualising the beta diversity–environmental heterogeneity relationship in running water systems. *Freshwater Biology*, 2015, 60(2), 223-235. <http://dx.doi.org/10.1111/fwb.12502>.
- HÉNAUT, Y., CORBARA, B., PÉLOZUELO, L., AZÉMAR, F., CÉRÉGHINO, R., HERAULT, B. and DEJEAN, A. A tank bromeliad favors spider presence in a neotropical inundated forest. *PLoS One*, 2014, 9(12), e114592. PMID:25494055. <http://dx.doi.org/10.1371/journal.pone.0114592>.
- HILL, J.M. and WEISSBURG, M.J. Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments. *Oecologia*, 2013, 172(1), 79-91. PMID:23250631. <http://dx.doi.org/10.1007/s00442-012-2488-4>.
- HILL, M.J., HEINO, J., THORNHILL, I., RYVES, D.B. and WOOD, P.J. Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. *Oikos*, 2017. In press. <http://dx.doi.org/10.1111/oik.04266>.
- HILLEBRAND, H. and BLECKNER, T. Regional and local impact on species diversity - from pattern to processes. *Oecologia*, 2002, 132(4), 479-491. PMID:28547633. <http://dx.doi.org/10.1007/s00442-002-0988-3>.
- INSTITUTO AGRONÔMICO DO PARANÁ – IAPAR. *Cartas climáticas do Estado do Paraná*. Londrina: IAPAR, 2000.
- INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA – IBGE. *Geografia do Brasil: região sul*. Rio de Janeiro: IBGE, 1990. vol. 2.
- JABIOL, J., CORBARA, B., DEJEAN, A. and CÉRÉGHINO, R. Structure of aquatic insect communities in tank-bromeliads in a East-Amazonian rainforest in French Guiana. *Forest Ecology and Management*, 2009, 257(1), 351-360. <http://dx.doi.org/10.1016/j.foreco.2008.09.010>.
- KEVAN, P.G. and BAKER, H.G. Insects as flower visitors and pollinators. *Annual Review of Entomology*, 1983, 28(1), 407-453. <http://dx.doi.org/10.1146/annurev.en.28.010183.002203>.
- KNEITEL, J.M. and MILLER, T.E. Resource and top predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. *Ecology*, 2002, 83(3), 680-688. [http://dx.doi.org/10.1890/0012-9658\(2002\)083\[0680:RATPRI\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2002)083[0680:RATPRI]2.0.CO;2).
- KNEITEL, J.M. and MILLER, T.E. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *American Naturalist*, 2003, 162(2), 165-171. PMID:12858261. <http://dx.doi.org/10.1086/376585>.
- LABANDEIRA, C.C. Pollination mutualisms by insects before the evolution of flowers. In J. TREFIL, ed. *McGraw Hill Encyclopedia of Science & Technology*.

- New York: McGraw-Hill Education, 2011, pp. 250-252.
- LAWTON, J.H. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, 1983, 28(1), 23-39. <http://dx.doi.org/10.1146/annurev.en.28.010183.000323>.
- LEGENDRE, P. and GALLAGHER, E.D. Ecologically meaningful transformations for ordination of species data. *Oecologia*, 2001, 129(2), 271-280. PMID:28547606. <http://dx.doi.org/10.1007/s004420100716>.
- LEGENDRE, P. and LEGENDRE, L. *Numerical ecology*. Amsterdam: Elsevier, 1998.
- LEGENDRE, P., BORCARD, D. and PERES-NETO, P.R. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, 2005, 75(4), 435-450. <http://dx.doi.org/10.1890/05-0549>.
- LEROY, C., CORBARA, B., PÉLOZUELO, L., CARRIAS, J.-F., DEJEAN, A. and CÉRÉGHINO, R. Ant species identity mediates reproductive traits and allocation in an ant-garden bromeliad. *Annals of Botany*, 2012, 109(1), 145-152. PMID:21984729. <http://dx.doi.org/10.1093/aob/mcr253>.
- MONTERO, G., FERUGLIO, C. and BARBERIS, I.M. The phytotelmata and foliage macrofauna assemblages of a bromeliad species in different habitats and seasons. *Insect Conservation and Diversity*, 2010, 3(2), 92-102. <http://dx.doi.org/10.1111/j.1752-4598.2009.00077.x>.
- NEUVONEN, S. and NIEMELÄ, P. Species richness and faunal similarity of arboreal insect herbivores. *Oikos*, 1983, 40(3), 452-459. <http://dx.doi.org/10.2307/3544318>.
- NICHOLLS, C.I. and ALTIERI, M.A. Plant biodiversity enhances bees and other insect pollinators in agroecosystems: a review. *Agronomy for Sustainable Development*, 2013, 33(2), 257-274. <http://dx.doi.org/10.1007/s13593-012-0092-y>.
- OBERDORFF, T., HUGUENY, B., COMPIN, A. and BELKESSAM, D. Non-interactive fish communities in the coastal streams of Northwestern France. *Journal of Animal Ecology*, 1998, 67(3), 472-484. <http://dx.doi.org/10.1046/j.1365-2656.1998.00211.x>.
