



The role of macrophyte architecture in driving periphytic algal communities in a lowland river in the Brazilian Amazon

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Abstract

Aquatic macrophytes have a key role in aquatic ecosystems because they can structure biotic communities by offering habitat for many aquatic organisms, especially periphytic algae. The aim of this study was to evaluate the periphytic algal structure (taxonomic diversity and functional traits) in two macrophytes with different architectures (*Nymphaea* L. and *Cabomba* Aubl.). We tested the hypothesis that architectures of the *Nymphaea* and *Cabomba* affect in a different way the periphytic algae community, increasing taxa richness and density in more complex substrate (*Cabomba*), and that the taxa composition, life form and adherence form are different between both types of macrophyte. In addition, we tested whether there is higher algae density without a fixed structure on complex substrate. The study was conducted in Caxiuanã National Forest, one of the largest protected areas in the Pará state, Eastern Amazon. The samplings were made in blocks with two levels (*Nymphaea* and *Cabomba*) under the same abiotic conditions. Our results showed that there was a significant difference in taxa richness and density between macrophytes, with higher values in *Cabomba*. We found more exclusive species in more complex substrate (70, *Cabomba*), than less complex substrate (19, *Nymphaea*). Furthermore, species composition, life form and adherence form also showed differences between macrophytes, with higher algae density without a fixed structure on *Cabomba*. These results indicated that when the source of algal propagules is the same (mixed bank of macrophytes), the habitat complexity tightly influenced the diversity of periphytic algae community.

Keywords *Cabomba* · Caxiuanã · *Nymphaea* · Periphyton · Substrate complexity

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1 Introduction

Aquatic macrophytes have been considered an important component in rivers, streams, lakes and reservoirs (Dodds and Biggs 2002; Jeppesen et al. 2012; Ferreira et al. 2013; Kelly et al. 2016). In these ecosystems, they are a favorable habitat for biotic colonization, which can be attributed to heterogeneity provided by their architectural complexity (Hinojosa-Garro et al. 2010; Dos Santos et al. 2013). Habitat complexity proposes that complex physical structures act to increase species richness by providing an increased number of habitat or resources (MacArthur and MacArthur 1961; Pierre and Kovalenko 2014). Then, more resources allow more species to coexist in a given area. However, the effects of habitat complexity may vary depending on what is perceived as a habitat by the species group studied. For example, macrophyte complexity is generated mainly by irregularities (e.g., crevices, projections) on the surface of some structures, which act as substrate and are important determinants of local species diversity for many organisms

groups, such as fish (Warfe and Barmuta 2006), macroinvertebrates (Walker et al. 2013) and periphytic algae (Dos Santos et al. 2013).

Periphytic algal communities are also important components of aquatic ecosystems because they contribute to the primary production and are the bases of food webs (Azim et al. 2005; Uieda and Motta 2007). They can be influenced by availability and diversity of substrates in the environment (Cattaneo et al. 1997), especially macrophytes (Biolo and Rodrigues 2013; Biolo et al. 2015), which are favorable substrate for its development and colonization (Burkholder 1996; De Souza et al. 2015). The morphological characteristics of macrophytes (including leaves, stems and roots) supply a structurally complex environment for periphytic algae because they provide places of shelter, feeding, and reproduction and, furthermore, contribute to avoiding grazing (Bergey 2005; Schneck et al. 2011; Fernandes et al. 2016). Therefore, macrophyte architecture becomes essential for the establishment and development of periphytic algae (Dos Santos et al. 2013). A complex architecture may offer increased abundance (Hao et al. 2017), biomass (Gross et al. 2003), species diversity (Biolo and Rodrigues 2013) and a particular species composition (Ferreiro et al. 2013) of periphytic algal community. The relationship between macrophytes and periphytic algae also can be influenced by the macrophyte specificity and physiology, like excretion, decomposition and production of allelopathic substances (Cattaneo and Kalff 1979; Burkholder 1996).

