Oecologia Australis (ISSN: 2177-6199)
Ahead of print (https://revistas.ufrj.br/index.php/oa/issue/view/1109/showToc)
Article ID: AO#66198
Published online: 17 JULY 2026

Seasonal variations in the macrophyte community of a wetland

SEASONAL VARIATIONS RESULT IN SLIGHT CHANGES IN THE MACROPHYTE COMMUNITY OF AN ATLANTIC FOREST WETLAND

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Abstract. Wetlands are shallow water ecosystems typically dominated by macrophytes. These plant communities play a crucial role in maintaining biodiversity and supporting key ecosystem functions. Their structure is regulated by environmental factors that vary across space and time, such as water temperature and depth. In the Atlantic Forest, climate seasonality is characterized by cyclic, predictable changes throughout the year. Given the importance of understanding the structure and dynamics of macrophyte communities, we analyzed whether the structure and composition of the macrophyte community in an Atlantic Forest wetland changed between hydrological seasons. The expeditions were carried out monthly between May 2019 and February 2020. We estimated macrophyte coverage in 150 plots of 2 by 2 m distributed in six standardized transects. Then, we applied multivariate techniques to summarize the seasonal variation in environmental variables and macrophyte coverage species composition. The composition of macrophyte assemblages showed slight differences between the wet and dry seasons, thus exhibiting mostly similar taxonomic compositions. The seasonal variation had little influence on the dynamics of the macrophyte community in the studied wetland. The analysis shows that the composition of the wetland remained relatively stable between the dry and wet seasons, likely due to the dominance of

abundant species that are not highly sensitive to seasonal variations. Additionally, the results suggest that factors beyond seasonal variations, such as water depth, biotic interactions, or anthropogenic impacts, may play a key role in shaping the structure of this macrophyte community. Understanding the structure and dynamics of macrophyte communities is essential for evaluating the functioning and resilience of wetlands. Identifying the drivers of community stability or change can improve our ability to predict ecosystem responses and inform more effective conservation and management strategies.

Keywords: Diversity, hydrophyte, Neotropical Wetland, floristic inventory, seasonality

INTRODUCTION

Wetlands are shallow-water ecosystems generally dominated by macrophytes (Valk 2012), encompassing freshwater, brackish, and saltwater ecosystems (Cabreira & Fabris 1948). They provide multiple ecosystem services, such as groundwater recharge, drinking water, and organic carbon storage (Junk et al. 2014), in addition to supporting terrestrial species (Chambers et al. 2008). Macrophytes are one of the primary producers in these environments, where they usually contribute to greater habitat heterogeneity and water body complexity, thereby favoring biodiversity and ecosystem functions (Dibble & Thomaz 2006).

The distribution and structure of macrophyte communities are regulated by environmental factors that vary both in space and time, such as depth and transparency (He et al. 2019). Different species are associated with specific habitats depending on their life form (*e.g.*, rooted-submerged, free-floating); therefore, their spatial distribution is determined by environmental variation (Schneider et al. 2018). For example, a decrease in depth can reduce the abundance of submerged species while increasing the abundance of amphibious ones (Mormul et al. 2015). On the other hand, increased transparency benefits submerged species but decreases the abundance of free-floating species (Canalli et al. 2023). These factors may vary across different spatial scales, such as within a lake, along a river course, or from a basin's headwaters to its mouth. They may also vary temporally in response to human impacts, such as mine tailings

(Leal et al. 2023, Silva et al. 2022), or due to natural climatic variability, including seasonal flood pulse (Junk & Wantzen 2004) or interannual climate variation (Hodson et al. 2011).

Seasonal variation in environmental factors, such as rainfall and solar radiation, can greatly shape aquatic ecosystems, changing limnological parameters (Mitchell & Rogers 1984, Wang et al. 2021), available resources (Eimers et al. 2008), and the structure of animal and primary producer communities (Thomaz et al. 2009, Mulderij et al. 2007, Muzaffar & Ahmed 2007, Walker et al. 2013, Ferreiro et al. 2011). In the wet season, rain can lead to an increase in depth and the input of sediments, leading to increased turbidity compared to the dry season (Mitchell & Rogers 1984). Depth and transparency impact the availability of light to macrophytes, which is essential to photosynthesis (Hudon et al. 2000). Increasing depth leads to a decrease in available light, resulting in a decrease in macrophyte biomass. In addition, changes in the photoperiod directly affect photosynthesis and the reproduction of macrophytes (Sultana et al. 2014, Spencer & Ksander 1995, Mitchell & Rogers 1984).