- PARADISE, C.J. Effects of pH and resources on a processing chain interaction in simulated treeholes. *Journal of Animal Ecology*, 2000, 69(4), 651-658. <http://dx.doi.org/10.1046/j.1365-2656.2000.00423.x>.
- PARADISE, C.J., BLUE, J.D., BURKHART, J.Q., GOLDBERG, J., HARSHAW, L., HAWKINS, K.D., KEGAN, B., KRENTZ, T., SMITH, L. and VILLALPANDO, S. Local and regional factors influence the structure of treehole metacommunities. *BMC Ecology*, 2008, 8(1), 22. PMID:19099587. <http://dx.doi.org/10.1186/1472-6785-8-22>.
- PETERMANN, J.S., FARJALLA, V.F., JOCQUE, M., KRATINA, P., MACDONALD, A.A.M., MARINO, N.A., DE OMENA, P.M., PICCOLI, G.C., RICHARDSON, B.A., RICHARDSON, M.J., ROMERO, G.Q., VIDELA, M. and SRIVASTAVA, D.S. Dominant predators mediate the impact of habitat size on trophic structure in bromeliad invertebrate communities. *Ecology*, 2015a, 96(2), 428-439. PMID:26240864. <http://dx.doi.org/10.1890/14-0304.1>.
- PETERMANN, J.S., KRATINA, P., MARINO, N.A.C., MACDONALD, A.A.M. and SRIVASTAVA, D.S. Resources alter the structure and increase stochasticity in bromeliad microfauna communities. *PLoS One*, 2015b, 10(3), e0118952. PMID:25775464. <http://dx.doi.org/10.1371/journal.pone.0118952>.
- QUINN, G. and KEOUGH, M. *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press, 2002.
- R DEVELOPMENT CORE TEAM. *R: a language and environment for statistical computing* [software]. Vienna: R Foundation for Statistical Computing, 2013 [viewed 4 July 2016]. Available from: <http://www.r-project.org>
- REISENMAN, C.E., RIFFELL, J.A., BERNAYS, E.A. and HILDEBRAND, J.G. Antagonistic effects of floral scent in an insect-plant interaction. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 2010, 277(1692), 2371-2379. PMID:20335210.
- REITZ, R. Bromeliáceas e a malária-bromélia endêmica. In: R. REITZ, ed. *Flora Ilustrada Catarinense*. Itajaí: BROM, 1983. 559 p.
- ROMERO, G.Q. and SRIVASTAVA, D.S. Food-web composition affects cross-ecosystem interactions and subsidies. *Journal of Animal Ecology*, 2010, 79(5), 1122-1131. PMID:20584097. <http://dx.doi.org/10.1111/j.1365-2656.2010.01716.x>.
- ROMERO, G.Q. and VASCONCELLOS-NETO, J. Spatial distribution and microhabitat preference of *Psecas chapoda* (Peckham & Peckham) (Araneae, Salticidae). *The Journal of Arachnology*, 2005b, 33(1), 124-134. <http://dx.doi.org/10.1636/M03-9>.
- ROMERO, G.Q. and VASCONCELLOS-NETO, J. The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae). *Journal of Animal Ecology*, 2005a, 74(1), 12-21. <http://dx.doi.org/10.1111/j.1365-2656.2004.00893.x>.
- ROMERO, G.Q. Geographic range, habitats, and host plants of bromeliad-living jumping spiders (Salticidae). *Biotropica*, 2006, 38(4), 522-530. <http://dx.doi.org/10.1111/j.1744-7429.2006.00173.x>.
- ROMERO, G.Q., PICCOLI, G.C., DE OMENA, P.M. and GONÇALVES-SOUZA, T. Food web structure shaped by habitat size and climate across

- a latitudinal gradient. *Ecology*, 2016, 97(10), 2705-2715. PMID:27859108. <http://dx.doi.org/10.1002/ecy.1496>.
- SCHULZ, G., SIQUEIRA, T., STEFAN, G. and ROQUE, F.O. Passive and active dispersers respond similarly to environmental and spatial processes: an example from metacommunity dynamics of tree hole invertebrates. *Fundamental and Applied Limnology*, 2012, 181(4), 315-326. <http://dx.doi.org/10.1127/1863-9135/2012/0365>.
- SCROK, G.J. and VARASSIN, I.G. Reproductive biology and pollination of *Aechmea distichantha* Lem. (Bromeliaceae). *Acta Botanica Brasílica*, 2011, 25(3), 571-576. <http://dx.doi.org/10.1590/S0102-33062011000300009>.
- SHERR, E.B. and SHERR, B.F. Significance of predation by protists in aquatic microbial food webs. *Antonie van Leeuwenhoek Journal of Microbiology*, 2002, 81(1-4), 293-308. PMID:12448728. <http://dx.doi.org/10.1023/A:1020591307260>.
