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Margin distance as a driving factor of macrophyte assembly in a tropical reservoir

Distância da margem como fator modulante da assembleia de macrófitas em um reservatório tropical

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Abstract: Aim: Evaluate the structure of the aquatic macrophytes assembly of the Jacarecica II Dam, Areia Branca, Sergipe, and verify if distance from the margin is a driver for species richness, and composition in this environment. **Methods:** We settled transects where we plotted quadrats and subplots. The transects were perpendicular in relation to the reservoir margin, and the first quadrat was placed on the margin with the four following ones completely over the water surface. We estimated cover area for each macrophyte species in each quadrat. Each species was also classified according to its life form. We calculated community indexes and tested the influence of the distance from the margin species, resulting in a richness of 14 species. The species with higher importance value were weedy and ruderal species (*Salvinia auriculata* and *Eichhornia crassipes*). The distance to the margin caused changes in macrophyte assembly and presented negative relation with species richness. **Conclusions:** The studied assembly presents few species, with some presenting great dominance. This dominance reflects the anthropization of these habitats. Besides, the species composition and richness are modified in the sense that emergent and free-floating species co-occur in marginal quadrats, but only free-floating species occur in quadrats that are in areas that are more distant from the reservoir margin.

Keywords: aquatic macrophytes; artificial reservoir; weed species; free-floating species.

Resumo: Objetivo: Avaliar a estrutura das assembleias de macrófitas aquáticas do reservatório Jacarecica II (Areia Branca, Sergipe) e verificar se a distância da margem é um fator estruturante da riqueza e composição de macrófitas nesse ambiente. **Métodos:** Nós instalamos transectos em que foram plotadas parcelas. Os transectos foram plotados perpendiculares em relação à margem e a primeira parcela foi alocada na margem e as outras quatro colocadas em áreas cobertas por água. Nós estimamos a área de cobertura de cada espécie de macrófita por parcela e cada espécie foi classificada de acordo com sua forma de vida. Nós calculamos índices fitossociológicos e testamos a influência da distância da margem na estrutura das assembleias de macrófitas. **Resultados:** Nós amostramos



10 espécies emergentes e quatro espécies flutuantes-livres de macrófitas aquáticas. As espécies com maiores valores de importância foram as espécies ruderais e invasoras (*Salvinia auriculata e Eichhornia crassipes*). A distância da margem alterou a assembleia de macrófitas e apresentou efeito negativo na riqueza de espécies. **Conclusões:** A assembleia estudada apresentou poucas espécies, sendo algumas muito dominantes. Essa dominância reflete a antropização desses habitats. Além disso, a composição e diversidade das espécies são modificadas no sentido de que as espécies emergentes e flutuantes livres co-ocorrem nas parcelas das margens, mas apenas as flutuantes livres ocorrem em parcelas mais distantes da margem.

Palavras-chave: plantas aquáticas; reservatório artificial; infestação; flutuantes livres.

14 macrophyte species in Jacarecica II Dam

Graphical Abstract



1. Introduction

Aquatic macrophytes can be defined as macroscopic plant species with distinct roots and shoots (Malthus, 2017) that occur on seasonally or permanently wet habitats (Padial et al., 2008). This definition includes a plethora of phylogenetically distinct lineages (Esteves, 1998), forming an ecological group composed of angiosperms, pteridophytes, and bryophytes (Bianchini Junior, 2003). Due to their high diversity, these plants hold relevant function on nutrients cycling and supply in continental aquatic ecosystems (Esteves, 1998), also providing food and habitat for the fauna (Trindade et al., 2010). Aquatic macrophytes present a wide variety of life forms that are usually distributed according to the depth of aquatic environments (Esteves, 1998; Pedralli, 2003; Pott & Pott, 2000).

Water depth is usually highly correlated with other limnological variables, productivity, and diversity of biological communities. In aquatic ecosystems, the variability of depth can modulate the concentration of phosphates, oxygen and the total amount of radiation that penetrates the water body (Esteves, 1998). In this way, the diversity of aquatic organisms responds to depth gradient, with relationships documented for phytoplankton, zooplankton, invertebrates and aquatic macrophytes (Jeppesen et al., 1997; Esteves, 1998; Noleto et al., 2019). Aquatic macrophyte richness and diversity are negatively related to depth and margin distance, what drives changes in species composition along the depth gradient (Alves et al., 2011; Noleto et al., 2019). The high diversity in marginal zone of tropical water bodies are related to the high diversity and dominance of emergent species that can survive to floods and dry seasons (Thomaz et al., 1999; Pott & Pott, 2000; Moura-Júnior & Cotarelli, 2019).

