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Bromeliad habitat regulates the richness of associated terrestrial and aquatic fauna

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Abstract Bromeliads harbour a great diversity of fauna species. The epiphytic habit of bromeliads is subject to higher temperatures and higher incidence of light than is the epigeic habit, so we expected individuals of the *Vriesea neoglutinosa* species to differ in terms of the composition, richness and abundance of their fauna associated with different bromeliad habits. We carried out a study in a *restinga* area on Marambaia Island, Brazil. We collected 32 bromeliads, of which 16 were epigeic and 16 were epiphytic, and found a total of 1125 individual animals of 88 morphospecies. Arthropods stood out in the sample, among which 68.2% were insects. Aquatic fauna was richer in epigeic bromeliads, and terrestrial fauna was richer in epiphytic bromeliads. As expected, species composition was different for aquatic and terrestrial fauna. The heterogeneity of the *restinga* environment and differences in the development stages of the fauna may be factors that influence its composition. Both bromeliad habits sustain fauna with several trophic guilds that compose a complex food web and depend on the bromeliad environment. As different habits lead to different fauna types, both epigeic and epiphytic bromeliads play a role in the maintenance of local biodiversity and are important for macrofauna conservation in *restingas*.

Key words: arthropods, food web, insects, species diversity, tank bromeliads.

INTRODUCTION

The Bromeliaceae family is endemic to the Neotropics and has over 3000 species, of which 803 occur in the Atlantic Forest (Martinelli *et al.* 2008). Many bromeliads have leaves arranged in imbricated whorls and an inverted cone shape (Benzing 1990). These characteristics provide them with a complex and heterogeneous architecture, allowing water accumulation in a central tank, or in leaf sheaths, in many species. Bromeliads provide a habitat to the local aquatic fauna, which is referred to as phytotelmata (Rocha *et al.* 2004; Jabiol *et al.* 2009). Local fauna can live their whole life or part of it in the phytotelmata. Terrestrial species can live on leaf surfaces or on litter, just as visitors (Frank & Lounibos 2009; Montero *et al.* 2010). Hence, bromeliads stand out in the environments where they occur, as they are key to biodiversity maintenance and enhancement (Rocha *et al.* 2000; DaRocha *et al.* 2016).

Arthropods comprise the predominant group of bromeliad-dwelling animals (Rocha *et al.* 2004; Frank *et al.* 2004; Zanin & Tusset 2007; Ospina-Bautista *et al.* 2008; Santos *et al.* 2009; Richardson & Richardson 2013). Other groups recorded include platyhelminthes, nematodes, mollusks, annelids and rotifers (Mestre *et al.* 2001; Frank *et al.* 2004; Zanin & Tusset 2007; Santos *et al.* 2009; Farjalla *et al.* 2012), in addition to vertebrates, such as anurans and lizards (Rocha *et al.* 2004). These groups include aquatic and terrestrial species. Several bromeliad-dwelling animals, usually aquatic species, are at immature development stages, which show the importance of bromeliads as nursery sites (Rocha *et al.* 2004; Santos *et al.* 2009). Moreover, detritivores compose the highest percentage of bromeliad-colonising taxa among aquatic species (Madeira *et al.* 1995; Santos *et al.* 2009; Montero *et al.* 2010), and this is probably due to detritus being the main

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nutrient resource in the bromeliad food chain (Brouard *et al.* 2012; Dézerald *et al.* 2014). Therefore, a larger amount of detritus offers more resources, as it increases the chances of more abundant and richer fauna (Richardson *et al.* 2000; Stuntz *et al.* 2002; González *et al.* 2014). Predators are usually also present in larger numbers in bigger plants (Armbruster *et al.* 2002; Srivastava *et al.* 2008; Brouard *et al.* 2012; Marino *et al.* 2012).

Physical differences among bromeliads, such as size, number of leaves and water volume, can result in differences in bromeliad fauna richness and abundance. Larger bromeliads favour the establishment of richer and more abundant fauna, both aquatic and terrestrial, than do smaller bromeliads (Richardson 1999; Armbruster *et al.* 2002; Araújo *et al.* 2008; Marino *et al.* 2012; Jocque & Field 2014). A larger number of leaves in a bromeliad promotes a larger and heterogeneous number of micro-habitats for fauna development, increasing fauna richness overall (Armbruster *et al.* 2002). Water volume is an important factor for aquatic bromeliad fauna by mediating processes such as sensitivity to drought, in which predators exhibit strong vulnerability, thus influencing the entire trophic web (Amundrud & Srivastava 2016). A larger amount of water favours increased richness and abundance of the associated aquatic fauna (Armbruster *et al.* 2002; Jabiol *et al.* 2009; Sodré *et al.* 2010; Dézerald *et al.* 2014; Cardoso *et al.* 2015).