There are many growth forms and life histories among the periphytic organisms that can favor to attach to different substrate types (Round et al. 1990; Burliga et al. 2004; Schneck and Melo 2012). Hence, species respond differently to the physical and environmental conditions, according to their biological characteristics (Bixby et al. 2009). More complex habitats provide large quantities and wide varieties of resources and high availability of physical refuges (Brown 2003). For instance, adnate species with prostrate growth forms have tight adhesion structures, features that allow them resistance to disturbance (Peterson and Stevenson 1992). On the other hand, other algae, such as motile and metaphytic species, are less resistant and may benefit mostly from the presence of refuges in more complex substrates (Schneck et al. 2011). Some filamentous algal species may present differentiated cells for attachment to substrates, which can favor their permanence in less complex substrates (Stevenson 1996). On the other hand, colonial algae do not present structures for adherence, but mucilage helps to entangle in periphytic matrices (Stevenson 1996).

Despite the great importance of the Amazon's global biodiversity, little is known about the ecology of periphytic algae for this biome. Some studies have demonstrated the importance of riverine flooding on structure, nutrient status and productivity of periphyton (Engle and Melack 1993;

Putz 1997; França et al. 2009), seasonality effects in the structure (Aprile and Mera 2007) and successional stages of these communities (França et al. 2011). Moreover, currently the knowledge about the ecology and taxonomy of diatoms has been more prominent for this biome (e.g., Diaz-Castro et al. 2003; Burliga et al. 2007; Ferrari et al. 2007; Melo et al. 2010; Pereira et al. 2013, 2015; Tremarin et al. 2013; Wetzel et al. 2010, 2012a, b, c; Azevedo et al. 2018).

Aquatic macrophytes species range from more complex structures to less complex structures, providing different substrates to periphytic communities (Dos Santos et al. 2013). To understand the role of substrate architecture in driving periphytic algae community (taxonomic diversity and functional traits), we compared two species of macrophytes, one with a simple physical structure (*Nymphaea* L.) and the other with a more complex one (*Cabomba* Aubl.). We hypothesized that architectures of the *Nymphaea* and *Cabomba* affect in a different way the periphytic algae community. Our predictions are as follows: (1) *Cabomba* has a higher richness and density compared to *Nymphaea*, (2) taxa composition, life form and adherence form are different between both macrophytes, and (3) there is higher algae density without a fixed structure on *Cabomba*, which allows these organisms to exploit crevices and, consequently, to have more refuges.

2 Materials and methods

Study area – Our study was carried out in the Anapu river basin, located in the surrounding of the Caxiuanã National Forest, one of the largest protected areas in the Pará state, Eastern Amazon. The area is covered by dense *terra firme* rainforest and lowland swamp forests (Lisboa et al. 1997). The local climate is of the “Am” type in the Köppen classification system (hot and humid tropical), with a short dry season between August and November, and a much longer rainy season, from December to July (Oliveira et al. 2008). Anapu river is a typical black water system, characterized by low pH and electrical conductivity and high concentrations of humic composts (Costa et al. 2002). The water flow has very low intensity and varies discreetly (rarely exceed 1 m), with little differentiation between seasons, but suffers a daily flood cycle caused by tide due to proximity to the Amazon estuary.

Tectonic activity during the upper Pleistocene and Holocene (Quaternary) associated with the transgression of the Atlantic Ocean during the last Wisconsin oscillation modified the geomorphology and hydrodynamics of the Anapu River and its tributaries, by blocking the normal drainage of these rivers (Behling and Da Costa 2000; Costa et al. 2002). Because of this geological event of valleys drowning of the Anapu river, the region is defined as a fluvial ria (Bertani

et al. 2015), showing a reduced annual flood pulse (Behling and Da Costa 2000). This process led to chemical changes in the water and the loss of flow, creating a continuous process of sediment deposition. The local streams and rivers have become lentic environments, with areas of unflooded *terra firme* forest reaching almost to the margins of the rivers (Behling and Da Costa 2000).