In anthropized environments, macrophyte assemblages can suffer great changes. For example, in artificial reservoirs these assemblies may become problematic in relation to ecosystem functioning (Thomaz & Bini, 2003), and to human activities (Esteves, 1998; Pedralli, 2003). These problems are mainly caused by weed species that undergo populational explosions driven by environmental modification, as the increase in nutrients concentration in the reservoir (Esteves, 1998; Thomaz & Bini, 2003; Pedralli, 2003). Populational explosions of weed macrophytes can lead to reductions in solar radiation and oxygen concentration in aquatic ecosystems (Esteves, 1998; Pompêo, 2008). Based on this information, monitoring aquatic macrophytes is a central tool to guarantee the adequate functioning or reservoirs, by recognizing weed species and/or detecting environmental changes (Pompêo, 2008).

The Jacarecica II Dam is an important reservoir found in the Sergipe State and is described as a potential source of species with high potential to colonize and become weeds in other areas (Almeida & Fabricante, 2021). The studies concerning the aquatic macrophytes of the Sergipe State are recent and limited to species checklists (Almeida & Fabricante, 2020, 2021). Added to that, the area is considered a knowledge gap about aquatic macrophytes in northeastern Brazil (Moura-Júnior & Cotarelli, 2019). Anyway, the studies of Sergipe show a high richness of emergent macrophytes and a low and limited composition of other life-forms with various weedy free-floating species (Almeida & Fabricante, 2020, 2021).

Therefore, our study aims to answer the following questions: (i) what are the macrophyte species that occur in Jacarecica II Dam, (ii) what are the dominant species in this reservoir, (iii) is the structure of the aquatic macrophyte assemblies modified by the distance from the reservoir margin? We expect that species with high cover areas and importance values, that we defined as dominant, will be those that are already considered as weedy species in the literature. We also hypothesized that the distance from the reservoir margin is a driver for macrophyte assemblies' richness and composition, with a change of these community parameters within the distance increase, since different life forms are ought to occupy different compartments in the transition between terrestrial and aquatic environments.

2. Material and Methods

2.1. Study area

The Jacarecica II Dam is an artificial reservoir that was created in 1987 based on the need of water supply for an irrigation area. The principal crops benefited by this irrigation perimeter are peanut, sweet-potato, banana, sugarcane, cowpeas, yam, and manioc. In 2021 the area presented a production of 8.247 ton that summed an estimated valued of R\$ 20 million. Besides the initial purpose of irrigation, the reservoir is also used to fisheries and entertainment. The reservoir waters are also being recently used to water provision to some Malhador villages, benefiting near 12 thousand people (COHIDRO, 2022).

The reservoir covers an area of 260 ha and can store up to 30.4 million cubic meters of water (COHIDRO, 2022). The region climate can be described as Tropical with dry summer (As) according to Köppen (Alvares et al., 2013) with a mean precipitation of 1411 mm and 23°C of mean temperature (COHIDRO, 2022). The soils around Jacarecica II Dam are classified as red-yellow podzolic soils (COHIDRO, 2022) with a mosaic of bare soil, cultivation zones and fragments of Atlantic Forest. Previous studies suggest that weedy macrophytes species may be profiting from the anthropic changes that occurred in the reservoir area (Almeida & Fabricante, 2021).

It is located in the *agreste* region of Sergipe, in the municipalities of Malhador and Areia Branca. This reservoir receives water from Jacarecica River, Marcela Stream and from lots of small water bodies that are originated in the national park of Serra de Itabaiana, a protected area neighboring the reservoir (Almeida & Fabricante, 2021). The data sampling occurred between January 3 and May 6, 2021, comprising the summer which are warm and dry months. Data sampling took place at three different points (Figure 1), where five, nine and six transects were installed, respectively.

