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RESEARCH ARTICLE

Effect of the structural complexity of aquatic macrophytes on epiphytic algal, macroinvertebrates, and their interspecific relationships

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Abstract

Aquatic macrophytes may have a significant effect on associated communities such as epiphytes and macroinvertebrates, which through the structural complexity of habitat, provide shelter, resources, and interspecific interactions. We tested the hypothesis that the structural complexity of macrophytes positively modifies epiphytes and macroinvertebrates and that the interspecific interactions of epiphytes and macrophytes positively influence macroinvertebrates by synergism of epiphyte availability and increased habitat complexity. The macrophytes presented different structural complexities, ranging from low (*Cyperus articulatus*), medium (*Nymphaea pulchella*) to high complexity (*Eichhornia crassipes* and *Ludwigia helminthorrhiza*). The richness, diversity, and biomass of epiphytes presented a significant difference and positive relationship with the increase of the structural complexity of the macrophytes. The synergism between the structural complexity of the macrophytes and the epiphytic biomass ($r^2 = 0.37$; $p = 0.0002$), increased the biomass of macroinvertebrates ($r^2 = 0.47$; $p = 0.003$). The functional traits of the epiphytes were directly related to the morphology of the macrophytes with the unicellular, pedunculated, and firmly adhered dominating. The dominance of these traits indicates the absence or low disturbance (e.g., rain) in the studied site. The responses of the functional characteristics of the epiphytes are important to understand ecosystem functioning and dynamics. Therefore, we conclude that epiphytes showed a positive relationship with the structural complexity of the macrophytes. Moreover, macroinvertebrates showed a positive relationship with the increased macrophyte morphological complexity and increased biomass of epiphytes. The management of macrophytes with different structural complexities can be a strategy to recover the biodiversity in tropical aquatic ecosystems.

Keywords Aquatic plants · Fractal dimension · Invertebrates · Periphyton · Trophic relation

Introduction

Macrophytes are important components of aquatic ecosystems since they act in nutrient cycling, serve as the substrate for biotic communities, and restore water quality (Choudhury et al. 2018). The structural complexity and diversity of aquatic plants are responsible for the increasing of habitat heterogeneity and consequently increasing the structural attributes (e.g., richness, diversity and biomass) of communities and ecological niches (MacArthur and MacArthur 1961; Ferreiro et al. 2011; Casartelli and Ferragut 2018). With an important role in structuring aquatic communities, macrophytes can also be used to manage and restore biodiversity in aquatic ecosystems (Thomaz and Cunha 2010). Habitat heterogeneity is a determining factor for aquatic systems, as it changes species dynamics and interactions, and influences ecosystem processes (Gianuca et al. 2017). Environmental variability is positively related to species diversity (Munguia et al. 2011) and consequently acts on biodiversity conservation and ecosystem functioning (Schuler et al. 2017).

Factors such as age, density, and depth of macrophytes are also responsible for the structure and distribution of

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epiphyte, macro, and microfauna communities (Lucena-Moya and Duggan 2011; Tarkowska-Kukuryk and Toporowska 2021). However, these factors are dynamic since they change depending on environmental conditions and over time (Grutters et al. 2015). Since macrophyte morphology is constant throughout their life cycles and through the fractal dimension, the effects of morphological complexity on adhered organisms can be measured (Casartelli and Ferragut 2018).

Aquatic ecosystems are increasingly going through the process of eutrophication, which is an important factor for aquatic biodiversity loss in temperate and tropical regions (Jeppesen 2005). Located in the tropics, the Brazilian semi-arid region usually features aquatic environments with low water levels and high concentrations of nutrients, that are strongly influenced by anthropogenic activities, high temperatures, and reduced rainfall throughout the year (da Costa et al. 2016). These conditions are ideal for cyanobacterial blooms, which decrease and limit light and can lead to the disappearance of submerged aquatic macrophytes, resulting in a change from clear to turbid water state (Seto et al. 2013; Jeppesen 2014).

Simply controlling the input of allochthonous nutrients is insufficient to restore a clear water state, since the releasing of nutrients from the sediments is an important factor in nutrient cycling that undermines the recovery of water quality (Osgood 2017). Therefore, studies should consider the relationships between macrophytes, epiphytes, phytoplankton, invertebrates, and fish to maintain or restore a clear water state (Mamani et al. 2019). This complex relationship may reduce nutrient concentrations, as well as increase habitat availability and resources for aquatic communities, which are important to maintain clear water states (Scheffer et al. 1993). Aquatic macrophytes are considered biological components in the freshwater ecosystems and have important roles in restoring water quality (Zhu et al. 2011; Li et al. 2015), therefore, they are widely used for ecological remediation of eutrophic lakes, polluted rivers, and other water bodies (Zhou et al. 2017). The increased habitat complexity through the manipulation of macrophytes can have significant effects on aquatic communities and trophic relationships in the ecosystem, maintaining the water quality (Ferreiro et al. 2013; Choi et al. 2014; Hao et al. 2017). Hence, Lv et al. (2019) observed that macrophytes reduced the concentrations of total nitrogen, total organic carbon, dissolved organic carbon, and increased the water transparency and species richness of periphytic algae. The authors suggested that higher diversity of macrophytes and periphytic algae can contribute to reduce nutrient concentrations and improve water quality. Triggering a cascade effect, higher biomass availability and diversity of periphytic algae provide positive conditions for macroinvertebrate establishment (Ferreiro et al. 2013; Wolters et al. 2018). In addition to increased food availability for herbivore invertebrates (e.g., periphytic algae) (dos Santos et al. 2013; Casartelli and Ferragut 2018), macrophytes can provide habitats with varying degrees of complexity (Wolters et al. 2018).

Studies about the influence of environmental factors and macrophyte complexity on epiphytes and macroinvertebrates are explored in rivers, flood plains, and lagoons (Thomaz et al. 2008; Walker et al. 2013; Matsuda et al. 2015). In contrast, few studies have used the functional characteristics of periphytic algae in tropical reservoirs. Studies of functional characteristics of the epiphyte community provide broader ecological generalizations because these organisms respond to the modifications caused by environmental and anthropic disturbances (Heino et al. 2013; Casartelli and Ferragut 2018). The use of epiphytic algae functional characteristics allows a clear assessment of the biotic and abiotic interactions of periphytic algae, which facilitates the understanding of the dynamics and functioning of the ecosystem (Louault et al. 2005).

Accordingly, we tested the hypothesis that the structural complexity of macrophytes influences species richness, diversity, and biomass of both epiphyte and macroinvertebrate communities. We further hypothesized that macroinvertebrate biomass is positively influenced by the interaction between epiphyte availability and increased complexity of macrophytes, and that the functional characteristics of the epiphyte community are directly related to macrophyte complexity.