The community structure of the bromeliad fauna is also affected by differences in habitat. Bromeliads under shaded habitats show greater richness than those under sunny habitats (Lopez & Rios 2001). The phytotelma community is also affected by vertical stratification, which provides variations in *taxon* occurrence and abundance (Zanin & Tusset 2007). Although some studies do not find a direct relation of bromeliad height from the soil to its associated fauna richness and abundance (Richardson *et al.* 2000; Mestre *et al.* 2001), there may be an indirect relation due to physical differences between epiphytes and epigeics, such as diameter (Melnychuk & Srivastava 2002). Epiphytes reach sites with greater light incidence within forests, but they are exposed to higher temperatures, higher water scarcity and lower nutrient input than epigeic bromeliads (Zotz & Hietz 2001). The variation in nutrient input and morphology of epigeic and epiphytic bromeliads are factors that favour the development of different fauna, with different composition, richness and abundance (Armbruster *et al.* 2002; Ospina-Bautista *et al.* 2008).

The different habits together promote the development of a great diversity of organisms (Rocha *et al.* 2004); however, how this affects the structure of the community is not yet known. Thus, the objective of the present study was to identify differences in the composition, richness and abundance of animals associated with bromeliads of the *Vriesea neoglutinosa* Mez species of epigeic and epiphytic habits. Our hypothesis is that individual *V. neoglutinosa* of epiphytic habit harbour fauna with a different, less rich and less abundant composition than do bromeliads of epigeic habit. We suggest that the lower water accumulation capacity, lower nutrient input, smaller size and smaller number of leaves of epiphytic bromeliads can explain the differences found between them and terrestrial bromeliads.

METHODS

Study area

The present study was carried out on Marambaia Island (23°02′S; 43°35′W), located on Sepetiba Bay, between the western region of Rio de Janeiro and part of the municipalities of Itaguaí and Mangaratiba, Brazil. Marambaia Island is a large portion of land of approximately 6 km that belongs to Restinga da Marambaia and is connected to the continent by a narrow sand strip. The northern portion faces the Sepetiba Bay, and the Southern portion is bathed by the Atlantic Ocean (Conde *et al.* 2005).

According to the Köppen system, the local climate is the Aw – Tropical Rainy Climate, with average temperatures above 20°C. The coldest months, between June and August, have an average minimum temperature around 18°C. December to March is the warmest period, with an average maximum temperature of approximately 30°C. The annual average rainfall is above 1000 mm. Rain is abundant mainly from November to March, when rainfall indices are above 100 mm (Mattos 2005).

The study was carried out on Praia Grande, a *restinga* beach facing the west of Marambaia Island. *Restingas* are plant formations on coastal sandy plains, and they harbour a diversity of species adapted to such environment with high salinity and temperatures. The shrubby–arboreal vegetation has a canopy reaching 13 m in height for the tallest trees as well as stretches covered with grasses. The vegetation height increases with the distance from the beach. In the shrubby–arboreal stretches, the understory is mainly dominated by bromeliad species, such as *Neoregelia cruenta* (Graham), *V. neoglutinosa* and *Bromelia antiacantha* Bertol., as well as by Cactaceae species. *V. neoglutinosa* occurs in an area far from the beach in some vegetation clusters formed by shrubby–arboreal species, with a dense leaf litter layer, which are separated from each other by bare soil or by soil covered with grasses. As these clusters are small and consist of few trees, the soil is not fully shaded, and there is intense light.

Study species

The *V. neoglutinosa* species is endemic to Brazil. It occurs in *restingas* and can take epigeic or epiphytic habits (Forzza *et al.* 2013). In *restingas*, bromeliads are distributed in sites with greater chances of germination and seedling establishment, such as inside clusters (Zotz 1997; Mantovani & Iglesias 2002). However, bromeliad seedlings are highly susceptible to mortality, and establishment success in *restinga* areas depends on high investment in asexual reproduction (Mantovani & Iglesias 2002).

Sampling

We collected individual *V. neoglutinosa* from different clusters and phorophytes in September 2012, totalling 16 epigeic and 16 epiphytic bromeliads (Fig. 1). Epigeic bromeliads were selected from different clusters to avoid clones, since there is a high rate of asexual reproduction in one same cluster (Mantovani & Iglesias 2002). The epiphytic bromeliads were collected 1.5–3 m above the ground from trunks and branches of different trees. We consider the collection of 16 bromeliads from each habit to be a sufficient sample with the least impact on the environment.

Fig. 1. Epigeic and epyphitic individuals of *Vriesea neoglutinosa* Mez. sampled in Praia Grande *restinga* on Marambaia Island, Brazil.