Sampling design – We collected periphytic algae from petioles of *Nymphaea* and *Cabomba*, which are two genera of macrophytes belonging to the families Nymphaeaceae and Cabombaceae, respectively. Both belong to the order Nymphaeales, which includes about 80 species, almost half of which belong to the genus *Nymphaea* (Bosch et al. 2008). Nymphaeales is a monophyletic group, representing one of the oldest strains among angiosperms (Judd et al. 2009). These two genera are fixed to the soil and are herbaceous, with floating stem, and are generally found in soils rich in organic material yet have distinct morphology. *Cabomba* is submerged and has a branched stem, with one or more branches per node, simple or branched. *Nymphaea* does not have a branched stem. The limbs of the leaves and flowers are elevated on the water surface through petioles and peduncles. Both macrophytes have distinct structural complexity, life form and substrate specificity (excretion, decomposition and production of allelopathic substances) (Judd et al. 2009). Due to the morphological characteristics, the architecture and complexity of these two macrophytes, we consider the two opposite complexities (more complex and less complex) as a main structuring factor on periphyton, without neglecting the other factors that occur in natural conditions.

We sampled six points along the Anapu river, with similar macrophyte banks (in size and richness) near the coastal areas of the river without shading by riparian vegetation. The six points represent six blocks, each one with two levels (*Nymphaea* and *Cabomba*) under the same conditions, totaling six samples for each macrophyte. The block sampling design allows samples from each bank to have the same pool of propagules. The distance between the sampling sites is 2 km, on average, covering approximately 3 km².

Limnological variables were measured at each site with multiparameter Horiba U-50 (temperature (°C), pH, conductivity (mS cm⁻¹), dissolved oxygen (mg L⁻¹) and total dissolved solids (mg L⁻¹)), just to confirm that the sites had similar physicochemical water characteristics (Table 1). In each point, we sampled one petiole from each macrophyte, and the sampling material was taken through scraping petioles using toothbrush and jets of distilled water (Algarte et al. 2014). The scraped areas were measured using ImageJ program, to be used in the density algae estimation, and the samples were fixed with 0.5% acetic Lugol.

The samples (material scraped) were quantified using sedimentation chambers in an inverted microscope (Utermöhl 1958) and sedimentation time followed Lund et al. (1958). The counting method consisted in random fields until reaching at least 100 individuals (cells, colonies or filaments) from the most dominant species and until the curve of species accumulation begins to decline (Ferragut and Bicudo 2012). The species density was estimated according to Ros (1979) using the scraped areas for estimation in a number of individuals per unit area (ind. cm⁻²). The classification system used was Round (1971). The functional traits of species were observed during the counting and identification of the species. We classified the periphytic algae according to two morphological functional traits: life form (non-motile unicellular, filamentous, flagellate, or colonial) and adherence form (motile, entangled, prostrate, stalked, or heterotrichous-differentiated basal cell) (Biggs et al. 1998; Bicudo and Menezes 2006; Schneck and Melo 2012; Dunck et al. 2016).

Data analysis – Initially, we checked the data for normality, and then we tested the differences in taxa richness and density of the periphytic algae between macrophytes with paired t tests (assuming normality), because each pair of samples (*Nymphaea* and *Cabomba*) was taken in the same macrophyte bank in a block sampling design (Schneck et al. 2011). A permutational multivariate analysis (PERMANOVA) based on 1000 permutations ($P < 0.05$) (Anderson 2001) was used to test differences in taxa composition, life form and adherence form of periphytic algae between macrophytes. A

Table 1 Physicochemical water characteristics from each sampled site

Site	Temperature (°C)	pH	Conductivity (mS cm ⁻¹)	Dissolved oxygen (mg L ⁻¹)	Total dissolved solids (mg L ⁻¹)
01	30.61	8.28	0.014	7.39	0.5
02	31.22	9.34	0.012	8.28	0.6
03	30.42	8.51	0.013	7.08	0.5
04	31.18	9.19	0.012	9.67	0.2
05	31.16	9.14	0.012	8.67	0.7
06	31.81	9.26	0.012	8.13	0.2

The six points representing six blocks, each one with two levels (*Nymphaea* and *Cabomba*)

principal coordinates analysis (PCoA) was conducted using the Bray–Curtis similarity index, with the taxa composition, life forms and adherence forms based on density data transformed into $\log(x + 1)$ values (Clarke and Warwick 1994) to visualize potential grouping patterns among the periphytic algal communities. We used a paired nonparametric Wilcoxon test ($P < 0.05$) to compare the density of motile algae between macrophytes given the non-normality of data was detected. This analysis was to verify if there is higher algae density without a fixed structure on more complex substrate. All analyses were conducted with the software R (R Core Team 2018).