Material and methods

Study area

The study was conducted in the Jazigo reservoir (8°00’S, 38°12’W), Serra Talhada, Pernambuco, Northeastern Brazil. The reservoir has a water accumulation capacity that exceeds 15 million m^3, an average depth of 4 m and is used for fishing and recreational activities. The climate of the region is classified as BSh according to the Köppen system, with average annual rainfall ranging from 600 to 700 mm, the average annual temperature of 26 °C, and hyperxerophilic caatinga type terrestrial vegetation (Alvares et al. 2013; APAC 2019). The aquatic vegetation is widely distributed in the coastal region and composed of the species *Pistia stratiotes* L., *Eichhornia crassipes* (Mart.) Solms, *Cyperus articulatus* L., *Nymphaea pulchella* DC, *Echinodorus palaefolius* (Nees et Mart.) Magbr., *Ludwigia helminthorrhiza* (Mart.) H. Hara and *Lemna minor* L. (data from this study).

Field and laboratory procedures

The sampling was performed quarterly in 2017 and 2018 in five different macrophytes beds, with four field expeditions ($n = 55$ samples), to analyze macrophyte, epiphyte, and macroinvertebrate communities. Water temperature (°C), dissolved oxygen (mg L^{-1}), salinity (ppt), pH, total dissolved solids (mg L^{-1}), and electrical conductivity (µS cm^{-1}) were measured in situ from the water subsurface in each macrophyte bank using a multiparameter probe (HANNA HI-9829 model). Water transparency was measured using a Secchi disk (*m*), light intensity (µmol photons m^{-2} s^{-1}) with a photometer (model LI-250A; LI-COR, Lincoln, NB, USA) and the depth with an echosounder (HONDEX; model PS7).

Samples were collected with a van Dorn bottle from the water subsurface. Water samples were transferred to the laboratory, where phytoplanktonic chlorophyll *a* (Bartram and Chorus 1999), total phosphorus (Strickland and Parsons 1972) (TP), nitrite ($N\text{-}NO_2$), nitrate ($N\text{-}NO_3$) (Mackereth et al. 1978), ammoniacal nitrogen ($N\text{-}NH_3 + N\text{-}NH_4^+$) (Koroleff 1976), and dissolved inorganic nitrogen (DIN) were analyzed. Dissolved inorganic nitrogen was measured as the sum of the nitrate, nitrite, and ammoniacal nitrogen concentrations. The trophic state index for Tropical/Subtropical reservoirs was calculated according to Cunha et al. (2013).

Determination of fractal dimension and biomass of macrophytes

Macrophytes were collected manually from each sampling point. A total of 55 macrophyte specimens (samples) were collected from four species with the following life forms: (1) free-floating: *Eichhornia crassipes* ($n = 20$) and *Ludwigia helminthorrhiza* ($n = 10$); (2) emergent: *Cyperus articulatus* ($n = 15$); and (3) fixed with floating leaves: *Nymphaea pulchella* ($n = 10$). At each sampling point, an individual of each macrophyte species was collected to analyze the fractal dimension, macrophyte biomass, and to collect periphytic algae and macroinvertebrates, with a total of five individuals per species collected in each sampling month. The individuals of each species were collected according to their presence at the time of collection. Only the floating macrophyte *Eichhornia crassipes* was present in all sampling months. Measurement of the structural complexity of the macrophytes was performed on the 55 specimens. The specimens were placed individually in aquariums with filtered water and photographed with a digital camera to better reflect the distribution and organization of the morphological structures. Images were produced in black and white and converted to JPEG.

The fractal dimension (*D*) was measured according to the Sugihara and May (1990) method, using the ImageJ program (Abràmoff et al. 2004). The fractal dimension was obtained from the slope of the relationship between Log N (number of occupied squares) and log 1/S (length of the side of the squares). This method involves a regular grid of squares with "*d*" dimension which measures the macrophyte structures (leaves, petioles, and roots) and the number of squares needed to cover the image (Halley et al. 2004). Subsequently, the macrophytes were dried in an oven at 60 °C until constant weight to determine their dry weight (DW).

Sampling, treatment, identification and quantification of epiphytes

Epiphytes were removed from the leaves, stems, or petioles of the 55 macrophytes specimens (area = 25 cm^2) by scraping with a soft bristle brush, scalpel, and jets of distilled water (150 mL), then they were preserved with acetic iodine lugol solution for quantitative and, preserved with 4% formalin solution, for qualitative analysis.

Epiphytic algae were identified through observations of morphological characteristics of organisms using specific taxonomic keys, such as Prescott and Vinyard (1982) for chlorophytes, John et al. (2002), for euglenophytes, Ettl (1978) for the xanthophyceans, Komárek and Anagnostidis (2005), Komárek and Cronberg (2001), and Komarek (2013) for cyanobacteria, Popovsky and Pfiester (1990) for dinoflagellates, Krammer and Lange-Bertalot (1991a, b) for diatoms. Permanent slides were prepared according to Carr et al. (1986) to identify diatoms.

Algae quantification was done under the Zeiss Axiovert (×400) inverted microscope, according to Utermöhl (1958). The settling time of the samples followed Lund et al. (1958), which were counted in transects with the count limit set by the species rarefaction curve and a minimum of 400 individuals of the most abundant species (Colwell et al. 2012). The density of species was estimated according to Ros (1979) and the results expressed in individuals per unit area (ind cm^{-2}). Biomass (µm^3 cm^{-2}) was estimated using the average biovolume of species obtained through geometric shapes and equations from Hillebrand et al. (1999) and was then multiplied by the average density of the species. The species richness (*S*), Shannon diversity index, and Pielou equitability were determined by the number of species and biomass in each sample (Magurran 2004). Filamentous and colonial individuals were counted as a single individual, when present, and the cell volume was calculated to estimate biomass.

Functional characteristics of algae

The algal community structure was characterized by 11 functional traits divided into three categories: life form (unicellular, filamentous, colonial and flagellar) (Graham and Wilcox 2000), the intensity of adherence to the substrate (firmly and loosely adhered) (Sládecková and Sládecek 1977) and form of adherence (mobile, entangled, prostrate, stalked and heterotrichous) (Biggs et al. 1998).

Sampling of associated macroinvertebrates

In the field, after the sampling of periphytic algae, the macroinvertebrates were removed from the leaves, stems, or petioles of the 55 macrophyte specimens collected using a soft-bristled brush and jets of distilled water from the pre-selected macrophytes from the epiphyte sampling. Subsequently, each sample was filtered in a collecting cup with 0.25 mm mesh opening and stored in flasks with 70% alcohol.

