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Dynamics of aquatic macrophytes and their contribution to carbon storage in La Zapatosa wetland, Colombia, under seasonal hydrological variation

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ABSTRACT

This study evaluated floristic composition, seasonal variation in macrophyte coverage (percentage of quadrat area occupied by each species), and the relationship between macrophytes, water physicochemical variables, and carbon stored in biomass in La Zapatosa Wetland (Cesar, Colombia), a RAMSAR site, during the rainy (October 2023) and dry (April 2024) seasons. Three stations (Chiriguaná, Chimichagua, and the Cesar River confluence) were sampled with two transects per station, each with five 1 m² quadrats; biomass was estimated gravimetrically, carbon by applying a fraction of 0.45 to ash-free organic matter, and physicochemical variables were measured in situ. Electrical conductivity ranged from 162 to 230 µS cm^{-1} in the rainy season and from 322 to 489 µS cm^{-1} in the dry season. Six genera in five families were identified, with higher richness and coverage in the rainy season. Floating species such as *Neptunia oleracea* and *Eichhornia azurea* dominated at higher water levels, whereas *Hymenachne amplexicaulis* tolerated water recession. Carbon stored in biomass, expressed as CO_2 equivalent, was highest in the rainy season at the Cesar River confluence (96.95 g m^{-2}), followed by Chimichagua (69.51 g m^{-2}) and Chiriguaná (60.07 g m^{-2}). Principal component analysis showed that stored carbon is modulated by tissue quality, architecture, and life form, and by gradients of turbidity, electrical conductivity, temperature, and pH. In the sectors evaluated, macrophytes store relevant amounts of carbon, although potential methane emissions must be considered; their conservation is key to enhancing wetland resilience to climate change.

Keywords: flood pulse, hydrophytes, multivariate ordination, plant biomass, Ramsar site.

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Dinâmica de macrófitas aquáticas e sua contribuição para o armazenamento de carbono na área úmida La Zapatosa, Colômbia, sob variação hidrológica sazonal

RESUMO

Avaliaram-se a composição florística, a variação sazonal da cobertura (porcentagem da área do quadrado ocupada por espécie) e a relação entre macrófitas, variáveis físico-químicas da água e carbono armazenado na biomassa na Área Úmida La Zapatosa (Cesar, Colômbia), sítio RAMSAR, durante as estações chuvosa (outubro de 2023) e seca (abril de 2024). Três estações (Chiriguaná, Chimichagua e a confluência com o rio Cesar) foram amostradas com dois transectos por estação, cada um com cinco quadrados de 1 m²; a biomassa foi estimada por gravimetria, o carbono aplicando uma fração de 0,45 à matéria orgânica livre de cinzas, e as variáveis físico-químicas in situ. A condutividade elétrica variou de 162 a 230 µS cm^{-1} na estação chuvosa e de 322 a 489 µS cm^{-1} na seca. Foram identificados seis gêneros em cinco famílias, com maior riqueza e cobertura na estação chuvosa. Neptunia oleracea e Eichhornia azurea (flutuantes) predominaram com níveis de água mais altos, enquanto Hymenachne amplexicaulis tolerou a recessão hídrica. O carbono armazenado na biomassa (CO_2 equivalente) foi maior na estação chuvosa na confluência com o rio Cesar (96,95 g m^{-2}), seguida de Chimichagua (69,51 g m^{-2}) e Chiriguaná (60,07 g m^{-2}). A análise de componentes principais mostrou que esse carbono é modulado pela qualidade do tecido, arquitetura e forma de vida, e por gradientes de turbidez, condutividade elétrica, temperatura e pH. Nos setores avaliados, as macrófitas armazenam carbono relevante, embora possíveis emissões de metano devam ser consideradas; sua conservação fortalece a resiliência da área úmida às mudanças climáticas.

Palavras-chave: biomassa vegetal, hidrófitas, ordenação multivariada, pulso de inundação, sítio Ramsar.