3 Results

For physicochemical water characteristics, the sites presented the following average values: temperature of 30.9°C (± 0.6), pH of 8.9 (± 0.5), conductivity of 0.012 mS cm^{-1}

(± 0.001), dissolved oxygen of 8.9 mg L^{-1} (± 1.5), and total dissolved solids of 0.7 mg L^{-1} (± 0.5) (Table 1).

We identified a total of 149 taxa of periphytic algae belonging to 11 classes, in which Bacillariophyceae and Zygnematophyceae were dominant (Supplementary material, Table S1). In the *Nymphaea* were recorded 79 taxa in total, in which 19 are exclusive of this treatment, while *Cabomba* had 130 taxa in total and 70 exclusive ones. Sixty taxa were found at both macrophytes. *Frustulia saxonica* Rabenhorst was the most abundant species on *Nymphaea* and consequently showed higher density ($201,845 \text{ ind. cm}^{-2}$). For *Cabomba*, *Nitzschia filiformis* (W. Smith) Van Heurck was the species that showed the highest density ($988,655 \text{ ind. cm}^{-2}$).

There was a significant difference in taxa richness ($t = 8.265$, $DF = 5$, $P < 0.001$) and density ($t = 2.332$, $DF = 5$, $P = 0.034$) between macrophytes (Fig. 1a–b). Taxa richness and density were higher in *Cabomba* with, on average, an additional 25 species and $157,141 \text{ ind. cm}^{-2}$, respectively, when compared to *Nymphaea*.