Understanding the factors that may influence macrophytes helps to identify the actions needed to sustain their diversity. Given the importance of understanding the structure and dynamics of macrophyte communities, in this study, we surveyed the macrophyte species in an Atlantic Forest wetland and analyzed whether there are differences in the community structure between the wet and dry periods. Since the Atlantic Forest climate seasonality is characterized by cyclic, predictable changes in temperature, rainfall, and solar radiation throughout the year, we expect that this strong climatic variation will lead to predictable changes in the macrophyte community. In this sense, we expect the highest species richness and coverage in the wet season, given the longer photoperiod and higher allochthonous nutrient input occurring in this season, compared to the dry season. We also expect that both seasons will exhibit different species compositions and richness. In addition, we provided a taxonomic key to subsidize future efforts to study aquatic macrophytes in the Atlantic Forest.

MATERIAL AND METHODS

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Study Area

The study area was located in a wetland in the Atlantic Forest in Southeast Brazil. The wetland Ribeirão das Crioulas (22º34' and 22º35' S, 42º16' and 42º17' W) is in the São João basin (Figure 1). This basin was drained and rectified in the 1950s and dammed in 1978, which increased the flooded area (Cunha 1991). The climate is characterized as hot and wet in the summer (December to March) and cold and dry in the winter (June to September) (Bernardes 1952). The Ribeirão das Crioulas is a Lowland Atlantic Forest, with secondary forests, anthropized fields, and exposed soil. The wetland shows environmental differences between the dry and wet seasons, such as differences in depth and water transparency (Supplementary Material S1-S3). The wetland is adjacent to the Juturnaíba dam and to a conservation unit intended for research and conservation activities (Poço das Antas Biological Reserve).

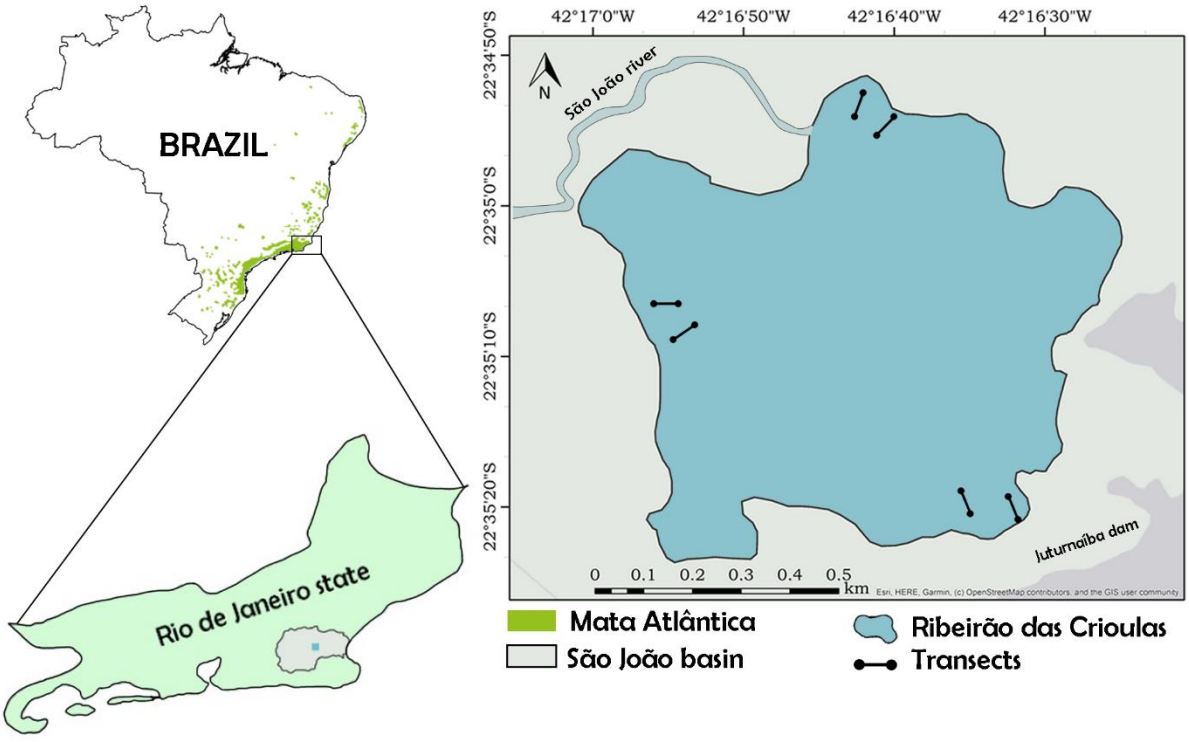

Figure 1. Map of Ribeirão das Crioulas wetland location with six transects sampled demarcated in line with dots.