1. INTRODUCTION

Anthropogenic climate change constitutes one of the main threats to the future of humanity, largely driven by high emissions of carbon dioxide (CO_2). In this context, among carbon-containing greenhouse gases released by human activities, CO_2 and methane (CH_4) stand out for their contribution to global warming. In response, the United Nations (2018) has established the reduction of greenhouse gas concentrations as a global priority, recognizing that such actions are essential to advancing sustainability as outlined in the 17 Sustainable Development Goals (SDGs) of the 2030 Agenda. In particular, SDG 13 (Climate Action) emphasizes the urgent need to adopt effective measures to address the impacts of climate change by strengthening the adaptive capacity and resilience of both natural and social systems. In this sense, Mohanty *et al.* (2024) point out that wetlands are directly linked to several targets of the 2030 Agenda: Target 6.6, which calls for protecting and restoring water-related ecosystems, including wetlands; Target 15.1, focused on the conservation and sustainable use of inland freshwater ecosystems; and SDG 13, given their role in climate regulation and carbon storage. These ecosystems also contribute to SDGs 12 and 14. The magnitude of this challenge is reflected in the accelerated global warming observed in recent years. In 2024, the global mean temperature reached a historic maximum, exceeding pre-industrial levels by approximately 1.55°C. This thermal increase has been accompanied by an intensification of extreme climate events, leading to unprecedented human displacement over a decade and a half, while exacerbating food insecurity, economic losses, and multiple forms of social instability (WMO, 2025). In this context, recent studies have demonstrated that the restoration of submerged macrophytes can play a relevant role in regulating carbon dynamics in aquatic ecosystems by

significantly reducing the production and emission of CO_2 and CH_4, improving water quality, and responding sensitively to environmental factors and dissolved organic matter (United Nations, 2025; Yin *et al.*, 2025; Ruane *et al.*, 2025).

Within the framework of climate change mitigation, the sustainable management of ecosystem services (ES), particularly those related to climate regulation and carbon sequestration, has become a key approach to reducing impacts and contributing to the achievement of SDG 13 (Yang *et al.*, 2020). In this regard, freshwater wetlands are of particular importance, as the presence of emergent macrophytes significantly enhances carbon fixation. Although similar processes occur in brackish wetlands, freshwater systems tend to exhibit greater efficiency due to the absence of salinity stress, which promotes more active and stable biogeochemical dynamics. Consequently, the conservation and restoration of these ecosystems emerge as priority strategies to enhance CO_2 sequestration and nitrogen regulation under climate change scenarios (Fang *et al.*, 2023).

Several studies, such as those conducted in Lake Taihu (China), have shown that submerged macrophytes, when developed under good water quality conditions and low nutrient concentrations, can contribute to reducing carbon dioxide emissions, highlighting their role in regulating the carbon cycle (Lei *et al.*, 2025). In this context, the La Zapatosa Wetland Complex in Colombia represents a system of particular interest for examining these dynamics, as it receives high inputs of sediments and organic matter from its watershed, altering its ecological balance and promoting the proliferation of aquatic species such as *Eichhornia crassipes*, *Limnocharis* sp., *Phalaris* sp., and *Paspalum fasciculatum*. Consequently, the dominance of these macrophytes, together with the trophic status of the water, raises questions regarding their influence on CO_2 capture and regulation, supporting the need to evaluate their role in carbon dynamics within this wetland (ONF Andina, 2013; Ramsar, 2023).

The scientific information available on La Zapatosa has focused on floristic composition, the seasonal dynamics of littoral vegetation, and the quality of floodplain vegetation (Instituto Humboldt; Fundación Omacha, 2015; Schmidt-Mumm and Janauer, 2014; García-Murcia *et al.*, 2024), whereas no estimates are available of the carbon stored in macrophyte biomass or of its relationship with water physicochemical variables under contrasting hydrological periods. This gap is consistent with that reported for the Neotropics, where descriptive studies predominate and those testing hypotheses about the ecosystem functioning of macrophytes are scarce (Padial *et al.*, 2008); moreover, inland wetlands have received less attention than coastal wetlands in the quantification of their carbon pools (Paredes-García *et al.*, 2021).

As a RAMSAR wetland, the La Zapatosa Wetland Complex requires research that supports its management through up-to-date scientific information. In this sense, understanding carbon dynamics in this ecosystem is essential due to its contribution to climate regulation and regional biogeochemical balance. Therefore, this study aimed to quantify carbon (C) stored in the biomass of macrophytes and to examine its relationship with water physicochemical variables, in order to provide a technical baseline to support environmental management, monitoring, and conservation strategies under climate change scenarios. For this purpose, principal component analysis (PCA) was used, a multivariate technique that summarizes correlated variables into a few uncorrelated components and that has been applied to discriminate plant species from multiple attributes (Pandey *et al.*, 2014) and to relate macrophyte groups to the environmental conditions of water bodies (Różańska-Boczula and Sender, 2025).

2. MATERIAL AND METHODS

2.1. Study design

This study adopted a longitudinal, descriptive–correlational design within a quantitative framework and was conducted during two contrasting climatic periods, corresponding to the dry and rainy seasons. This methodological approach enabled the examination of the

association between carbon stored in macrophytes, water physicochemical characteristics, and the typology of the evaluated plant species (Hernández Sampieri *et al.*, 2014).