We placed the bromeliads in individual plastic bags with approximately 200 mL of alcohol 70° in order to kill the animals present in the central or lateral tanks. We dissected the bromeliads leaf by leaf and collected the associated fauna by using tweezers and brushes and placed them in flasks containing alcohol 70° for each bromeliad. For each individual *V. neoglutinosa*, we measured the bromeliad height, the largest diameter and the smallest diameter using a measuring tape (1-mm accuracy) and counted the number of leaves. Height was the measurement of the bromeliad base to the apex of the highest leaf. The largest diameter and the smallest diameter were measured from the apex of the outermost leaf to its opposite side on the largest and smallest circumferences, respectively. We used these measurements in the cone volume formula to calculate bromeliad volume:

$$V_{\mathrm{br}} = \frac{\pi * r_{\mathrm{ma}} * r_{\mathrm{me}} * h}{3}$$

where r_{ma} is the largest radius (the largest diameter divided by 2); r_{me} is the smallest radius (the smallest diameter divided by 2); and h is the bromeliad height.

We separated the fauna collected from each bromeliad into morphospecies and counted the number of individuals (*N*) under a stereoscopic microscope. The morphospecies were identified at the most specific taxonomic level whenever possible. The identification keys found in Costa *et al.* (2006), Segura *et al.* (2011) and Rafael *et al.* (2012) were used for identification of orders, in general. Taxonomy experts identified the families, genera and species of more abundant groups.

Statistical analysis

All analyses were performed using the R software, version 3.5.2 (R Development Core Team, 2015). We calculated the alpha, beta and gamma diversity of the fauna associated with epigeic and epiphytic bromeliads. Alpha diversity represents the average diversity of the fauna associated with each individual *V. neoglutinosa* for each habit (epiphyte and epigeic). Gamma diversity represents the diversity of the whole landscape; that is, all samples pooled. Beta diversity is a measure of the change in diversity across samples, and it is calculated using the formulas proposed by Baselga (2010) in which the Sorensen coefficient was the measure of total beta diversity, the Simpson coefficient was the measure of species turnover between samples, and the nestedness coefficient was the measure of nesting resulting from differences in species richness. We used the 'betapart' package in R (Baselga *et al.* 2020).

We tested differences between epigeic and epiphytic bromeliads using t-tests. We utilised habit as a predictor variable, and diameter, height, volume and number of leaves as response variables. Since the aquatic and terrestrial fauna represent distinct ecosystems, we classified the fauna morphospecies as terrestrial or aquatic, according to

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their observed habit, as confirmed by their identification or their morphological characteristics. We used generalised linear models (GLM) to test the differences in richness and abundance of the associated fauna. We analysed total, terrestrial and aquatic morphospecies separately. We utilised Poisson distribution in models with richness as a dependent variable and quasi-Poisson distribution (after residual analysis) in models with abundance as a dependent variable. Bromeliad habit, volume and number of leaves and their interactions were the predictor variables. The models were summarised by the ANOVA function using the chi-squared test. In the abundance models, we excluded an outlier value, which proved to previously influence the data strongly. We calculated pseudo-R^2 values with pseudo-R^2 maximum likelihood for models with Poisson distribution using the pR^2 function of the 'pscl' package in R (Jackman 2020).

In order to determine the fauna species associated with epigeic and epiphytic individuals, an indicator species was analysed using the multipatt function of the 'indicspecies' package in R (De Cáceres *et al.* 2010) for terrestrial and aquatic fauna separately. We assessed the heterogeneity of the composition of the fauna associated with epigeic and epiphytic bromeliads using model-based analysis of multivariate data by the 'mvabund' package in R (Wang *et al.* 2020). We analysed composition for total fauna and terrestrial and aquatic fauna separately. Our prediction was that the fauna would have different compositions of epigeic and epiphytic bromeliads.

RESULTS

We recorded a total of 1125 individuals of 88 morphospecies in 32 bromeliads (Table 1). Epigeic bromeliads showed 49 morphospecies (16 aquatic and 33 terrestrial morphospecies), and epiphytic bromeliads had 57 morphospecies (11 aquatic and 46 terrestrial morphospecies). In the epigeic bromeliads, total beta diversity was 0.88 (βSIM = 0.83; βNES = 0.05), and in the epiphytic bromeliads, it was 0.91 (βSIM = 0.88; βNES = 0.03). Epigeic bromeliads had a larger diameter, greater height and volume than did the epiphytes. They did not differ in number of leaves. The total species richness was not influenced by bromeliad habit ($P = 0.80$; pseudo-$R^2 = 0.20$; Fig. 2a) and nor by physical variables. However, bromeliad habit influenced species richness of aquatic morphospecies ($P < 0.001$; pseudo-$R^2 = 0.36$; Fig. 2b) and terrestrial morphospecies ($P = 0.009$; pseudo-$R^2 = 0.36$; Fig. 2 c). Total macrofauna abundance was influenced by bromeliad volume ($P = 0.016$; Fig. 3a), and so was that of terrestrial morphospecies ($P = 0.003$; Fig. 3b). Aquatic morphospecies abundance, however, was not influenced by bromeliad habit and nor by physical variables.