The macroinvertebrates were identified using a stereoscopic microscope and optical microscope to the lowest taxonomic level, when possible, using specific bibliographies, such as Pérez (1988) and Trivinho-Strixino (2011). After identification, species abundance, diversity, and richness were calculated as previously mentioned. The biomass was estimated from the number of individuals per dry weight of macrophytes.

Data analysis

The permutational multivariate analysis of variance (PERMANOVA; $\alpha = 0.05$) was used to determine possible changes in abiotic variables in different months and macrophyte banks. The normality and homoscedasticity were evaluated using the Kolmogorov–Smirnov and the Bartlett tests, respectively. The one-way factorial analysis of variance (ANOVA) and Tukey's a posteriori test was applied to abiotic data. Fractal dimensions of macrophytes and structural attributes of epiphytes and macroinvertebrates were used to detect any significant differences. The normality and homoscedasticity were evaluated using the Kolmogorov–Smirnov method and the Bartlett test, respectively. The Jaccard index (J) was used to calculate the similarity between macrophyte species through a matrix of presence and absence of algae.

Linear regressions were to determine the relationship between structural attributes (richness, biomass, equitability, and diversity) of periphytic algae and macroinvertebrates with the fractal dimensions of macrophytes and dry weight. The radio-loud quasars (RLQ) analysis (Dolédec et al. 1996) was used to evaluate the relationship between the environmental variables, fractal dimensions of the macrophytes, and the functional traits of epiphytes. The RLQ is based on the ordering of three separate arrays (species biomass, environmental variables, and functional traits of the species) and it is an extension of co-inertia analysis that searches for a combination of traits and environmental variables of maximal co-variance, which is weighted by the biomass of species epiphytes. We explore the co-variance between environmental variables (R table) and species traits (Q table), constrained by the biomass of each species (L table) as observed in each macrophyte. The Tukey's a posteriori test permutation was carried out to verify the significance of relationships (Dray and Legendre 2008).

A multiple regression model was used to verify possible relationships between environmental variables (e.g., temperature, salinity, and macrophytes) and epiphytic algae with the macroinvertebrates. All analyses were performed in the R program (R Development Core Team 2014). The package Ade4 (Chessel et al. 2004) was used to construct the functional distance matrix for the RLQ analysis, and the Vegan package (Oksanen 2011) was used for ANOVA and PERMANOVA.

Results

Abiotic variables

The water capacity of the reservoir showed low variation (19.86%) with a maximum of 100% and a minimum of 80.14% of the total reservoir accumulation capacity. The mean rainfall was 29.87 mm. The water temperature, pH, conductivity, dissolved oxygen, total dissolved solids, and salinity showed no significant differences between the months (PERMANOVA, $F = 3.41$; $p > 0.05$). Likewise, the nutrients did not present significant variations throughout the studied months. The total phosphorus value was the highest in August 2017 with 51.39 $\mu g\ L^{-1}$ and the lowest in November 2018 with 33.25 $\mu g\ L^{-1}$ (Table 1). The trophic state index showed that the reservoir was mesotrophic, with a mean of $54.60 \pm 2.56\ \mu g\ L^{-1}$.

Fractal dimension of macrophytes

The difference in the fractal dimensions between the macrophytes was significant (ANOVA; $F = 105.4$; $p < 0.002$). *Cyperus articulatus* presented the lowest fractal complexity (LC) ($D = 1.72$), *Nymphaea pulchella* (MC) a medium complexity ($D = 1.83$), while *Eichhornia crassipes* (HC1) and *Ludwigia helminthorrhiza* showed the highest complexity (HC2) ($D = 1.85$ and $D = 1.91$, respectively). No difference was observed in the fractal dimension between specimens of each macrophyte species ($F = 1.23$; $p = 0.41$) or between months ($F = 1.43$; $p = 0.84$). The Tukey's a posteriori test showed that *C. articulatus* (LC) had a significant difference between macrophytes with medium (MC) and high complexities (HC1 and HC2), while *L. helminthorrhiza* (HC2) significantly differed from *E. crassipes* ($p = 0.002$, HC1) and *N. pulchella* ($p = 0.002$, MC).

Table 1 Mean values (± standard deviation) of the limnological parameters of the water of the macrophyte beds in the reservoir Jazigo, Pernambuco, Brazil

Abiotic variables	2017		2018	
	August	November	March	June
Precipitation (mm)	0.70	3.60	118	0.80
Water temperature (°C)	23.98 ± 0.44	28.21 ± 0.68	30.36 ± 0.19	24.96 ± 0.11
pH	8.10 ± 0.51	7.98 ± 0.12	8.04 ± 0.06	8.05 ± 0.10
Conductivity (µS cm^{-1})	84.71 ± 40.82	218.14 ± 1.09	256.63 ± 19.62	165.00 ± 4.37
Dissolved oxygen (mg L^{-1})	5.85 ± 1.46	4.58 ± 0.24	3.74 ± 0.56	8.64 ± 1.11
Total dissolved solids (mg L^{-1})	33.33 ± 13.11	109.16 ± 0.75	132.41 ± 4.27	86.30 ± 2.51
Salinity (ppt)	0.10	0.10	0.10	0.12
Ligth intensity (µmol fótons m^{-2} s^{-1})	748.80 ± 458.50	548.23 ± 272.21	426.35 ± 312.66	1081.61 ± 415.63
Nitrate (µg L^{-1})	125.49 ± 16.16	14.09 ± 4.14	2.60 ± 1.94	12.22 ± 2.82
Nitrite (µg L^{-1})	9.66 ± 1.02	10.96 ± 1.22	0.43 ± 0.20	10.43 ± 1.03
Ammonia (µg L^{-1})	37.66 ± 8.02	18.06 ± 0.72	20.12 ± 0.72	17.81 ± 0.62
Dissolved inorganic nitrogen (µg L^{-1})	172.82 ± 9.15	43.11 ± 6.09	23.16 ± 1.41	32.76 ± 4.73
Total phosphorus (µg L^{-1})	51.39 ± 4.27	33.25 ± 8.55	46.85 ± 2.13	38.27 ± 5.63
Secchi (m)	1.00 ± 0.36	1.06 ± 0.30	1.54 ± 0.65	1.33 ± 0.60
Depth (m)	1.57 ± 0.12	1.15 ± 0.42	2.44 ± 0.21	1.51 ± 0.40
Trophic state	56.16 (eutrophic)	55.39 (mesotrophic)	50.78 (ultraoligotrophic)	56.07 (eutrophic)

Structure of the epiphyte community

A total of 82 taxa of periphytic algae were recorded, which were found in *Eichhornia crassipes* (73 taxa), *Ludwigia helminthorrhiza* (53 taxa), *Nymphaea pulchella* (50 taxa) and *Cyperus articulatus* (39 taxa). The four macrophytes shared the largest number of taxa ($S = 24$), compared to the number of taxa shared between *E. crassipes*, *N. pulchella*, and *C. articulatus* ($S = 17$), and between *E. crassipes* and *N. pulchella* ($S = 12$), thus reflecting the greater similarity between *E. crassipes* and *L. helminthorrhiza* ($J = 0.61$), and low similarity between *N. pulchella* and *C. articulatus* ($J = 0.45$).