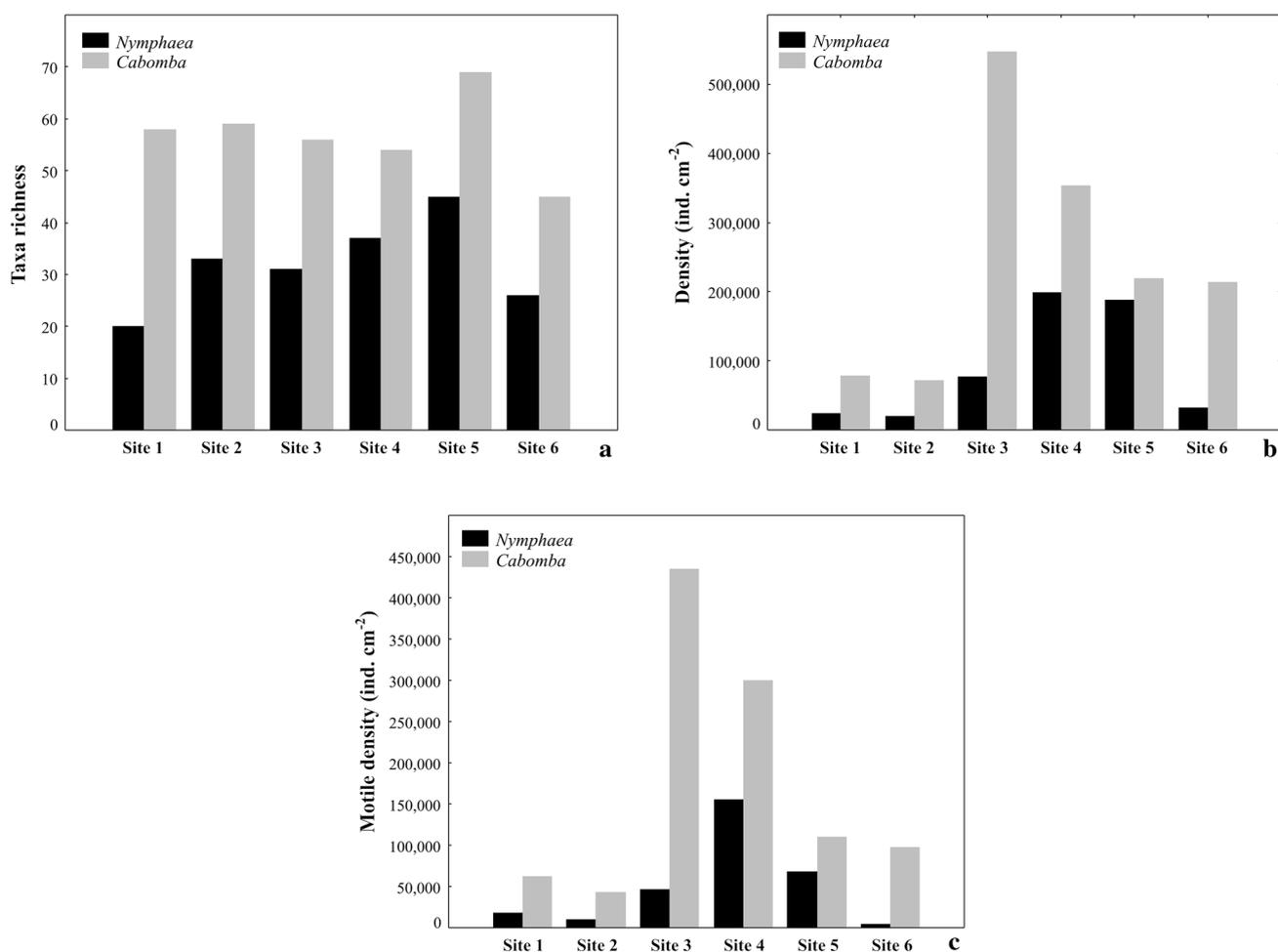


Fig. 1 Taxa richness (a), total density (b) and motile form density (c) of periphytic algae for *Nymphaea* and *Cabomba*

PCoA showed separation of the communities between macrophytes, and PERMANOVA confirmed that species composition ($pseudo-F = 3.877$, $P = 0.001$), life form ($pseudo-F = 15.998$, $P = 0.002$) and adherence form ($pseudo-F = 5.614$, $P = 0.023$) were different between the two treatments (Fig. 2a–c).

Unicellular was the most dominant life form at both macrophytes, with 53 species and 528,900 ind. cm^{-2} in *Nymphaea* and 99 species and 1,464,457 ind. cm^{-2} in *Cabomba* (Fig. 3a). On the other hand, colonial form was not found in *Nymphaea* and it was found in lower abundance in *Cabomba* (only 3 species and 603 ind. cm^{-2}). In *Nymphaea*, flagellate form presented the lowest abundance (only 3 species and 90 ind. cm^{-2}). As for the adherence form, all types were found at both macrophytes; however, motile species were the most abundant form, with 8 species and 302,555 ind. cm^{-2} in *Nymphaea* and 12 species and 1,049,061 ind. cm^{-2} in *Cabomba* (Fig. 3b). Nonetheless, when testing this density, we found differences between the two macrophytes ($W = 21$, $P = 0.016$; Fig. 1c), showing that there was higher

algae density without a fixed structure on complex substrate (*Cabomba*).

4 Discussion

The hypothesis that architectures of the *Nymphaea* and *Cabomba* affect in a different way the periphytic algae communities was supported in our study. Taxa richness and density were higher on *Cabomba*, and taxa composition, life form and adherence form were different between both types of macrophyte. Thereby, the macrophyte architecture was an important factor for influencing different diversity metrics of periphytic algal assemblages. In addition to the distinct structural complexity of the two macrophyte species, they have distinct life form and substrate specificity that together may have influenced the periphytic algae communities.

In comparison with *Nymphaea* species, the higher habitat complexity in *Cabomba* architecture provides many refuges and habitats for algae colonization and, consequently,