- SMITH, L.B. and DOWNS, R.J. Bromelioideae (Bromeliaceae). *Flora Neotropica*, 1979, 14(3), 1493-2142.
- SOUZA FILHO, E.E. and STEVAUX, J.C. Geomorphology of the Paraná River Floodplain in the reach between the Paranapanema and Ivaí Rivers. In: A.A. AGOSTINHO, L. RODRIGUES, L.C. GOMES, S.M. THOMAZ and L.E. MIRANDA, eds. *Structure and functioning of the Paraná River and its floodplain*. Maringá: Eduem, 2004, pp. 9-13.
- SOUZA, M.C. and KITA, K.K. Formações vegetais ripárias da planície alagável do alto rio Paraná e Mato Grosso do Sul, Brasil. In: A.A. AGOSTINHO, S.M. THOMAZ, L. RODRIGUES and L.C. GOMES, eds. *A planície de inundação do alto rio Paraná: Site 6*. Maringá: Nupélia/PELD/CNPq, 2002, pp. 197-201.
- SRIVASTAVA, D. and BELL, T. Reducing horizontal and vertical diversity in a food web triggers extinctions and impacts functions. *Ecology Letters*, 2009, 12(10), 1016-1028. PMID:19702635. <http://dx.doi.org/10.1111/j.1461-0248.2009.01357.x>.
- SRIVASTAVA, D. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, 1999, 68(1), 1-16. <http://dx.doi.org/10.1046/j.1365-2656.1999.00266.x>.
- SRIVASTAVA, D. Habitat structure, trophic structure and ecosystem function: interactive effects in a bromeliad-insect community. *Oecologia*, 2006, 149(3), 493-504. PMID:16896779. <http://dx.doi.org/10.1007/s00442-006-0467-3>.
- SRIVASTAVA, D.S., KOLASA, J., BENGTSSON, J., GONZALEZ, A., LAWLER, S.P., MILLER, T.E., MUNGUÍA, P., ROMANUK, T., SCHNEIDER, D.C. and TRZCINSKI, M.K. Are natural microcosms useful model systems for ecology? *Trends in Ecology & Evolution*, 2004, 19(7), 379-384. PMID:16701289. <http://dx.doi.org/10.1016/j.tree.2004.04.010>.
- TALAGA, S., DÉZERARD, O., CARTERON, A., PETITCLERC, F., LEROY, C., CÉRÉGHINO, R. and DEJEAN, A. Tank bromeliads as natural microcosms: a facultative association with ants influences the aquatic invertebrate community structure. *Comptes Rendus Biologies*, 2015, 338(10), 696-700. PMID:26302833. <http://dx.doi.org/10.1016/j.crvi.2015.05.006>.
- TORREIAS, S.R.S. and FERREIRA-KEPPLER, R.L. Macroinvertebrates inhabiting the tank leaf terrestrial and epiphyte bromeliads at Reserva Adolpho Ducke, Manaus, Amazonas. *Brazilian Archives of Biology and Technology*, 2011, 54(6), 1193-1202. <http://dx.doi.org/10.1590/S1516-89132011000600015>.
- WALKER, E.D., KAUFMAN, M.G. and MERRITT, R.W. An acute trophic cascade among microorganisms in the tree hole ecosystem following removal of omnivorous mosquito larvae. *Community Ecology*, 2010, 11(2), 171-178. PMID:25342946. <http://dx.doi.org/10.1556/ComEc.11.2010.2.5>.
- WERNER, E. and PEACOR, S. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 2003, 84(5), 1083-1100. [http://dx.doi.org/10.1890/0012-9658\(2003\)084\[1083:AROTI\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2003)084[1083:AROTI]2.0.CO;2).
- WHITTAKER, R.H. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 1960, 30(3), 279-338. <http://dx.doi.org/10.2307/1943563>.
- WHITTAKER, R.H. Evolution and measurement of species diversity. *Taxon*, 1972, 21(2/3), 213-251. <http://dx.doi.org/10.2307/1218190>.
- WILLIAMS, D.D. *The biology of temporary waters*. Oxford: Oxford University Press, 2006.
- WINEGARDNER, A.K., JONES, B.K., NG, I.S.Y., SIQUEIRA, T. and COTTENIE, K. The terminology of metacommunity ecology. *Trends in Ecology & Evolution*, 2012, 27(5), 253-254. PMID:22325446. <http://dx.doi.org/10.1016/j.tree.2012.01.007>.
- ZELLWEGER, F., ROTH, T., BUGMANN, H. and BOLLMANN, K. Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure. *Global Ecology and Biogeography*, 2017, 26(8), 898-906. <http://dx.doi.org/10.1111/geb.12598>.
- ZOTZ, G. and THOMAS, V. How much water is in the tank? Model calculations for two epiphytic bromeliads. *Annals of Botany*, 1999, 83(2), 183-192. <http://dx.doi.org/10.1006/anbo.1998.0809>.

Received: 26 March 2017

Accepted: 16 October 2017