The species richness differed significantly between the macrophytes (Fig. 1a). Macrophytes with low complexity showed lower richness and differed significantly among the other macrophytes, which showed higher species richness. The equitability did not differ between the macrophytes (Fig. 1b). Species diversity significantly differed among macrophyte species ($F = 5.64$; $p = 0.002$). Only LC differed from MC, HC1, and HC2 ($p = 0.01$; $p = 0.003$; $p = 0.02$, respectively), and the most complex species (*L. helminthorrhiza*) showed greater diversity (Fig. 1c), but this trend was not significant. Epiphyte biomass differed significantly between the macrophyte complexities ($F = 25.78$; $p = 0.007$). Regarding the differences between macrophytes, only the LC macrophyte differed from MC, HC1, and HC2 ($p < 0.05$, Fig. 1d). Species richness showed a positive relationship with the structural complexity (Fig. 2a). Conversely, the equitability did not show a relationship to the fractal dimension (Fig. 2b). Moreover, diversity showed a positive relationship with macrophyte complexity ($r^2 = 0.32$; $p = 0.0004$) (Fig. 2c). Epiphyte biomass showed positive relationship with increased structural complexity ($r^2 = 0.41$; $p = 0.002$; Fig. 2d). Linear regressions showed that only epiphytic algae biomass was positively correlated with the dry weight of macrophytes (Table 2).

The dominant life forms of epiphytes in macrophytes were unicellular (60.79%) and filamentous (31.75%) (Table S1). In August, filamentous algae were dominant with rapid substitution by unicellular forms throughout the study, except in August (Fig. 3a). Regarding the intensity and form of adherence, the algae that were firmly adhered and stalked were dominant (Fig. 3b, c). Stalked (44.42%) and entangled (41.06%) forms of adherence showed higher biomass, followed by prostrated (14.38%). The first two axes of RLQ analysis accounted for 96.32% (first axis) and 0.24% (second axis) of the inertia with the variables (Fig. 4). The first axis was more correlated with temperature, higher complexity, and conductivity (positively), and the second axis was more correlated with dissolved oxygen and luminous intensity (positively), besides low complexity and DIN (both negatively) (Fig. 4a). The relationships of functional traits on the first axis were correlated to the filamentous and heterotrichous forms (both positively) and the second axis was correlated to colonial (negatively), prostrated, loosely adhered and entangled species (positively) (Fig. 4b). The loosely adhered and entangled species were positively correlated to the highest values of luminous intensity and dissolved oxygen; the prostrated species were correlated to macrophytes with medium structural complexity. The

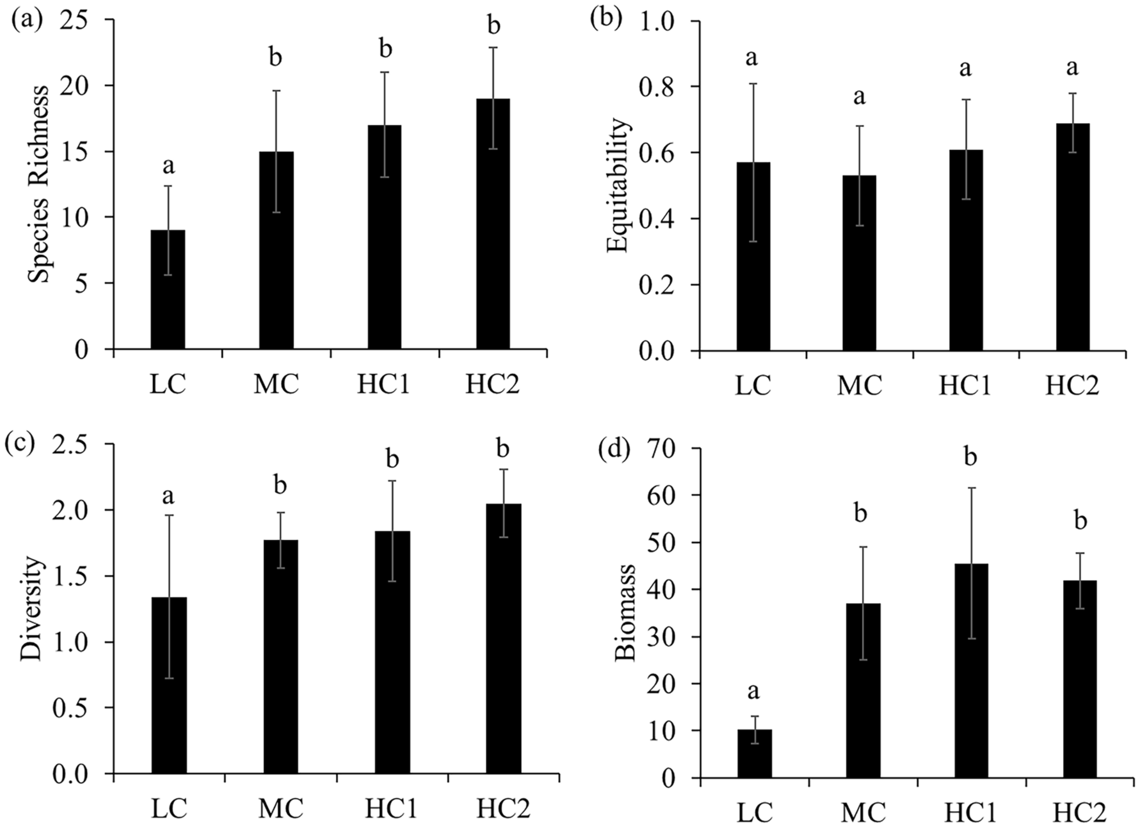


Fig. 1 Structural attributes of epiphytic algae in different species of aquatic macrophytes: **a** species richness, **b** equitability, **c** species diversity (bits ind^{-2}), and **d** biomass ($\times 10^5$ µg^3 cm^{-2}). *LC Cyperus articulatus*, *MC Nymphaea pulchella*, *HC1 Eichhornia crassipes*, *HC2 Ludwigia helminthorrhiza*. Letters indicate significant differences ($\alpha = 0.05$)

colonial species were related to nitrate, ammonia, dissolved inorganic nitrogen, and macrophytes with low complexity; while unicellular, heterotrichous, and filamentous species were related to conductivity, temperature and macrophytes with high structural complexity (Fig. 4).