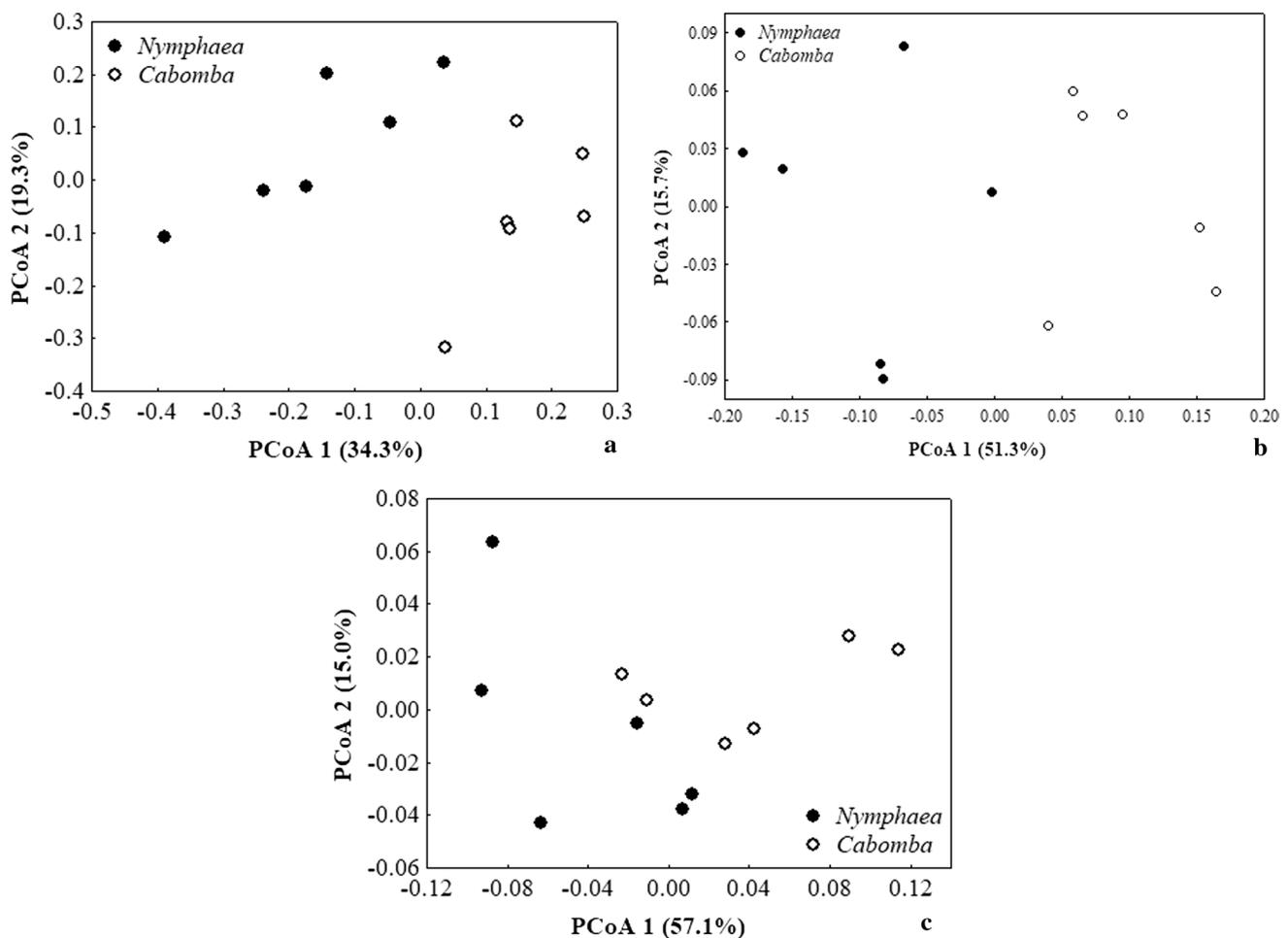


Fig. 2 Principal coordinates analysis (PCoA) of the taxa composition (a), life form (b) and adherence form (c) of periphytic algae