Sampling design

The expeditions were carried out monthly between May 2019 and February 2020 (except August 2019), including samplings in the dry season from May to September and in the wet season from October to February. We standardized six transects (2 x 50 m) divided into 25 plots (2 x 2 m), ultimately generating 150 plots per month and 1350 plots in total. Environmental variables were sampled in each plot, including pH, relative air humidity, water temperature, room temperature, transparency, rainfall, wind speed, and photoperiod (Supplementary Material S3). The transects were marked perpendicularly to the shoreline to encompass the greatest depth variation possible. We established two transects close to the entrance of the São João River, two in the middle of the wetland and two nearby to the Juturnaíba dam (Figure 1).

Macrophyte coverage in each transect was calculated as the sum of the area in each plot (2 x 2 m) using a quadrat. The coverage of each plot can be up to 4 m² because they can have different life-forms and occupy different portions of the water column (Figure 2). The species were identified based on herbarium material and specialized bibliography (Ichaso 1966, Diego-Pérez et al. 2001, Barros & Xavier 2007, Wagner et al. 2007, Baleeiro et al. 2017, Canalli & Bove 2017, Correia & Bove 2017, Guimarães et al. 2017, Lourenço & Bove 2017; Moreira & Bove 2017) and then registered in the herbarium R (Thiers 2016, see http://sweetgum.nybg.org/ih). The life form was classified by the position in the water column and the rooting mode as amphibious, emergent, floating-rooted, floating-free, submerged-rooted, submerged-free, and epiphytic (Irgang et al. 1984) (Figure 2c). One should note that these life forms represent the categories that the species could be classified in, but not all life forms were found in the sampling site. Several macrophyte species exhibit more than one life form according to the literature (Bove et al. 2003). We classified them based on the life form observed at the study site.

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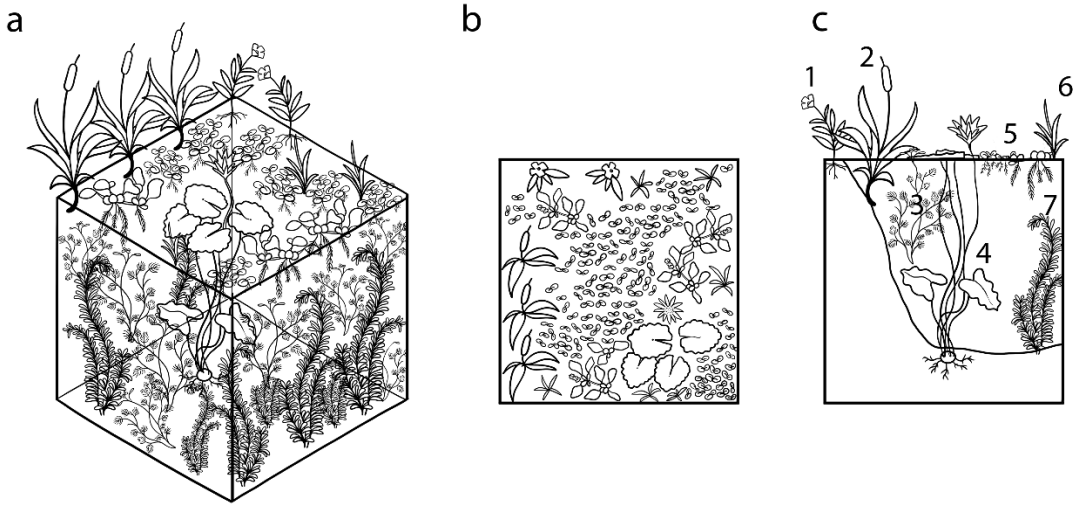

Figure 2. Life-forms and coverage of macrophytes in aquatic environments. a) Slanted view of a longitudinal section demonstrating a plot with coverage above 100%. b) Upper view of plot. c) Longitudinal section with species of all life forms of macrophytes. Amphibious (1), emergent (2), submerged-free (3), floating-rooted (4), floating-free (5), epiphytic (6), and submerged-rooted (7). Canalli, Y. M (2024).

Data analysis

The species frequency was calculated as the number of times each species occurred in the transect, and coverage was the area occupied by each species. We assessed the sampling sufficiency through a rarefaction approach using the Chao 2 index (Chao 1987, Béguinot 2016, Magurran 2004). This index interpolates the data from species number and abundance and extrapolates them, showing the expected number of species if more samples were taken.