The morphospecies belong to the Arthropoda, Mollusca and Chordata phyla. The groups showing the largest number of morphospecies were Insecta (68.18%; $S = 60$) and Arachnida (20.45%; $S = 18$; Fig. 4a). Numerically, the Insecta class also predominated, corresponding to 92.27% of the individuals ($N = 1038$). Orders Coleoptera (41.68%; $N = 469$), Blattodea (22.13%; $N = 249$), Diptera (10.31%; $N = 116$) and Hymenoptera (9.24%; $N = 104$) were the most abundant (Fig. 4b). A larva of the Coleoptera order, Scirtidae family, showed an abundance of 410 individuals, whereas in the Blattaria order, *Pinaconota bifasciata* (Saussure, 1862) showed an abundance of 185 individuals. All the other morphospecies showed abundance of fewer than 70 individuals. For aquatic morphospecies, indicator species results showed the Coleoptera family Hydrophilidae as an epigeic habit indicator (IndVal = 0.658; $P = 0.03$). As to terrestrial morphospecies, indicator species results showed Blattaria *Nyctibora sericea* Burmeister, 1838 as an epiphytic habit indicator (IndVal = 0.639; $P = 0.03$). The model-based analysis of multivariate data showed bromeliad habit affecting the composition of aquatic ($P = 0.001$), terrestrial ($P = 0.001$) and aquatic and terrestrial macrofauna together ($P = 0.001$).

DISCUSSION

The inventory of the macrofauna associated with terrestrial and epiphytic *V. neoglutinosa* bromeliads in the *restinga* of Praia Grande showed similar richness to that in other studies (Richardson 1999; Stuntz *et al.* 2002; Frank *et al.* 2004). Considering the number of species and individuals recorded in such studies, bromeliads act to maintain local biodiversity and can also amplify it (Cruz-Angón *et al.* 2009; Gonçalves-Souza *et al.* 2010; Angelini & Silliman 2014). In *restinga* areas, where environmental physicochemical conditions are restrictive and selective to different groups of organisms (Franco *et al.* 1984), the role played by *V. neoglutinosa* and other bromeliads in the study area is important in maintaining biodiversity.

Aquatic and terrestrial morphospecies richness was influenced by bromeliad habit. Epigeic bromeliads showed more aquatic species, while epiphytic bromeliads supported more terrestrial species. The fauna associated with epiphytic plants is subject to more restrictive environmental conditions, such as higher light incidence, higher temperature, water scarcity and lower nutrient input, than is the fauna associated with epigeic plants (Lopez & Rios 2001; Zotz & Hietz 2001). These characteristics should be more restrictive for aquatic fauna. Epigeic bromeliads have a larger size, which allows more water and detritus accumulation and harbouring richer aquatic fauna. Light incidence, as occurs in epiphytes, is related to decreased input of allochthonous material in the bromeliad tank (Farjalla *et al.* 2016), although

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Table 1. List of morphospecies associated with bromeliads of the *Vriesea neoglutinosa* species in Restinga da Marambaia by development stages (A = adult; N = nymph; L = larva; J = juvenile; F = female; M = male), bromeliad habit (Ep = epiphytic; T = epigeic), frequency (number of epigeic and epiphytic bromeliads with the morphospecies, respectively, when it occurred in both) and morphospecies habit