Macroinvertebrate community structure

A total of 26 taxa were identified and 5172 individuals were counted, distributed in *E. crassipes* (2234), *N. pulchella* (1780), *L. helminthorrhiza* (647), and *C. articulatus* (511) (Table S2). The species of mollusk *Melanoides tuberculatus* (Müller, 1774), *Biomphalaria straminea* (Dunker, 1848), *Gundlachia radiata* (Guilding, 1828), larvae of Chironomidae, and Copepoda Calanoida were the most representative in terms of biomass. The macrophytes with greater morphological complexity shared the largest number of macroinvertebrate species ($S = 26$) and had 11 unique taxa. The highest similarity (Jaccard index) was observed between *E. crassipes* and *L. helminthorrhiza* ($J = 1$) and the lowest similarity between *E. crassipes* and *C. articulatus* ($J = 0.25$). Species richness differed significantly (Fig. 5a, ANOVA; $F = 28.39$; $p = 0.001$) with only LC macrophyte different from MC and HC2 (Fig. 5a). The equitability of macroinvertebrates showed significant differences between HC2 and MC ($F = 85.69$; $p = 0.001$, Fig. 5b), and species diversity in HC2 differed from LC, MC, and HC1 (Fig. 5c). Biomass of MC differed from all macrophytes (Fig. 5d).

The richness of macroinvertebrates showed a positive relationship with macrophyte complexity ($r^2 = 0.42$, $p = 0.0001$; Fig. 6a), while the LC macrophyte showed lower richness and differed significantly from the other complexities ($p < 0.05$). In addition, the HC macrophyte differed significantly from MC and LC. The diversity of macroinvertebrates differed significantly (ANOVA; $F = 17.69$; $p < 0.05$) and showed a positive relationship with the structural complexity of macrophytes (Fig. 6b). The biomass and equitability increased significantly with the increased macrophyte complexity ($r^2 = 0.41$; $p = 0.003$) (Fig. 6c, d, respectively). Linear regressions showed that no structural attributes of macroinvertebrates had a significant relationship with the dry weight of macrophytes (Table 2). Multiple regression models showed a strong relationship between macroinvertebrates and the explanatory variables ($r^2 = 0.63$, $p = 0.001$). Macroinvertebrates showed a positive relationship with diatoms ($r^2 = 0.47$; $p = 0.003$), entangled algae ($r^2 = 0.27$; $p = 0.05$), and fractal dimension of macrophytes ($r^2 = 0.37$;

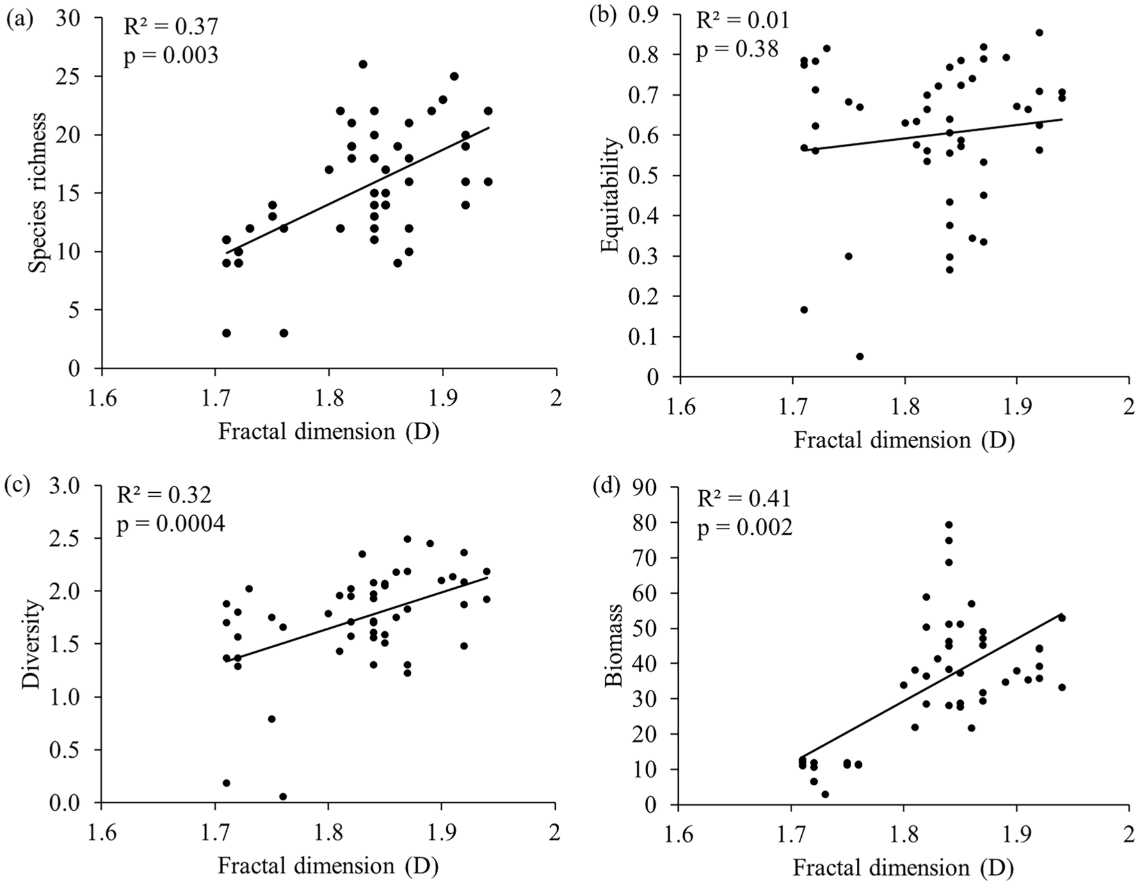


Fig. 2 Relationship between the fractal dimension of the macrophytes and **a** species richness, **b** equitability, **c** species diversity (bits ind^{-2}), and **d** biomass ($\times 10^5$ µg^3 cm^{-2}) of algae

Table 2 Multiple regression of the structural attributes of epiphytic algae and macroinvertebrate with the dry weight (g) of aquatic macrophytes

Structural attributes	Epiphytic algae		Macroinvertebrates	
	r^2	p	r^2	p
Richness	0.05	0.09	0.01	0.43
Equitability	0.01	0.49	0.07	0.06
Diversity	0.02	0.84	0.001	0.77
Biomass	0.15	0.07	0.22	0.0006$^+$

$^+$Positive relationship

$p=0.0002$), while it did not show a significant relationship with the other explanatory variables ($p>0.05$).