2.2. Data sampling

We settled a total of 20 transects that were perpendicularly placed in relation to the water reservoir along the study site margin (Ferreira et al. 2010). Each transect was 5 meters long and was placed 20 m apart from the others. We divided the transects into five sampling quadrats of 1 m². These quadrats were divided in distance groups, with the reservoir margin as a reference point: D1 (0 m), D2 (1 m from the margin), D3 (2 m from the margin), D4 (3 m from the margin), D5 (4 m from the margin). The first quadrat (D1) was placed to allow the other quadrats (D2 to D5) to be completely inserted over the water body (Figure 2). Water depth have a strict relationship with the distance to margin (Ferreira et al., 2010; Noleto et al., 2019), so in this study we use distance to margin as a proxy for depth.



Figure 1. Map with the location of Jacarecica II Dam, where we sampled aquatic macrophyte assemblages. Five transects where installed in point 1, nine in point 2 and six in point 3.



Figure 2. Transects and quadrats system applied to the sampling of aquatic macrophyte assemblies of the Jacarecica II Dam, Areia Branca, Sergipe, Brazil.

To evaluate species cover, we divided each 1 m^2 quadrat in 100 subplots (0.01 m x 0.01 m) and counted the number of subplots filled by each species. We considered as macrophytes all the plant species with distinct roots and shoots (Malthus, 2017) that were present inside the water body or in contact with the water, including those species that occurred on saturated wet soil (Irgang & Gastal, 1996).

Due the limitations imposed by the COVID-19 pandemic we were not able to collect and deposit plants as vouchers in herbarium collections. The species determination was performed through the comparison of photographs that were taken in the field and material previously sampled in the same region (Almeida & Fabricante, 2020, 2021). Whenever necessary, the images were sent to specialists to obtain the correct name for

each species. We built the taxonomic classification based on APG IV (Chase et al., 2016) and used the Brazilian Flora and Funga (Jardim Botânico do Rio de Janeiro, 2022) to obtain the most correct species and author names. We classified all the sample species in the lifeforms proposed by Pott & Pott (2000) as it follows: emergent, fixed floating, free floating, fixed submersed, free submersed, and epiphytes. We also used the list of aquatic macrophytes from Northeastern Brazil to identify ruderal species (Moura-Júnior et al., 2013).

2.3. Data analysis

We calculated the absolute and relative values of frequency and cover, for each species (Müller-Dombois & Ellenberg, 1974). Cover was obtained by multiplying the total number of subplots that species occur by 0.01 (the area of a subplot in m²). Importance index was calculated summing relative values of cover and frequency. All relative metrics was calculated as the ratio between absolute metric and the sum of entire community (Müller-Dombois & Ellenberg, 1974). Based on these results we applied the word "dominant" to classify those species that presented high values of the importance index in the context of the studied assemblies.

We used generalized linear mixed model (GLMM) with Poisson distribution to test if the richness decreases as the distance to margin increase. In the models the richness of quadrats are used as response variable and distance to margin as a predictor variables with fixed effect. To account the dependence of quadrates of the same transect, the transects was included in model as a random effect (Bates et al., 2015). This test was implemented using the function 'glmer' available in the *lme4* package (Bates et al., 2015).

To test for differences on the macrophyte assemblies composition among the quadrats we built an incidence matrix and calculated the distance among quadrats of different margin distances with Jaccard dissimilarity with the function 'metaMDS', we graphically represented the groups in a Non-metric Multidimensional Scaling (NMDS). Based on this matrix, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) using the distance to margin as predictor variable to determine if the macrophytes species composition change in the distance gradient. Additionally, we also performed pairwise tests to verify the difference between groups. These analyses were implemented using the function 'adonis'. To test if the multivariate dispersion (the average distance of individual samples for their group centroid in a multivariate space) are different between groups we used permutational analysis of multivariate dispersions (PERMDISP; Anderson et al., 2006). This analysis was implemented using the function 'betadisper'. Pairwise comparisons and significance differences in dispersion between groups were permuted with 9999 permutations of PERMDISP results with the function 'permutest' (Oksanen et al., 2021). All these functions are available on the vegan package (Oksanen et al., 2021). All analysis was done in R Software (R Core Team, 2021). The R script and data are available in https:// doi.org/10.5281/zenodo.7738151.