	Development stage	Bromeliad habit	Frequency	Habitat
Arthropoda				
Arachnida				
Acari				
Hydracarina	A	Ep	1	Aquatic
Indet	A	Ep	1	Terrestrial
Araneae				
Anyphaenidae – *Aysha borgmeyeri* (Mello-Leitão, 1926)	J/F/M	T/Ep	1/2	Terrestrial
Clubionidae – *Elaver* sp.	J	T	1	Terrestrial
Corinnidae – *Corinna* sp.	J	Ep	1	Terrestrial
Corinnidae – *Tupirinna* sp.	J	T	1	Terrestrial
Ctenidae – *Ctenus* sp.	J	Ep	1	Terrestrial
Ctenidae – *Phoneutria* sp.	J	T	1	Terrestrial
Eutichuridae – *Cheiracanthium inclusum* (Hentz, 1847)	J	Ep	2	Terrestrial
Linyphiidae – *Eurymorion* sp.	J	T	1	Terrestrial
Salticidae – *Breda bicruciata* (Mello-Leitão, 1943)	F	Ep	1	Terrestrial
Scytodidae – *Scytodes fusca* Walckenaer, 1837	J/F	Ep	3	Terrestrial
Selenopidae – *Selenops melanurus* Mello-Leitão, 1923	F	Ep	1	Terrestrial
Sparassidae – *Stasina americana* Simon, 1887	J	Ep	1	Terrestrial
Tetragnathidae – *Chrysometa* sp. n. aff. *minuta*	F	Ep	1	Terrestrial
Theridiidae – *Cryptachaea* sp.	J	Ep	1	Terrestrial
Theridiidae – *Faiditus* sp.	J	T	1	Terrestrial
Pseudoscorpiones	A	T/Ep	1/1	Terrestrial
Chilopoda				
Scolopocryptopidae	A	T/Ep	2/2	Terrestrial
Oryidae	A	Ep	1	Terrestrial
Diplopoda				
Rhinocricidae	A	T/Ep	2/4	Terrestrial
Polyxenidae	A	Ep	1	Terrestrial
Crustacea				
Decapoda				
Armasis cf. *angustipes*	A	T	1	Aquatic
Isopoda				
Oniscidae	A	T/Ep	3/4	Terrestrial
Insecta				
Blattaria				
Blaberidae – *Pinaconota bifasciata* (Saussure, 1862)	N/A	T/Ep	11/10	Terrestrial
Ectobiidae – *Lophoblatta* sp.	N/A	T/Ep	8/9	Terrestrial
Ectobiidae – *Nyctibora sericea* Burmeister, 1838	N/A	T/Ep	1/7	Terrestrial
Coleoptera				
Cerambycidae	L	Ep	3	Terrestrial
Chrysomelidae	A	Ep	1	Terrestrial
Curculionidae	A	T/Ep	2/1	Terrestrial
Curculionidae – Scolytinae	A	Ep	1	Terrestrial
Elateridae sp1	L	T	1	Terrestrial
Elateridae sp2	L	T	3	Terrestrial
Elateridae sp3	A	T	1	Terrestrial
Elateridae sp4	A	Ep	1	Terrestrial
Elateridae sp5	A	Ep	1	Terrestrial
Hydrophilidae	L	T/Ep	8/2	Aquatic
Nitidulidae	A	Ep	1	Aquatic
Scarabaeidae sp1	L	T	1	Terrestrial
Scarabaeidae sp2	A	T	1	Terrestrial
Scirtidae sp1	L	T/Ep	14/12	Aquatic
Scirtidae sp2	A	T/Ep	5/3	Aquatic
Staphylinidae	A	T	1	Terrestrial
Tenebrionidae – Alleculinae sp1	A	Ep	1	Terrestrial

Table 1. *Continued*

	Development stage	Bromeliad habit	Frequency	Habitat
Tenebrionidae – Alleculinae sp2	A	Ep	1	Terrestrial
Diptera				
Ceratopogonidae sp.	L	Ep	2	Aquatic
Chironomidae	L	T	1	Aquatic
Chironomidae – *Chironomus* sp.	L	T	1	Aquatic
Chironomidae – *Polypedilum*	A	T/Ep	1/1	Terrestrial
Chironomidae – *Polypedilum kaingangi* Pinho, Mendes & Andersen, 2013	L	T/Ep	12/6	Aquatic
Chironomidae – *Polypedilum marcondesi* Pinho & Mendes, 2010	L	T	1	Aquatic
Culicidae	A	Ep	1	Terrestrial
Empididae	L	T	1	Aquatic
Ephydridae sp1	L	T	4	Aquatic
Ephydridae sp2	L	T	1	Aquatic
Stratiomyidae	L	T	1	Aquatic
Tabanidae	L	Ep	1	Aquatic
Tipulidae sp1	L	T/Ep	10/4	Aquatic
Tipulidae sp2	P	Ep	1	Terrestrial
Hemiptera: Heteroptera	A	Ep	1	Terrestrial
Hymenoptera				
Camponotus sp1	A	T	1	Terrestrial
Camponotus sp2	A	Ep	1	Terrestrial
Cephalotes pusillus (Klug, 1824)	A	T	1	Terrestrial
Crematogaster sp.1	A/P/L	T	1	Terrestrial
Crematogaster sp.2	A	Ep	1	Terrestrial
Neoponera aff. *villosa* (Fabricius, 1804)	A	Ep	1	Terrestrial
Odontomachus hastatus (Fabricius, 1804)	A	Ep	1	Terrestrial
Pachycondyla striata Smith F., 1858	A	T	1	Terrestrial
Paratrechina sp.	A	T	1	Terrestrial
Pheidole sp1	A	T	1	Terrestrial
Pheidole sp2	A	T	1	Terrestrial
Pheidole sp3	A/P	Ep	3	Terrestrial
Isoptera				
Termitidae sp1	A	T/Ep	3/3	Terrestrial
Termitidae sp2	A	T/Ep	2/1	Terrestrial
Termitidae sp3	N	Ep	1	Terrestrial
Lepidoptera				
Lepidoptera sp1	P	Ep	1	Terrestrial
Lepidoptera sp2	P	T	1	Terrestrial
Mantodea: Thespidae	A	Ep	1	Terrestrial
Odonata				
Coenagrionidae	N	T/Ep	7/3	Aquatic
Pseudostigmatidae				
Orthoptera				
Gryllidae sp1	N	T/Ep	1/4	Terrestrial
Gryllidae sp2	A	Ep	1	Terrestrial
Trichoptera	L	T	4	Aquatic
Indeterminado: Indet sp1	L	Ep	2	Aquatic
Mollusca				
Gastropoda	A	T	2	Aquatic
Vertebrata				
Anura				
Rhinella ornata (Spix, 1824)	A	T	1	Terrestrial
Scinax cuspidatus (Lutz, 1925)	A	Ep	3	Terrestrial
Scinax sp.	A	Ep	2	Terrestrial