Discussion

Our study showed that the structural complexity of macrophytes is important in the structuring of the algal and macroinvertebrate communities, with higher values of richness, diversity, and biomass in macrophytes with high morphological complexity. The presence of macrophytes with different morphologies is important for the heterogeneity of habitats in aquatic ecosystems (Thomaz and Cunha 2010; Fontanarrosa et al. 2013), creating several microhabitats and interstitial spaces that provide resources and niches that favor the fixation, colonization, and abundance of algae and macroinvertebrates (MacArthur and MacArthur 1961; Matsuda et al. 2015; Pettit et al. 2016). The functional characteristics of the epiphytes showed significant relationships with the morphology of the macrophytes, despite the physicochemical conditions of the water being related to some functional traits.

The morphological complexity of macrophytes is determined by the organization of leaves, stems, petioles, and roots, which characterize each macrophyte life form and species. The macrophyte *Cyperus articulatus* has simple morphology, with petioles below the water surface and inflorescence emerging above the surface, which provides few microhabitats and showed low diversity, richness, and biomass of algae and macroinvertebrates. In other studies, algal biomass was low due to the simple morphology of

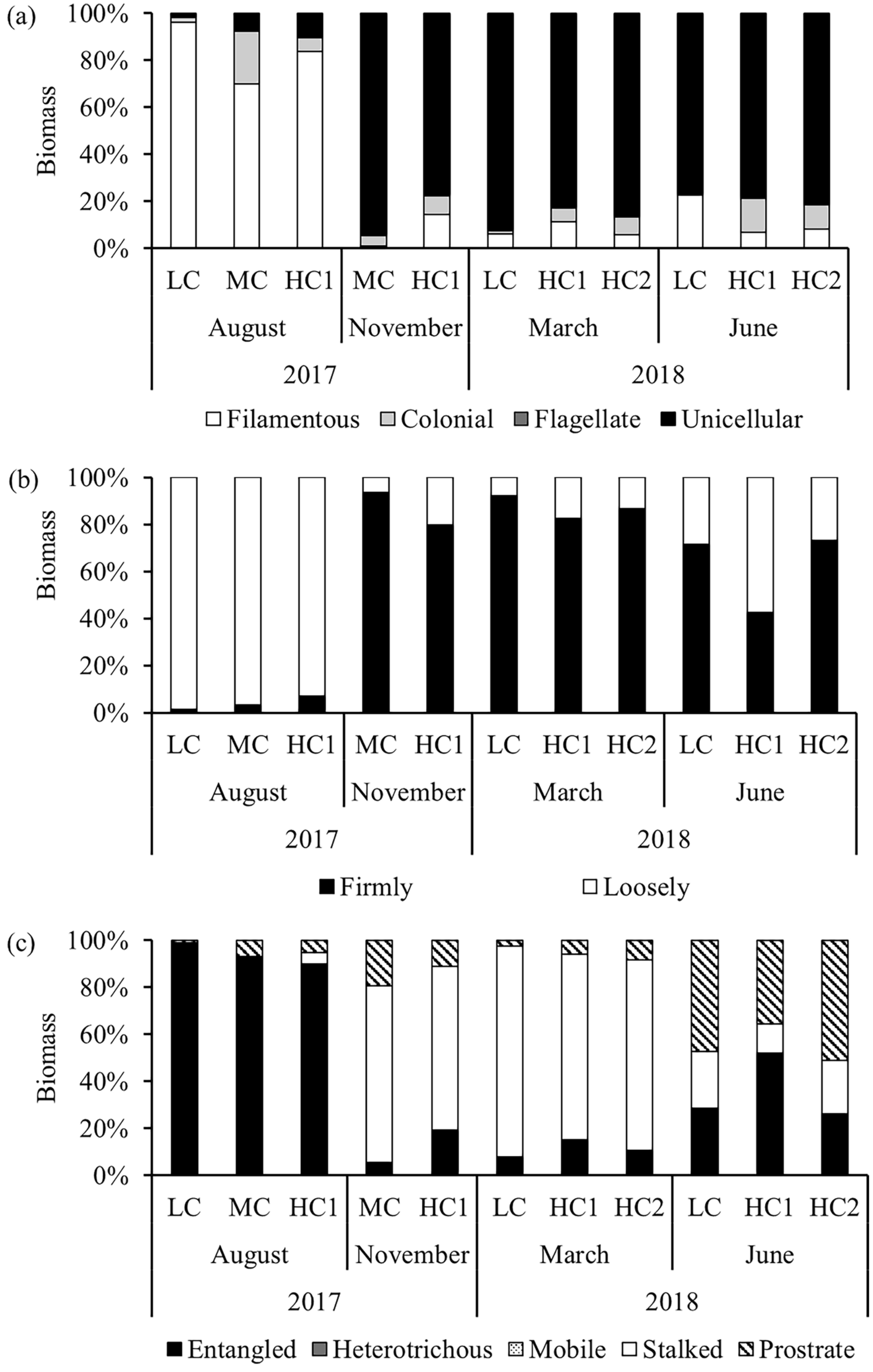
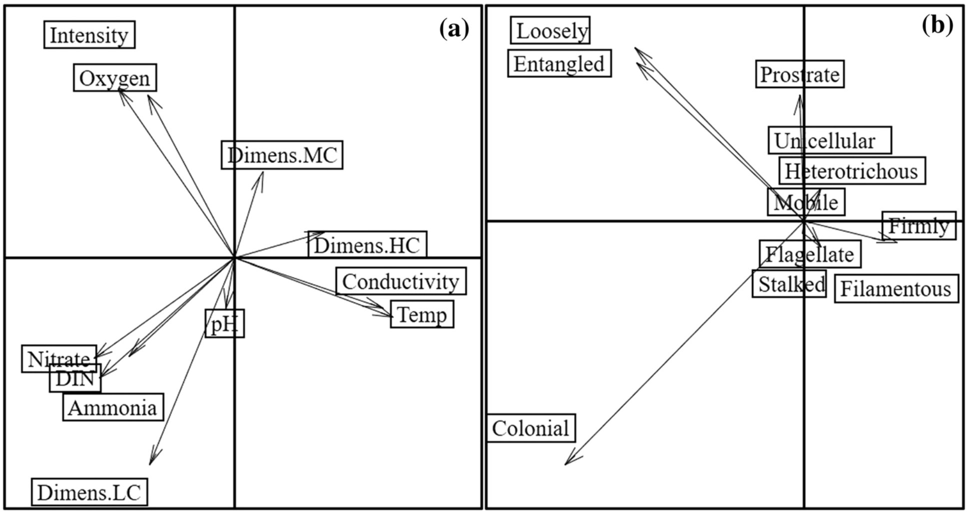