3. Results

We sampled 14 species that belonged to 10 families (Table 1). One species of the Cyperaceae family was not determined in lower taxonomic

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levels. The most representative families were Asteraceae, Cyperaceae, Poaceae and Salviniaceae, represented by two species each. We Only found emergent and free floating macrophytes, each group represented by ten and four species, respectively. The most common species in the distance from the margin gradient were the free-floating ones, *Azolla filiculoides* Lam., *Lemna aequinoctialis* Welw., *Eichhornia crassipes* (Mart.) Solms, and *Salvinia auriculata* Aubl., that occurred in quadrats comprising the five distances from the margin (Table 1).

Free-floating species as *S. auriculata* (21.91 m²), *E. crassipes* (19.06 m²), *L. aequinoctialis* (5.6 m²) and the emergent *Bulbostylis* sp (5.11 m²) (Table 2) presented high absolute covers (AC). The relative cover (RC) highlights *S. auriculata* and *E. crassipes*, that presented values of 36.2% 31.49% respectively. The most frequent species are the same with the highest values of cover. In relation to the importance index, the species with the highest values and considered as dominant are *S. auriculata* (64.06) and *E. crassipes* (51.39) which together have 57.73% of the index (Table 2).

The quadrat species richness decreases towards the deeper sampled areas (Figure 3A; Table 3 - GLMM). The NMDS show that macrophytes composition differ between distance groups which the groups D1 and D2 hold all species and the other groups keep subsets from this composition with D4 and D5 showing the same composition. The ordination well represents the distance matrix with a stress of 0.137 (Figure 3B). We found significant modification pattern of macrophyte assemblies in relation to the distance of the margin of the reservoir (Pseudo F = 9.53, p < 0.001 - PERMANOVA, Figure 3B). Also, the results showed that the distance of the margin decreases the heterogeneity of species composition of macrophytes (F= 3.18; p= 0.02 - PERMIDISP). We found that only the margian group (D1) was significantly different and presented a higher multivariate dispersion when compared to groups D3, D4 and D5 (Table 4; Figure 3C). In other words, the composition of macrophytes of the margin is more heterogeneous than two meters from this place.

4. Discussion

Our results show that the studied area present a high level of ruderal dominant species. This flora only present two life forms (free-floating and emergent plants). In relation to aquatic macrophytes

Fable 1. Aquatic macrophyte species sampled in Jacarecica II Dam, Areia Branca, Se	ergipe, Brazil
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Family/ Species		Distance from the reservoir margin				-	Р
		D2	D3	D4	D5	г	ĸ
ARACEAE							
Lemna aequinoctialis Welw.	1	1	1	1	1	FL	Ν
ASTERACEAE							
Eclipta prostrata (L.) L.	1	0	0	0	0	Е	Y
Enydra radicans (Willd.) Lack	1	0	0	0	0	Е	Ν
BORAGINACEAE							
Heliotropium indicum L.	1	0	0	0	0	Е	Y
CYPERACEAE							
Bulbostylis sp.	1	1	0	0	0	Е	Ν
Cyperaceae sp1	1	1	1	0	0	Е	Ν
ONAGRACEAE							
Ludwigia erecta (L.) H. Hara	1	1	0	0	0	Е	Y
POACEAE							
<i>Eragrostis</i> cf. <i>hypnoides</i> (Lam.) Britton, Sterns & Poggenb.	1	1	0	0	0	Е	Ν
Urochloa humidicola (Rendle) Morrone & Zuloaga		0	1	0	0	Е	Y
POLYGONACEAE							
Polygonum lapathifolium L.	1	0	0	0	0	Е	Y
PONTEDERIACEAE							
Eichhornia crassipes (Mart.) Solms	1	1	1	1	1	FL	Y
RUBIACEAE							
Pentodon pentandrus (Schumach. & Thonn.) Vatke	1	0	0	0	0	Е	Ν
SALVINIACEAE							
Azolla filiculoides Lam.	1	1	1	1	1	FL	Ν
Salvinia auriculata Aubl.	1	1	1	1	1	FL	Y

D1 - 0 m from the reservoir margin, D2 - 0 m from the reservoir margin, D3 - 2 m from the reservoir margin, D4 - 3 m from the reservoir margin, D5 - 4 m from the reservoir margin. F – Life Form (FF – Free Floating and E - Emergent). R - Ruderal Species (Y -yes and N - no).

Table 2.	Phytosociological	parameters of th	e aquatic	macrophytes	assembly	of Jacarecica	II Dam,	Areia	Branca,
Sergipe,	Brazil.								