it maintains the same production of algae biomass, regardless of bromeliad exposure (Marino *et al.* 2011). The composition of the aquatic macrofauna is based on the detritus chain, and therefore, its richness is smaller among epiphytic individuals. *Restingas* are environments that are also subject to high

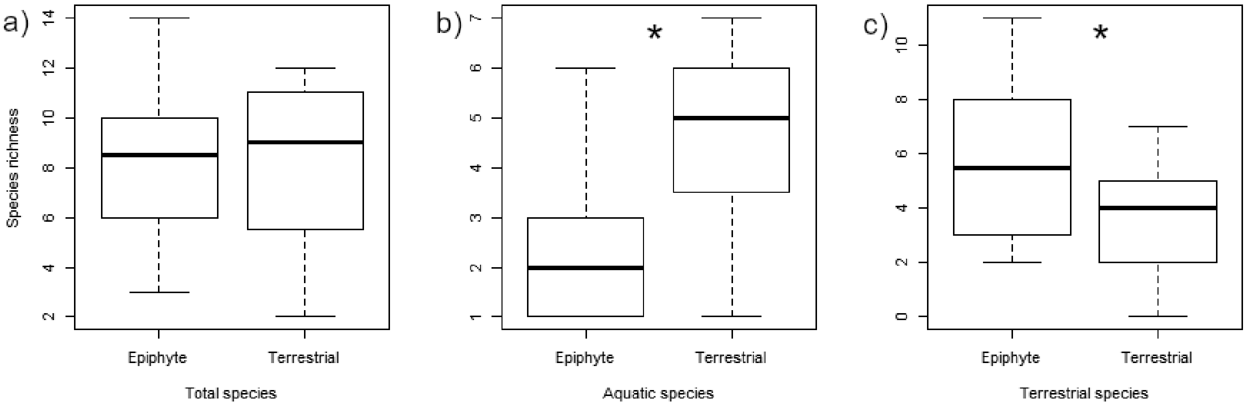

Fig. 2. Richness of total (a), aquatic (b) and terrestrial (c) morphospecies associated with epiphytic and epigeic bromeliads of *Vriesea neoglutinosa* Mez. The centre line marks the median. The lower and upper box parts mark the first and third quartiles. The lower and upper stems show the quartiles minus 1.5× the interquartile range (Q – 1.5IQR). Asterisks mark significant differences ($P < 0.05$).

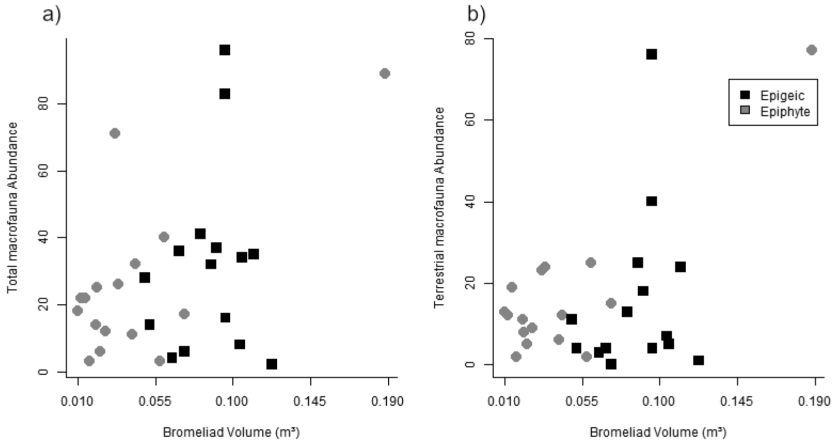

Fig. 3. Relationship between bromeliad volume and total macrofauna abundance (a) and terrestrial macrofauna abundance (b) for epigeic (dark square) and epiphyte bromeliads (grey circle) of the *Vriesea neoglutinosa* Mez species.

temperatures and water scarcity (Scarano 2002; Rocha *et al.* 2004; Cogliatti-Carvalho *et al.* 2010), which imposes restrictions to colonisation. For the terrestrial fauna, the restrictive characteristics imposed by epiphytes are not an additional hindrance. They can change their location if conditions become unfavourable. Besides, water accumulation capacity, even of a small amount, as in epiphytes, advances their use by terrestrial fauna, behaving as a refuge in *restingas* (Richardson & Richardson 2013; Hénaut *et al.* 2014).