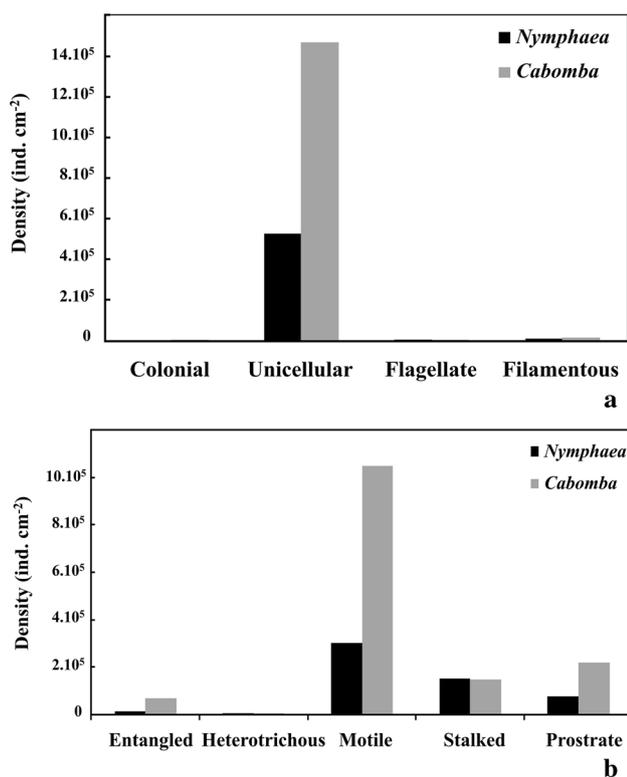


Fig. 3 Density of periphytic algae by life forms (a) and adherence form (b) in *Nymphaea* and *Cabomba*

increases the algal richness and density. Many studies found positive effects of the substrate complexity on periphytic algae provided by macrophyte architecture (Lucena-Moya and Duggan 2011; Schneck et al. 2011; Fernandes et al. 2016; Osório et al. 2019). Considering our results, the morphological characteristics of *Cabomba* support an increase in periphytic density and taxa richness, because this macrophyte provide greater varieties, sizes, and shapes of habitat for these organisms, potentially facilitating the coexistence of different periphytic algal species. Although this study did not evaluate the physiological characteristics of the macrophytes, such as the production and transfer of organic compounds to their periphery, this aspect can likewise relate to increment in periphytic algae diversity (Pip and Robinson 1984). Besides, the *Cabomba* provides a wide and favorable area for periphytic algae colonization according to its size and structure and also can improve nutrients for periphytic community (Kahlert and Pettersson 2002; Murdock and Dodds 2007).

In situ physical factors interact to produce responses by periphytic algae community. For example, a change in level of light intensity on microenvironment can affect vertical colonization of these organisms (Villeneuve et al. 2010). That is, the occurrence of certain species depends on the solar radiation that penetrates the water column as well

as the self-shading within the periphytic algal community (Müller 1996; Albay and Akçaalan 2008). *Nymphaea* has a large leaf area above its petiole, which leads to a reduction in light intensity on its submerged petiole and consequently on the periphytic algae diversity that it hosts. On the other hand, *Cabomba* has a small leaf and may support higher accumulation of periphytic algae due to greater input of solar radiation on its petiole. In addition, both young and mature periphytic algae can be affected by the lower level of light intensity, enhancing the number of algal cells on macrophyte (Villeneuve et al. 2010).

Another mechanism that could account for the positive relationship between substrate complexity and periphyton diversity is the accumulation of organic matter on macrophyte. Generally, the greater the leaf dissection and intricate branching of a submerged macrophyte, the larger and more varied was the periphyton associated with it (Bergey 1999). In addition, low current speed such as found in Anapu river favors the accumulation of organic matter. Thereby, *Cabomba* has an architecture and environmental conditions that can be closely related to organic matter deposition on its leaves, providing more nutrients for periphytic community, and consequently leading to an increase in richness and density when compared to *Nymphaea*. It may even explain the highest abundance of *Nitzschia filiformis* in *Cabomba* because this species can develop an optional heterotrophy strategy (Tuchman 1996), being able to explore the organic matter in abundance.

The differences found in periphytic algae taxa composition between macrophytes *Nymphaea* and *Cabomba* may be due to selection of some taxa regarding the macrophyte species (Santos and Ferragut 2018). Moreover, it can also be explained by the colonization process, as reported in other studies (Fernandes et al. 2016; Elias et al. 2017). Periphytic algae species can show substrate preferences during the colonization stage on macrophytes (Schneck et al. 2011). Furthermore, environments with a greater structural complexity host species with different functional characteristics, yielding greater diversity than in homogeneous areas due to the increased availability of niches (Pacini et al. 2009; Fernandes et al. 2016). This may also help explain why the number of exclusive taxa was higher in substrates with a higher complexity (*Cabomba*) than substrates with a less complexity (*Nymphaea*).