We applied the Hellinger transformation with the aim of reducing the dominance effect in the dissimilarity patterns of the most common species in relation to the rare ones while maintaining the patterns between them and decreasing the raw values. The Bray-Curtis coefficient was used to construct the dissimilarity matrices. This index varies from 0 (no dissimilarity) to 1 (completely dissimilar). Then, we explored the similarity patterns in species composition using a non-metric multidimensional scaling (NMDS) ordination graphic in each transect and colored-coded the points according to each season.

We applied the Permutation Multivariate Analysis of Variance (PERMANOVA) on the transformed matrix to test whether the dissimilarity between seasons was greater than the dissimilarity within those seasons. PERMANOVA was carried out using the summed coverage of all species in each transect per sampling month and considering 10,000 permutations (Anderson, 2017). Finally, we applied the Similarity Percentages Analysis (SIMPER) to measure the contribution of each species to the total dissimilarity between seasons.

We calculated the Inverse Simpson Index for each transect across seasons, followed by a t-test to evaluate whether species dominance significantly differed between the dry and wet seasons ($p < 0.05$).

To assess the relationship between macrophyte community composition and environmental variables, we conducted a Redundancy Analysis (RDA). This multivariate technique was selected to explore how environmental factors, such as water depth and pH, influence macrophyte composition across the transects. Before the analysis, species coverage data were transformed using the Hellinger method to reduce the influence of coverage species, while environmental variables were standardized using Z-score transformation. A Forward Selection was applied to identify the subset of environmental variables that significantly explained variation in macrophyte composition. The transects were separated by seasons, wet and dry, allowing us to examine if variation in macrophyte composition is explained by environmental gradients.

The analyses were performed in the adespatial (Dray et al. 2006), vegan (Oksanen et al. 2022), iNEXT (Hsieh et al. 2016), and ggplot2 (Wickham 2014) packages in the R environment (R Core Team 2020).

RESULTS

We identified 14 species classified in 11 taxonomic families (Table 1) among angiosperms and fern species. We provide a dichotomous key to facilitate the identification of species occurring in Ribeirão das

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Crioulas in Supplementary Material S4. The comparison between observed species richness (Mao Tau) and the Chao 2 estimator suggests that sampling effort was sufficient, as both curves showed a tendency to stabilize and converge with increasing sampling effort (Supplementary Material S5)

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Table 1. Plant family, species, life form, relative frequency, coverage of all transects, and occurrence in each season at Ribeirão das Crioulas, state of Rio de Janeiro, Brazil.

Family	Species	Life Form	Relative Frequency (%)	Coverage (m^2)	Wet	Dry
Alismataceae	*Hydrocleys nymphoides* Buchenau	Rooted-floating	3.33	40.12	X	X
Cabombaceae	*Cabomba furcata* Schult. & Schult.f.	Free-submerged	38.78	1068.24	X	X
Cyperaceae	*Cyperus blepharoleptos* Steud.	Free-floating	3.47	12.92	X	X
	Cyperus gardneri Ness	Epiphyte	29.09	115.28	X	X
Hydrocharitaceae	*Egeria densa* Planch.	Free-submerged	30.42	468.84	X	X
Lentibulariaceae	*Utricularia breviscapa* C.Wright ex Griseb.	Free-submerged	3.47	26.20	X	X
	Utricularia foliosa L.	Free-submerged	20.79	320.12	X	X

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Nymphaeaceae	*Nymphaea caerulea* Savigny	Rooted-floating	5.62	87.92	X	X
Onagraceae	*Ludwigia* sp. L.	Amphibious	0.074	0.04		X
Plantaginaceae	*Bacopa monnieri* (L.) Pennell	Amphibious	0.22	3.84	X	
Poaceae	Poaceae gen.	Amphibious	1.18	15.36	X	X
Pontederiaceae	*Pontederia azurea* Sw.	Rooted-floating	39.15	840.48	X	X
	Pontederia crassipes Mart.	Free-floating	7.84	39.76	X	X
Salvinaceae	*Salvinia auriculata* Aubl.	Free-floating	70.83	1972.44	X	X

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Of all plots, 1,275 were occupied by at least one macrophyte. Seventy-five plots were not occupied by any macrophyte, and 631 plots exhibited more than 100% coverage. On average, 94.3% of plots were covered by one to nine species (mean ± SD: 2.77 ± 1.34), and the coverage ranged from 0 to 31.8 m² (mean ± SD: 4.63 ± 4.16). The wet season showed the highest total coverage and frequency (3063.32 m², 1787), while the dry season displayed the lowest values (2490.72 m², 1541). The number of species in the dry and wet seasons did not differ, with 13 species each. The Inverse Simpson Index indicated no significant difference in species diversity between the wet and dry seasons ($t = 1.76$, $p = 0.09$).