Species	AF	RF [%]	AC ^(m2)	RC [%]	IVI	RIVI [%]
Salvinia auriculata	56	27.86	21.91	36.20	64.06	32.03
Eichhornia crassipes	40	19.90	19.06	31.49	51.39	25.70
<i>Bulbostylis</i> sp.	16	7.96	5.11	8.44	16.40	8.20
Azolla filiculoides	21	10.45	2.03	3.35	13.80	6.90
Lemna aequinoctialis	8	3.98	5.6	9.25	13.23	6.62
Cyperaceae sp1	15	7.46	2.02	3.34	10.80	5.40
Eragrostis cf. hypnoides	10	4.98	1.58	2.61	7.59	3.79
Ludwigia erecta	10	4.98	0.49	0.81	5.78	2.89
Urochloa humidicola	7	3.48	1.25	2.07	5.55	2.77
Enydra radicans	4	1.99	0.86	1.42	3.41	1.71
Polygonum lapathifolium	6	2.99	0.13	0.21	3.20	1.60
Eclipta prostrata	4	1.99	0.27	0.45	2.44	1.22
Pentodon pentandrus	2	1.00	0.16	0.26	1.26	0.63
Heliotropium indicum	2	1.00	0.05	0.08	1.08	0.54

AF – Absolute frequency value, RF – Relative frequency value, AC – Absolute cover value, RC – Relative cover value, IVI – Importance Index, RIVI – Relative Importance Index.

Table 3. Results of GLMM that tested the effect of distance to margin in macrophytes richness at Jacarecica II Dam, Areia Branca, Sergipe, Brazil.

	Estimate	Std. Error	X ²	p-value
(Intercept)	2.18	0.15	14.17	<0.0001
Distance	-0.63	0.06	-10.11	< 0.0001



Figure 3. A – Relationship between the richness of macrophytes and the distance to margin; B - Non-metric dimensional scaling showing the nested pattern of the composition of aquatic macrophyte assemblies in relation to the distance from the margin of the reservoir in Jacarecica II Dam, Areia Branca, Sergipe. The ellipses show the 95% confidence interval. C – Differences on the the mean multivariate dispersion, among the distance to the margin groups, in which 1 represents the margin itself and 5 represents 5 m far towards the center of the reservoir.

Table 4. Permuted p-value of pairwise comparisons inmultivariate dispersion of macrophytes assemblage inJacarecica II Dam.

	D1	D2	D3	D4
D2	0.096			
D3	0.0021	0.2221		
D4	0.0029	0.1616	0.7329	
D5	0.0071	0.3323	0.9991	0.7819

D1 - 0 m from the reservoir margin, D2 - 1 m from the reservoir margin, D3 - 2 m from the reservoir margin, D4 - 3 m from the reservoir margin, D5 - 4 m from the reservoir margin. Result in bold corresponds to significant values (p<0.05).

assembly structure *S. auriculata* and *E. crassipes* are dominant in the reservoir, presenting the higher values for the phytosociological parameters and importance index. The richness of macrophyte species decrease as distance to margin increase. Our data show that distance to margin modulate the macrophyte assemblies. All these findings support our hypothesis and demonstrate that margin distance modulates richness and composition of macrophytes. In addition, our study presents the first study that aims to understand ecological processes driving aquatic macrophytes assemblies in Sergipe.

The total species richness is low when compared to other studies that were carried in the similar areas. For example, the Marcela weir, reservoir located upstream in relation to the Jacarecica II Dam, 24 aquatic macrophyte species were identified (Almeida & Fabricante, 2020), and the National Park of Serra de Itabaiana, a protected area that is limited by the Jacarecica II Dam, presented a richness of 63 species (Almeida & Fabricante, 2021). The predominance of the Cyperaceae family in aquatic macrophyte floras is common in the earlier published works (Moura-Júnior et al., 2011; Araújo et al., 2012; Almeida & Fabricante, 2021) and reinforces the place of this family as the most representative in the aquatic macrophyte flora of Northeastern Brazil (Moura-Júnior & Cotarelli, 2019). However, this result needs to be interpreted with care, due to field time limitations, our study did not sample the entire reservoir extension.