The community structure showed that *Frustulia saxonica* was the most abundant taxon in *Nymphaea*. *F. saxonica* is a diatom that has specialized structures for attachment to the substrate producing mucilaginous matrices (Round 1991). This condition is important and necessary for attachment to a smooth substrate, such as the petiole of *Nymphaea*. Therefore, the highest density values for this species are partly related to their specialized structures that confer a competitive advantage over other species in a lentic system (Biggs

1996; Bichoff et al. 2016). On the other hand, *N. filiformis* showed the highest abundance in *Cabomba*. For being moderately mobile and having a benthic habit (Kociolek 2011), this species is more susceptible to loss or substrate release due to physical disorders (Biggs et al. 1998). For this reason, more complex habitats, such as *Cabomba*, favor their establishment and protection from disturbances, which may explain their predominance on this substrate, when compared to *Nymphaea*. Besides that, *N. filiformis* can develop an optional heterotrophy strategy (Tuchman 1996) that may increase its possibilities to exploit nutrients from different sources.

We also found differences in the periphytic life form between two substrates; however, unicellular forms (such as species of the *Actinella* F. W. Lewis) were the most abundant at both *Nymphaea* and *Cabomba*. Unicellular species are smaller in size compared to other periphytic life forms. Smaller cell size has faster cell division and growth rate (Cox 1991) and thus can colonize substrates at a quicker rate than other life forms. These organisms also have large surface area/body volume ratio, which favors the ability to obtain and metabolize nutrients more rapidly than other life forms (Niklas 2000; Bajpai 2019). This can explain why unicellular life form was abundant at both macrophytes, as they have an ability to colonize quicker due to faster growth rate and can exploit resources unavailable to non-mobile species. The filamentous species are favored by vertical growth in the periphytic matrix, which allows greater access to light and nutrients from the water column (Dunck et al. 2013). This life form has higher light and nutrient requirements and is late colonists compared to other life forms (Steinman and McIntire 1990; Peterson and Stevenson 1992). Thus, its low density at both macrophytes can be due to disturbance caused by constant flow of residents' boats in the river, favoring the growth of unicellular forms. These forms are generally associated with rapid environmental changes (Dunck et al. 2019) and can reproduce faster due to its metabolism.

Colonial forms (*Gloeocapsa* sp., *Merismopedia* sp. 1 and *Merismopedia* sp. 2), although in lower abundance, were found exclusively on *Cabomba*, which is the macrophyte with more complex architecture. Generally, the presence of mucilage in the colonial forms facilitates the permanence in the tangles provided by the leaves and peduncles of the macrophytes. Thus, the *Cabomba* growth form and architecture provide more structure to settle (Schneck et al. 2011), favoring species without a fixed structure on substrates (Liess and Hillebrand 2004). This might explain why our results showed only colonial forms on more complex substrate. On the other hand, its low density may be due to successional stage, because colonial forms are not pioneering colonizers (Biggs 1996), and because of constant physical disturbance by boats, the periphytic algae communities may not be in

advanced successional stage. In addition, colonial forms are usually present in phytoplankton, which is a source of propagules for periphyton.

The predominant adherence form at both macrophytes was motile algae; however, the density was significantly different between them, higher in *Cabomba*. These results corroborate our hypothesis that periphytic algae without a fixed structure would be predominant on more complex substrate, such as *Cabomba*. The most structurally complex substrates (as found in *Cabomba* entangled architecture) can be more efficient for biofilm formation and accumulate more sediment than simpler one (Bergey 1999; Gómez-Ramírez et al. 2019). Therefore, motile algae can move vertically on crevices to exploit resources and obtain protection from grazers or disturbances (Underwood et al. 2005; Murdock and Dodds 2007). Such characteristics combined with the greater structural complexity of the substrate can explain higher density of motile algae in *Cabomba*.

In summary, our results demonstrated the importance of substrate type when the source of algal propagules is the same, in a mixed bank of macrophytes. The macrophyte architecture providing a wider variety of microhabitats could enhance periphytic algae community diversity. *Cabomba* seems to have an important morphological structure compared to *Nymphaea* for the community organization. The life forms and adherence forms may have the same predominance between the substrates, though present with distinct densities.

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Author contributions All authors contributed to the study conception and design. H. Leão quantified the biological material, analyzed the results and wrote the manuscript. LCR Esdar complemented the discussion and revised the language. B. Dunck reviewed and complemented the paper.

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