The families with the highest number of species were Cyperaceae, Lentibulariaceae, and Pontederiaceae, including two species each. *Salvinia auriculata* showed the highest coverage and frequency (1972.44 m², 957). *Ludwigia* sp. displayed the lowest coverage and frequency (0.04 m² coverage, occurring in only one plot). *Salvinia auriculata* and *C. furcata* were the species with the highest coverage in the dry season, whereas *S. auriculata* and *P. azurea* dominated in the wet season (Figure 3).

The species were classified into the following life-forms: amphibious (1 species), epiphyte (1 species), free-floating (4 species), free-submerged (4 species), and rooted-floating (3 species). Other life-forms were not observed in the local aquatic flora. *Bacopa monnieri* was not recorded in the dry season, and *Ludwigia* sp. was not recorded in the wet season.

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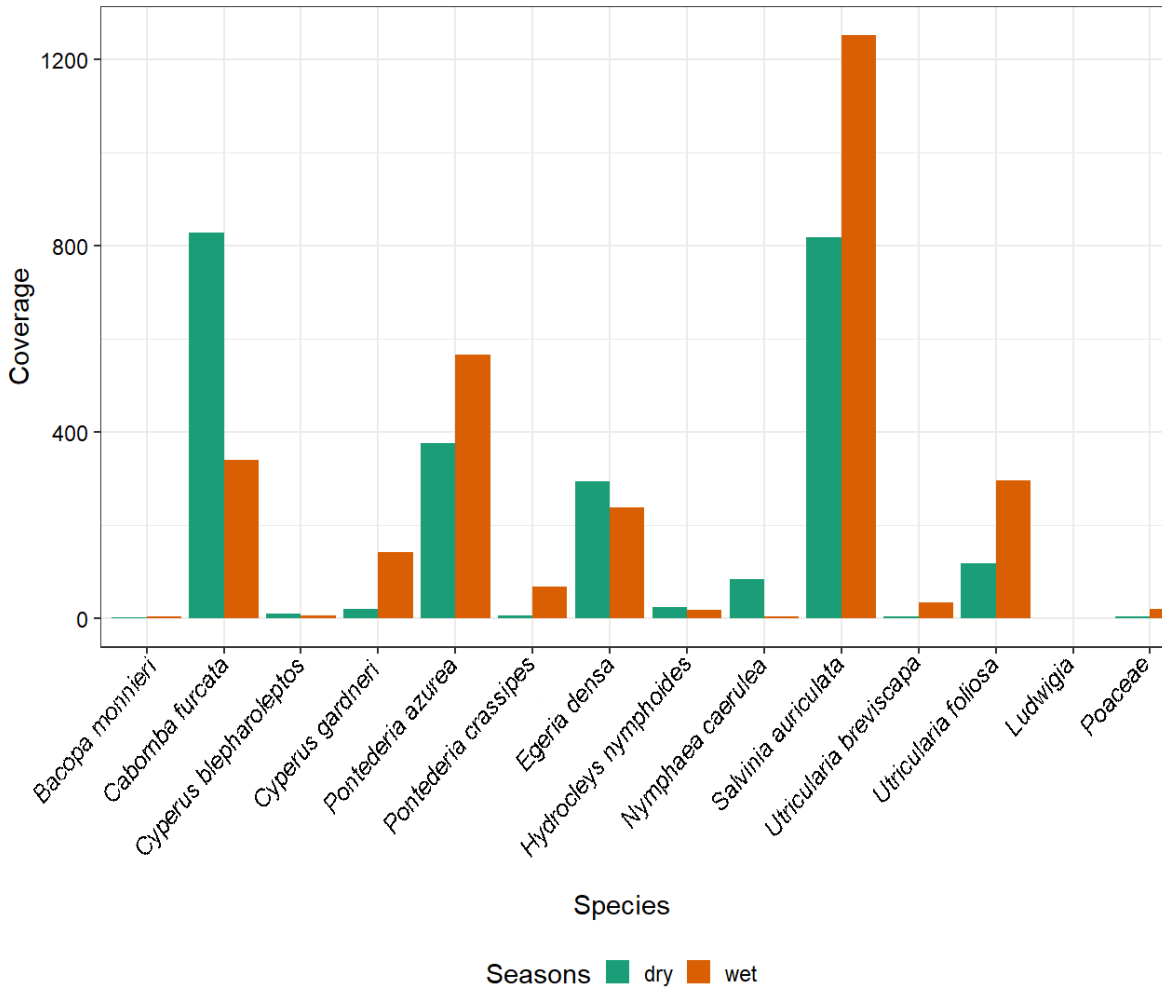

Figure 3. Plant species cover (m²) across all transects during the wet and dry seasons in Ribeirão das Crioulas, Rio de Janeiro State, Brazil.