The species that showed the highest frequency, cover, and index of importance values were those considered as ruderals (Moura-Júnior et al., 2013), that present weedy potential and cause problems in other regions of the world (Thomaz & Bini, 2003; Pompêo, 2008). The dominance of the free-floating species *S. auriculata* and *E. crassipes* may cause ecological problems to the reservoir, as the reduction of light availability for the water

column (Thomaz & Bini, 2003), the decrease of oxygen concentration, chemical changes in the water composition, and the production of toxic gases (Esteves, 1998; Pedralli, 2003). Summed to these problems, high cover of these plants may generate problems for the human populations that use the reservoir, as difficulties for navigation, water supply provision, and sports practices, as well as the maintenance of habitats that are conducive for the development of disease vectors (Esteves, 1998).

The high growth of free-floating species is linked to the fact that reservoirs generally receive high discharges of sediment and nutrients (Thomaz & Bini, 1998), what may favor the population explosions of these opportunist free-floating species (Esteves, 1998; Thomaz & Bini, 2003; Pedralli, 2003). Besides the natural discharges of nutrients and sediments from the streams that feed the Jacarecica II Dam, this area is intensely used by the population, and is a destination for household effluents (Almeida & Fabricante, 2021). In this sense, it is expected that the high concentration of nutrients and sediments that the dam receives drive the dominance of free-floating species (Bini et al., 1999).

We observed that species richness decreases as distance to margin increase. This pattern is explained by the presence of emergent species that can survive the water saturated soils of margin (Pott & Pott, 2000) that is combined with the presence of free-floating species that arrive on the shore due the action of wind and water level changes (Thomaz & Bini, 1998). As the emergent plants are one of the most representative aquatic macrophyte groups in Northeastern Brazil (Moura-Júnior & Cotarelli, 2019), as well as in the Jacarecica II Dam (Almeida & Fabricante, 2021), they add value to the richness of reservoir margins (Boyd, 1971; Thomaz et al., 1999). Even free-floating plants have the ability of occupy areas beyond the water body (Thomaz & Bini, 1998), there are few free-floating species in the studied reservoir. Moreover, other lifeforms that could increase the specie richness far from the margin are absent in Jacarecica II Dam.

The distance influence on the aquatic macrophytes assemblies composition is also justified by the life forms that are found in the Jacarecica II Dam. The differences in composition pattern that we found arises from differences between margin plots and all others. Changes in species composition as distance from margin and depth increase are expected once succession of the life forms of aquatic macrophytes is an already well described pattern (Pott & Pott, 2000; Alves et al., 2011; Noleto et al., 2019). This pattern occurs even in the case of this study where few free-floating plants dominates the assemblage and other life forms are absent. The reduction in heterogeneity of species composition of macrophytes shows once again the low floating species richness and the absence of submerged species in shallower places.

In any case, the compositional modifications and the reduction of heterogeneity found raise other questions. The first question to be raised is whether the dominance of ruderal species justifies the reduction in floating species richness, the absence of submerged species and the homogeneity in composition far from margin? Another question is whether there are submerged and floating species that we did not sample, since another study has already shown that there are few other species in the reservoir. Finally, this study was carried out on a small scale and in a short period of time, is it possible that these patterns are maintained on other banks of the reservoir and in the rainy season when the water level rises?

The Jacarecica II Dam is a very explored reservoir, and exists under severe antrhopic pressures (Almeida & Fabricante, 2021). This environmental situation reflects on the aquatic macrophytes assemblies, that present few species and are dominated by species that cover the entire water surface in some areas of the reservoir. In this scene, we propose that new studies should evaluate the impact of the chemical conditions of the reservoir on the aquatic macrophytes assemblies structure over time. It is also necessary to monitor ruderal species to understand if they cause problems for water use in the reservoir.

5. Conclusions

The aquatic macrophyte assembly of Jacarecica Dam II is formed by few free-floating and emergent species. The structure of this assembly highlights the dominance of some species known for their weedy behavior and this dominance points to an unbalanced ecosystem due to the anthropization of this reservoir. Richness decrease in areas far from the margin and the composition of the macrophyte assemblies in the Jacarecica Dam II shows differences caused by the margin plots which have the higher richness and variability in species composition. This information shows that distance to margin have importance in the macrophyte assemblies. Additionally, new studies are needed to identify possible sampling gaps and whether the observed patterns in this study are maintained throughout the reservoir at other times of the year.

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