Morphospecies abundance did not differ between bromeliad habits. However, bromeliad volume affected total abundance and terrestrial morphospecies abundance. Bromeliad volume was used as a proxy for water accumulation capacity. It was expected to influence aquatic species abundance more strongly. However, the volume had no influence on it. This can be explained by the amount of water being a limiting factor for terrestrial species, which must look for the resources that they need in the *restinga*. Or the increase in the available area *per se* leads to an increased number of individuals in the bromeliad (Armbruster *et al.* 2002). Another possibility is that the larger volume allows the contribution of more food resources (Marino *et al.* 2011; Farjalla *et al.* 2016) and, consequently, sustains a more complex trophic web. The absence of a direct variable to measure the amount of water hampers conclusions about its effect on macrofauna abundance, and it was a limitation to our study.

The composition of the fauna associated with epigeic and epiphytic bromeliads differed for aquatic species, terrestrial species and total macrofauna. Scirtidae larvae, Chironomidae larvae, *P. bifasciata* (Blaberidae) and *Lophoblatta* sp. (Ectobiidae) are species that provide great contribution and occur in both terrestrial and epiphytic bromeliads. However, most

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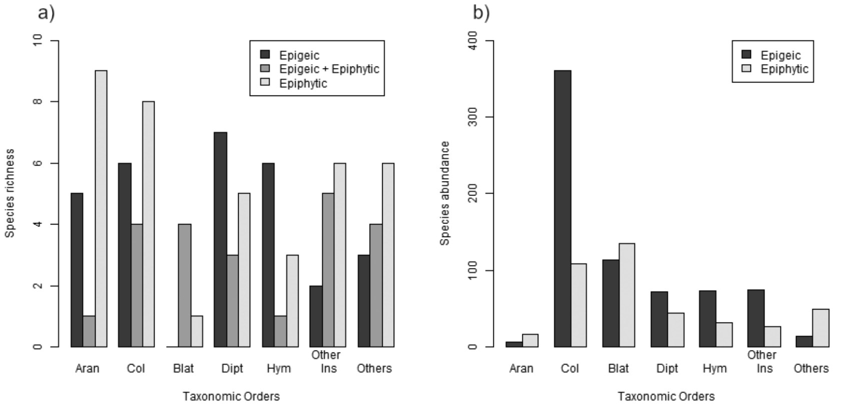

Fig. 4. Richness (a) and abundance (b) of fauna groups associated with the tank of epigeic (black), epiphytic (light grey) or both (dark grey) types of bromeliads of the *Vriesea neoglutinosa* Mez species sampled in the *restinga*.

morphospecies occurred in only one habitat (78.4%, Table 1). This result also explains the high turnover between epigeic and epiphytic bromeliads. *Restingas* are highly heterogeneous environments (Mantovani & Iglesias 2002). Such environmental heterogeneity changes the microclimatic conditions of each tank, enabling colonisation by different species. This explains the small similarity within groups.

In addition to differences in terrestrial and aquatic fauna, the different composition for the total fauna may be due to changes in the development phases between the epigeic and epiphytic habitats. Epiphytes harbour greater richness of terrestrial fauna, and epigeic bromeliads harbour greater richness of aquatic fauna. However, most terrestrial species were adults (60.6%, Table 1), while most aquatic species were immature (77.3%, Table 1). The role of tank bromeliads in harbouring immature aquatic fauna is well known (Jabiol *et al.* 2009; Jocque & Field 2014; Cardoso *et al.* 2015; Albertoni *et al.* 2016; Céréghino *et al.* 2018), and they can be called fauna nurseries. This is expected, considering that insects are the vast majority of bromeliad-colonising organisms, and they divide into life stages, with some species having immature aquatic stages (Rafael *et al.* 2012). However, in adulthood, some of the species move to a terrestrial habitat.

Scirtidae larvae and Blattaria species greatly contributed to both habits. They are detritivorous organisms that are very common in bromeliad communities (Richardson 1999; Mestre *et al.* 2001; Santos *et al.* 2009; Albertoni *et al.* 2016), where they play a basal role in the food web and are crucial to maintaining it (Kitching 2001; Santos *et al.* 2009). This high contribution highlights the relevance of the detritus chain in the trophic web of the associated community (Santos *et al.* 2009; González *et al.* 2014). Through the detritus chain, there is a redistribution of nutrients to other members of the fauna, which allows the increase in trophic levels. The trophic-level variety helps compose a more complex trophic structure (Starzomski *et al.* 2010; Hammill *et al.* 2015). The presence of different trophic guilds interacting in bromeliad tanks shows the role of *V. neoglutinosa* as a site for foraging and nutrient obtainment.