The composition of the macrophyte community showed a statistically significant but slight difference between wet and dry seasons (PERMANOVA; $p = 0.017$, $R^2 = 0.063$), indicating mostly similar taxonomic composition given the low explanatory power (Figure 4). The SIMPER analysis demonstrated that *S. auriculata*, *C. furcata*, and *P. azurea* contributed most to the dissimilarity observed between seasons (Supplementary Material S6). *Salvinia auriculata* had greater average

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coverage in the dry season (41.7% vs. 37.1% in the wet season), explaining 17.9% of the dissimilarity between seasons. In contrast, *C. furcata* (11.3% vs. 37.6% in the wet season) showed higher coverage in the wet season. Instead, some transects sampled in different seasons were more similar to each other in relation to their community compositions than some transects from the same season.

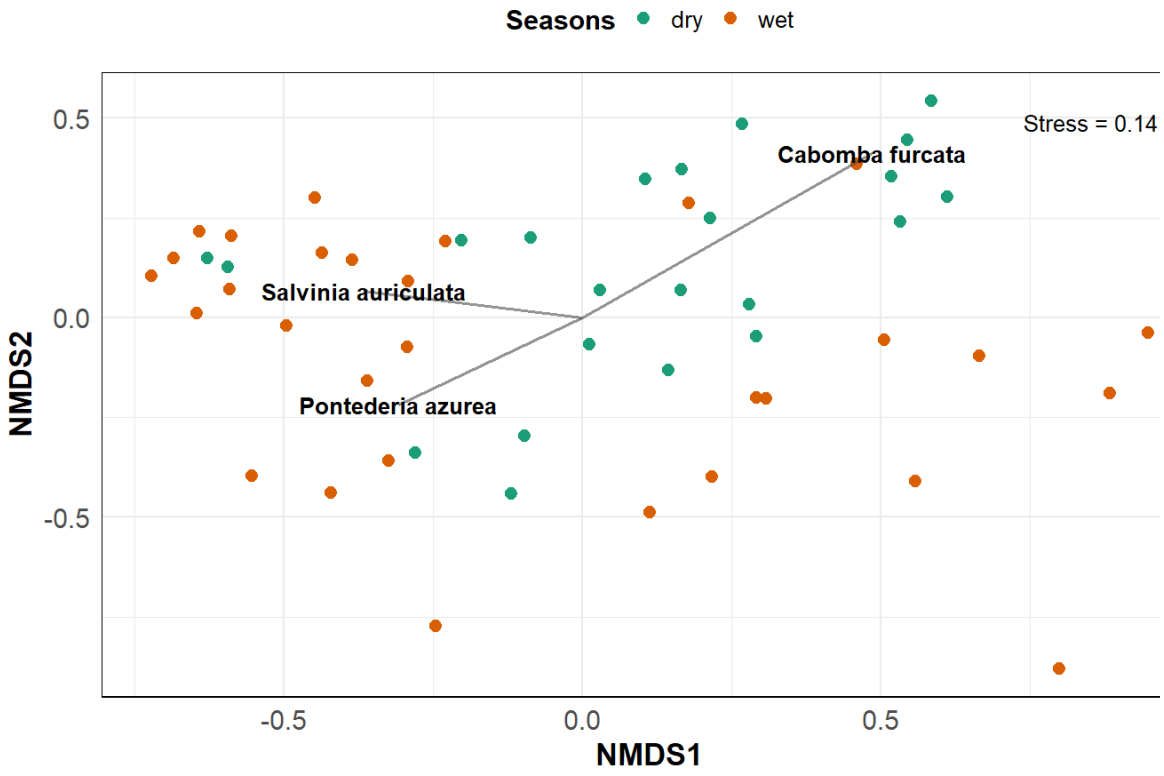

Figure 4. Non-metric multidimensional scaling (nMDS) ordination based on Bray-Curtis dissimilarities in macrophyte community composition per transect, showing seasonal variation between the wet and dry seasons at Ribeirão das Crioulas, Rio de Janeiro state, Brazil. Species vectors indicate the main contributors identified by SIMPER analysis. Stress value=0.14.

The Redundancy Analysis (RDA) showed that environmental variables explained 23.14% of the total variation in macrophyte community composition (R^2adj = 0.2314), and the constrained model was statistically significant (F = 2.77, p = 0.001). Among the constrained axes, only the first

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(RDA 1) was significant (F = 15.06, p = 0.001), indicating that most of the explained variation is concentrated along this gradient (Supplementary Material S7). A forward selection identified photoperiod, relative air humidity, and pH as the most important environmental variables contributing to the explained variation in community composition (Figure 5). The variables relative humidity and photoperiod were primarily related to the wet season and pH to the dry season, although there was a slight distinction between the periods.