Fig. 3 Relative biomass of the **a** life forms, **b** adherence intensity, and **c** form of adherence of the epiphytic community in the macrophytes throughout the study months (August and November/2017) and (March and June/2018). *LC Cyperus articulatus*, *MC Nymphaea pulchella*, *HC1 Eichhornia crassipes*, and *HC2 Ludwigia helminthorrhiza*

macrophytes (Gosselain et al. 2005; Pettit et al. 2016). Our results indicate that the richness, diversity, and biomass of algae and macroinvertebrates are influenced by the structural complexity of macrophytes. The floating macrophytes *L. helminthorrhiza* and *E. crassipes*, which have high morphological complexity, favored the increase of richness, diversity, and biomass of periphytic algae and macroinvertebrates. This fact may be related to the greater availability of microhabitats and resources that more complex macrophytes provide for periphytic algae and macroinvertebrates (Bell

Fig. 4 RLQ ordering of the distribution of environmental variables (a) and functional traits of algae (b) in the reservoir. Intensity—Luminous intensity (μmol photons m^{-2} s^{-1}), Dimens.LC—Low complexity, Dimens.MC—Mean Complexity, Temp—Temperature °C, DIN—Dissolved inorganic nitrogen (μg L^{-1}), and Dimens. HC—High complexity



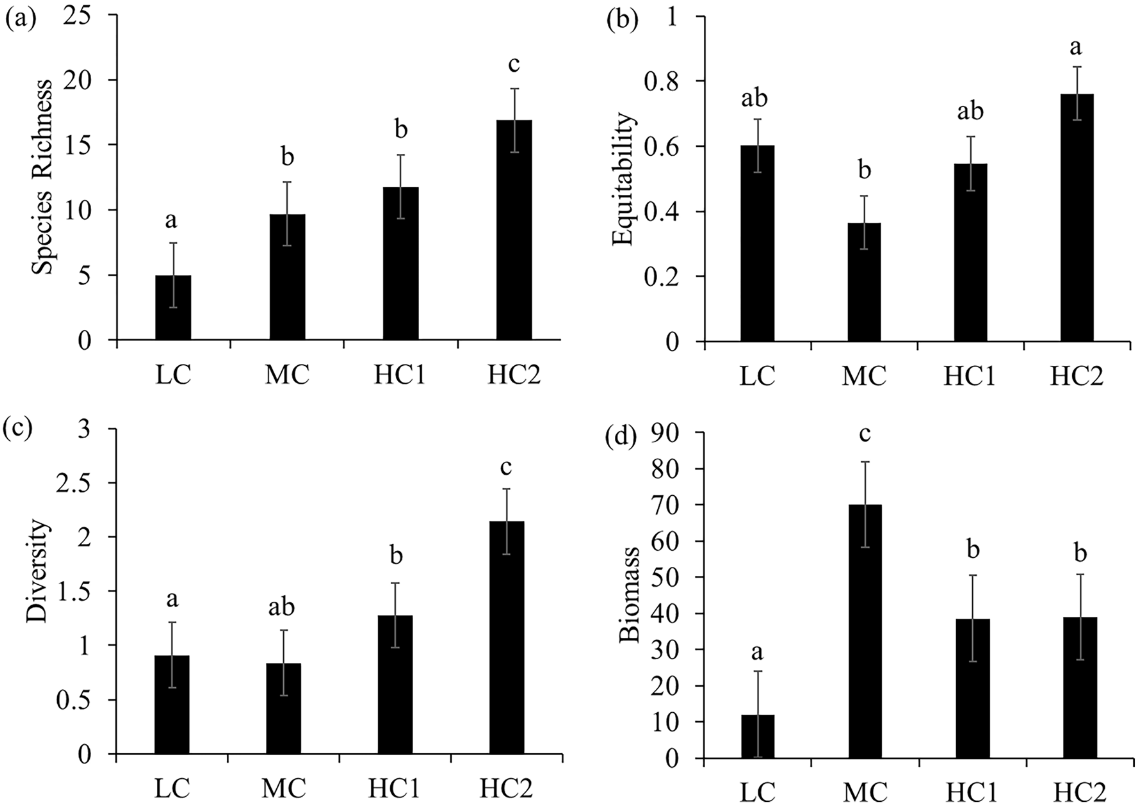


Fig. 5 Structural attributes of macroinvertebrates in different species of aquatic macrophytes: **a** species richness, **b** equitability, **c** species diversity (bits ind^{-2}), and **d** biomass (ind g^{-1}). Letters indicate significant differences ($\alpha = 0.05$)

et al. 2013; Casartelli and Ferragut 2018). Macrophytes increase habitat heterogeneity and, consequently, biodiversity of aquatic ecosystems (Alahuhta 2015), while the spatial complexity, promoted by the structural architecture of macrophytes, increases the colonization area and facilitates access to light for periphytic algae (Pettit et al. 2016).

The morphological complexity of macrophytes plays an important role in the structuring of aquatic communities, promoting changes in the composition and biotic interactions, as observed by Tokeshi and Arakaki (2012) and in the present study. Furthermore, Schneck et al. (2011) and Wolters et al. (2018) observed the same in streams and rivers. The diversity of complex structures is essential for a