Predator species, such as spiders, showed great richness ($S = 15$ morphospecies). Spiders were more frequent in epiphytic bromeliads (70.8% of the individuals). In terrestrial bromeliads, Odonata were frequent predators of the aquatic ecosystem. Some studies have indicated that predators are more sensitive to the area size because they depend on its being previously occupied by their prey (Holt *et al.* 1999). Odonates are more frequently present in large than in small bromeliads (Petermann *et al.* 2015), as are the terrestrial bromeliads in our study. Spiders do not depend on resources directly obtained from bromeliad tanks, but on the fauna of the surrounding environment, and, therefore, can establish well on epiphytes. Terrestrial species of predators, such as spiders, can affect the richness and abundance of species in the aquatic ecosystem due to the consumption of ovipositor females (Romero & Srivastava 2010; Omena *et al.* 2017; Dejean *et al.* 2018). This can affect the whole trophic web, including aquatic predators such as odonates (Omena *et al.* 2017).

Diptera species also greatly contributed to the richness and abundance of bromeliad-associated macrofauna, a common result in several studies (Frank & Lounibos 2009; Jabiol *et al.* 2009; Júnior *et al.* 2017; Céréghino *et al.* 2018). We did not find any Culicidae larvae, which are quite frequent in studies in the field (Jabiol *et al.* 2009; Parker *et al.* 2012; Júnior *et al.* 2017; Céréghino *et al.* 2018). We only observed a single adult individual. Chironomidae and Tabanidae were the most frequent diptera species in our study. Chironomidae species also are common in

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studies (Sodré *et al.* 2010; Júnior *et al.* 2017; Céréghino *et al.* 2018). Chironomidae species play variable ecological roles (Frank & Lounibos 2009) and require further taxonomic and behavioural studies (Frank & Lounibos 2009; Sodré *et al.* 2010). The *Polypedilum* species may feed on debris and, to a lesser extent, on algae (Silva *et al.* 2008). We find species of *P. kaingangi* (Pinho, Mendes & Andersen, 2013) and *P. marcondesi* (Pinho & Mendes, 2010) only described for Santa Catarina state. This is the first record of such species in Rio de Janeiro state. This reinforces the importance of greater taxonomic efforts, since we will be able to find several new records of occurrence and even new species (Frank *et al.* 2004; Sodré *et al.* 2010).

The fauna associated with *V. neoglutinosa* showed species at different development stages. The presence of immature stages, mainly in the aquatic ecosystem, points out the role played by tank bromeliads, such as *V. neoglutinosa*, as a nursery for fauna. Bromeliads make water available in the *restinga* environment, where this resource is limited (Cogliatti-Carvalho *et al.* 2010). This role is essential for the maintenance of the species diversity in the area. Bromeliads are necessary for the species development and the achievement of the reproductive phase (Rocha *et al.* 2004; Santos *et al.* 2009). The large amount of terrestrial macrofauna, composed mainly of adults, shows the essential role played by bromeliads even at stages that do not depend directly on water availability for their development. Bromeliads provide stable conditions in the long term and are a refuge for terrestrial invertebrates under drought conditions (Richardson & Richardson 2013). The terrestrial organisms found among the bromeliad fauna are also characteristic of the forest soil fauna (Richardson & Richardson 2013). Hence, besides nurseries, bromeliads can also be called terraria due to the terrestrial fauna that they harbour.

In conclusion, *V. neoglutinosa* harbours rich and abundant fauna, composed of several taxa and with the predominance of insects. It can be considered a biodiversity amplifier in the *restinga* of Praia Grande. The bromeliad fauna represents several life cycle stages, from larvae to adults, and forms a complex food web, composed of different trophic guilds. Hence, bromeliads play a major role in the maintenance of the local diversity, acting as a nursery and terrarium for many species. Terrestrial bromeliads harbour richer aquatic fauna than do epiphytic bromeliads while epiphytes shelter richer terrestrial fauna than terrestrial bromeliads. As terrestrial and epiphytic *V. neoglutinosa* show different fauna compositions and richness, they play complementary roles. Each habit is responsible for the maintenance of part of the biodiversity and life cycle stages present in the *restinga*, and the conservation of both habits is necessary for macrofauna conservation.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Bianca Ferreira da Silva Laviski: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (lead); Visualization (equal); Writing-original draft (lead). **Ícaro de Moraes Monteiro:** Conceptualization (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing-original draft (supporting). **Luiz Carlos Pinho:** Data curation (equal); Methodology (equal); Writing-original draft (supporting). **Renner Luiz Cerqueira Baptista:** Data curation (equal); Methodology (equal); Writing-original draft (supporting). **Antonio José Mayhé-Nunes:** Data curation (equal); Methodology (equal); Writing-original draft (supporting). **Francisco Racca-Filho:** Data curation (equal); Methodology (equal); Writing-original draft (supporting). **André Felippe Nunes-Freitas:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing-original draft (equal).

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