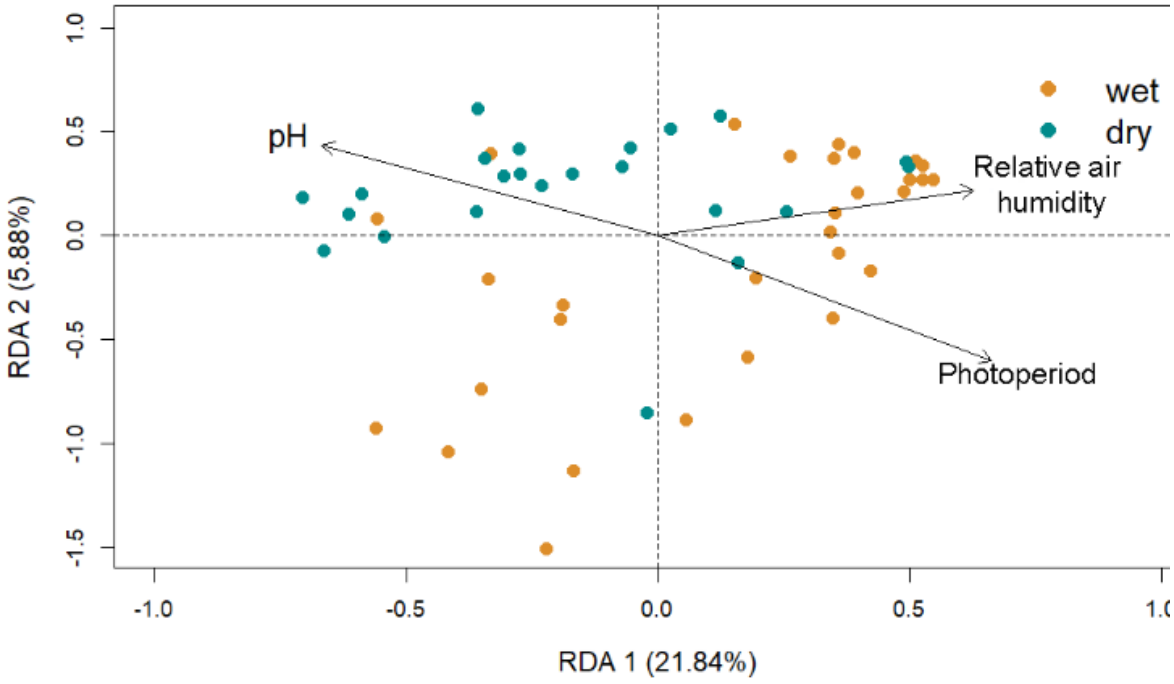

Figure 5. Redundancy Analysis (RDA) showing the relationship between macrophyte community composition per transect and environmental variables selected by forward selection (photoperiod, pH, and relative air humidity) at Ribeirão das Crioulas, state of Rio de Janeiro, Brazil. Arrows represent environmental gradients, and sample scores indicate the distribution of transects in relation to these variables.

DISCUSSION

This study evaluated the effect of seasonal changes in a macrophyte community in the Atlantic Forest wetland. Seasonal changes can act as stressors and signal the onset of favorable or unfavorable

conditions for different species, influencing composition and richness. However, we observed only slight variations in the frequency and composition of the macrophyte community in the Ribeirão das Crioulas wetland between hydrological seasons. This can be explained by the fact that we observed large variations in the structure and composition of the macrophyte community within the same season, with some transects from the same season being more different from each other than transects from different seasons.

The increased rainfall during the wet season was accompanied by decreased pH and increased photoperiod, which made us expect community changes between periods because they impact certain species differently (Supplementary Material S1 and S3). Free-floating species tend to increase coverage in less transparent water, while free-submerged species increase coverage in high water transparency (Canalli et al. 2023). Rooted-floating species, on the other hand, need to stretch to lift leaves and flowers to the surface and, therefore, greater depths of the wet season can make it difficult for these species to establish (Schneider et al. 2015). Photoperiod affects macrophyte flowering; some species flower in short photoperiods and others in long photoperiods, which is another reason why seasonal changes can modify community composition (Spencer & Ksander 1995).