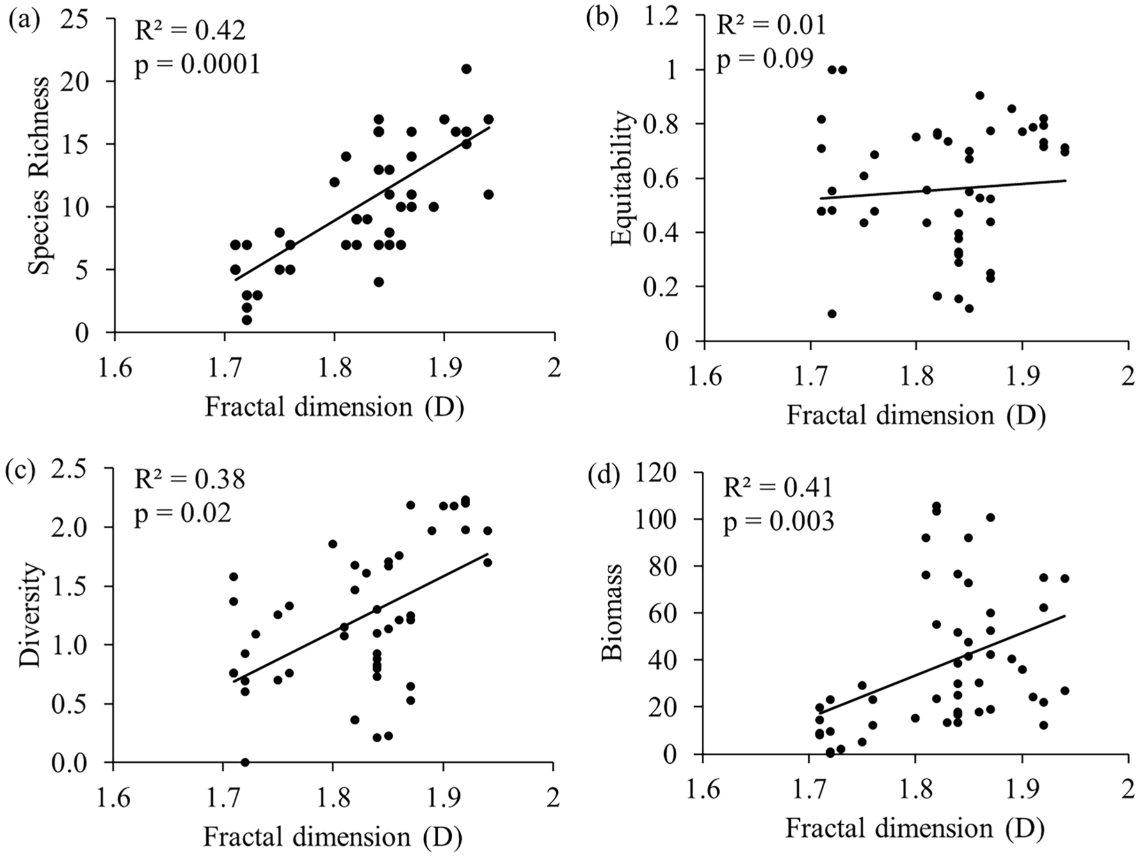


Fig. 6 Relationship between the structural complexity of macrophytes and **a** species richness, **b** equitability, **c** species diversity (bits ind^{-2}), and **d** biomass of macroinvertebrates (ind g^{-1})

high variety of niches and increasing species richness (Pierre and Kovalenko 2014). Therefore, habitat complexity is important for maintaining biodiversity because its simplification can result in species losses. Fernandes et al. (2016) observed that the periphytic algae assemblages were different among the macrophytes investigated, even among those occurring in the same sampling sites, thus they believe that the algae developed colonization mechanisms for the different substrates. Therefore, periphytic algae may be related to the morphology and roughness of macrophytes, as suggested by other studies (Thomaz et al. 2008; Sultana et al. 2010).

The increased availability of niches promoted by macrophytes with higher morphological complexity was important for increasing the structural attributes of algae and macroinvertebrates. This is because the increase in physical spaces leads to more complex habitats and creates habitable interstitial spaces that provide a greater diversity of niches (Tokeshi and Arakaki 2012). The increased niches, promoted by the morphological complexity of macrophytes, allows different species with diverse requirements to colonize these microhabitats (Osório et al. 2019). Some studies show that the biomass, richness and diversity of algae and macroinvertebrates are higher in macrophytes with higher biomass. However, we did not observe this pattern in our study. In addition, we observed that only the epiphyte biomass positively correlated with the macrophyte biomass (dry weight), since the other structural attributes of algae and macroinvertebrates did not show a significant relationship. Biomass and macrophyte volume can be used to measure habitat availability for aquatic organisms (Rennie and Jackson 2005). However, da Silva and Henry (2020) observed that the abundance and richness of macroinvertebrates were higher in the macrophyte with the lowest root biomass compared to the macrophyte with the highest biomass. Similar results were found in a comparative study of the fauna associated with floating macrophytes, in which *Salvinia molesta* (low biomass) sheltered a higher density of macroinvertebrates than *E. crassipes* (high biomass) (Diarra et al. 2018).

The functional groups of periphytic algae based on adaptive strategies were more sensitive to changes in macrophyte complexity. For periphytic algae, the groups defined by the adaptive strategies vary more in relation to the environmental changes when compared to taxonomic groups at the family or class levels (dos Santos et al. 2013; Rangel et al. 2016). Typically, responses at higher taxonomic levels (family or class) occur during strong disturbances

(Cottingham and Carpenter 1998). Our results showed that the functional characteristics responded to the complexity of macrophytes and physicochemical variables. Moreover, we did not observe a relationship between functional groups and macrophyte life forms, but we observed a direct relationship with the morphological complexity of macrophytes.

Usually, the metaphytic species (entangled) *Aulacoseira granulata* var. *angustissima*, *Phormidium hamelii* and *Pseudanabaena* sp. were predominant and correlated to light intensity and dissolved oxygen. These species have no fixation structures to adhere them to the substrates and are located more superficially in the periphytic matrix, being more susceptible to strong disturbances (Passy and Blanchet 2007; Dunck et al. 2016), which did not occur during the study period. In addition, the stalked algae also presented high biomass throughout the study. The predominance of the stalked functional group occurs in environments without nutrient restriction and is where diatoms typically predominate (Lange et al. 2011). Pedunculated algae are easily consumed by herbivorous macroinvertebrates due to their location and exposure in the periphytic matrix. Pedunculated diatoms grow rapidly in environments with low nutrient availability but are quickly consumed by herbivores (Vadeboncoeur and Power 2017). This may explain the positive relationship between macroinvertebrate biomass and diatoms. In our study, the herbivores, represented by mollusks, Chironomidae, and Copepoda Calanoida were probably responsible for the positive relationship between macroinvertebrates and diatoms.

The lack of strong disturbances, with no intense rainfall and stability of water level in the reservoir, promoted the dominance of firmly adhered species, such as *Gomphonema gracile* (stalked) and *Synedra ulna* (prostrate). Due to such adhesion, firmly adhere species are more resistant to disturbances and remain in the periphytic matrix, providing substrate for other species to adhere (Tuji 2000; Passy and Blanchet 2007). Moreover, the presence of macrophytes with high structural complexity protects the epiphytic algae against disturbances and favor the growth of species with different adaptive strategies (Squires et al. 2009; Casartelli and Ferragut 2015). Our results also demonstrated that macrophyte structural complexity is an important factor influencing the macroinvertebrate community structure. Increased macrophyte complexity provides greater variety, size, and form of epiphytes that can be consumed by herbivorous macroinvertebrates (Taniguchi et al. 2003; Casartelli and Ferragut 2018). Therefore, increased biomass of epiphytes with different life forms and adherence, along with the macrophyte complexity synergistically influenced herbivorous invertebrates.

The structural complexity of the macrophytes showed strong positive effects on periphytic algae (Fig. 2) and macroinvertebrate (Fig. 6) community structure. Therefore, we conclude that the heterogeneity of the habitat, promoted by the structural complexity of macrophytes, is fundamental for increasing the richness, biomass, and diversity of epiphytic algae and macroinvertebrates. The functional characteristics of the epiphytic algae were related to some physicochemical variables in the water and the morphology of macrophytes. Macroinvertebrates were positively influenced by the increased algae biomass and macrophyte morphology.

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Data availability statement Data, associated metadata, and calculation tools will be made available on request to the corresponding author (ariadne_moura@hotmail.com).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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