Despite the environmental variation between seasons, macrophytes responded with slight changes in community composition, indicating that this community might be structured by conditions unrelated to seasonal variation. Other environmental properties, such as soil or topography, mostly related to spatial gradients (locality, biome) might be important to determine community composition (Grimaldo et al. 2016, Alahuhta et al. 2018, Santos & Thomaz 2007, Thomaz 2002, Duarte & Kalff 1986). This might happen because deep and shallow areas persist over the seasons (Y. Canalli; pers. obs.), shaping different community compositions in the same season (Maseko et al. 2018, Zhang et al. 2018). In Ribeirão das Crioulas, increased depth reduced the abundance of some species, leading to a negative response from the community, while transparency promoted a turnover of species

according to their life forms along the gradient (Canalli et al. 2023). This interpretation is further supported by the RDA, which indicated that environmental variables explained only a small proportion of the total variation in macrophyte community composition, with photoperiod, relative air humidity, and pH identified as the main predictors shaping community structure.

From a conservation perspective, the understanding that spatial variation is the primary component of macrophyte diversity implies that impacts altering spatial variation need to be better assessed and addressed. Most macrophyte species benefit from shallow environments, such as *H. nymphoides,* which is a regionally rare species that could disappear with increasing depth, while *U. foliosa* benefits from deeper environments (Canalli et al. 2023). This is an important finding, as it suggests that management and conservation strategies focused on wetland macrophytes must consider the spatial variation of aquatic ecosystems and maintain their spatial heterogeneity.

The homogenizing effect of common species with high coverage may also be one of the factors for the low dissimilarity between seasons. Highly dominant species mask the differences in community composition, as they comprise the greatest contribution to the dissimilarity indices than rare species (Vitule & Pozenato 2012). Studies indicate that the contribution of common species as predictors of community response to environmental changes is much greater than the contribution of rare species (Lyons et al. 2005). It has been observed that even removing up to 50% of the rarest species does not significantly change community structure patterns, suggesting that common species are important, while rare species are less relevant for understanding community responses to environmental changes (Brasil et al. 2020). The high coverage of *S. auriculata* also indicates possible eutrophication, and because it has high coverage in both seasons, it indicates that even if the concentration of nutrients changes between seasons, it might not be a limiting factor (Maseko et al. 2018).

Despite the strong presence of *S. auriculata*, the extensive coverage of macrophytes in some plots was linked to the presence of various life-forms distributed across different layers of the water column. In a given plot, it is possible to have 100% coverage of free-floating species such as *S. auriculata*, 100% coverage of epiphyte species such as *C. gardneri,* and 100% coverage of free-submerged species such as *C. furcata.* This pattern is generated by resource sharing, a common process in biological communities, in which species can coexist by using different resources (Gross et al. 2009). For aquatic macrophytes, an important factor facilitating co-occurrence is the partitioning of the vertical space of the water column, which is possible due to species of different life-forms (Schneider et al. 2018). Sharing resources is important to promote the coexistence of different life-forms that impact aquatic ecosystems, increasing the number of other species (Thomaz & Cunha 2010).

It is important to highlight that the study was conducted over a single annual cycle. Extending the temporal scale of research would make it possible to evaluate whether seasonal responses vary between years and to identify potential interannual differences in macrophyte community composition (Kõrs et al. 2012). Additionally, it is relevant to consider the specific characteristics of the study area, which is located at the edge of a reservoir and surrounded by agricultural fields, cattle farming, and possibly affected by sewage from nearby communities (Morais et al. 2016). We also need to consider that the site is located within the Atlantic Forest biome, which has been under intense anthropogenic pressure for many centuries (Solórzano et al. 2024). These anthropic factors may exert a significant influence on the macrophyte community and should be further investigated in future studies to assess their influence on macrophyte community composition.

Moreover, future studies should further explore the role of dominant and generalist species in driving temporal stability in macrophyte communities (Moi et al. 2021). These species are often highly tolerant to environmental changes and can persist even under strong anthropogenic pressures.

Their ability to thrive under a wide range of conditions allows them to remain present year-round, which may lead to reduced seasonal turnover and a more homogenized community structure. Quantifying the influence of these species is important to understand the mechanisms behind the observed temporal stability, as their dominance may mask seasonal signals of the rare species.

ACKNOWLEDGMENTS

We are grateful to the Ewê-Odé support network for their feedback on this manuscript and CAPES for the doctoral grant to YMC. CMS has been supported by CNPq (Processo: 301772/2018-5).

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Submitted: 17 November 2024

Accepted: 16 June 2026

Published: 17 July 2026

Oecologia Australis (ISSN: 2177-6199)
Ahead of print (https://revistas.ufrj.br/index.php/oa/issue/view/1109/showToc)
Article ID: AO#66198
Published online: 17 JULY 2026

Associate Editor: Ivan Carneiro