2.2. Study area

The study area for the assessment of carbon storage by macrophytes was the La Zapatosa Wetland Complex (LZWC), a lentic ecosystem of high ecological relevance located in the confluence region of the Cesar and Magdalena Rivers in Colombia (Figure 1). This complex, designated as a RAMSAR site in 2018 (Decree 1190 of 12 July 2018) and listed as Ramsar Site No. 2521 (Ramsar, 2023), extends across the municipalities of Chiriguaná, Chimichagua, Curumaní, Pailitas, and Tamalameque, in the department of Cesar, and El Banco, in the department of Magdalena. It is also recognized as the largest continental wetland in the country (Ramsar, 2023).

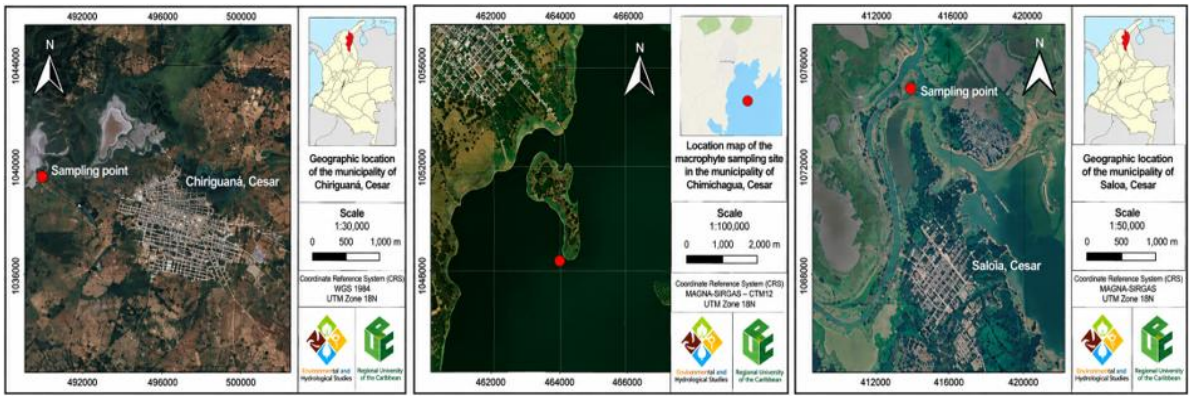


Figure 1. Geographic location of the three macrophyte sampling points in the La Zapatosa Wetland Complex (department of Cesar, Colombia; Ramsar Site No. 2521): P1, Chiriguaná, 9°22'06.5" N, 73°37'38.1" W; P2, Chimichagua, 9°14'36.4" N, 73°48'20.5" W; P3, Cesar River confluence, 9°12'27.6" N, 73°43'56.4" W.
Source: Moscote Vides (2024).

Geographically, the main body of the complex lies between 9°00'–9°18' N and 73°40'–73°56' W (ONF Andina, 2013), with the central coordinates of the Ramsar site at 9°07' N and 73°47' W; however, the site comprises approximately 1,900 swamps and associated water bodies (Ramsar, 2023), so some peripheral sectors, such as Chiriguaná, where station E1 was located, lie north of this range. The complex lies at about 30 m a.s.l. (Schmidt-Mumm and Janauer, 2014). The Ramsar site covers 121,725 ha (Ramsar, 2023), while the water surface of the main swamp has a mean extent of approximately 35,000 ha, which increases by about 14,500 ha during high-water periods (Schmidt-Mumm and Janauer, 2014). The IDEAM bathymetric survey recorded a mean depth of 4.15 m for a water level of 6.60 m at the Belén gauging station, with depths greater than 12 m in the Cesar River channel near its confluence with the Magdalena; the flooded area varies from approximately 150 km² in the dry season to 350 km² in the rainy season, with volumes ranging from less than 300 to nearly 2,000 million m³ (IDEAM, 2007).

Regarding climatic conditions, the area has a warm tropical climate, with a mean annual temperature of 28.4°C (range 27–30°C) and mean annual precipitation of 1,956 mm (1,000–2,600 mm), distributed in a bimodal regime: a first rainy and rising-water period between May and July (about 2.6 m above the mean level), a short drier period between July and September, the main high-water period between October and December (about 5 m above the mean level, with maximum rainfall in October), and the main dry season between January and April (Schmidt-Mumm and Janauer, 2014; Ramsar, 2023). Hydrologically, the complex is fed by the Cesar and Magdalena Rivers, whose regime controls seasonal water-level fluctuations. During

high water, the greater discharge of the Magdalena dams the Cesar River and favors macrophyte development in the connecting channel (Schmidt-Mumm and Janauer, 2014). Soils originate from recent alluvial fans, colluvial deposits, alluvial terraces, and lacustrine deposits (Ramsar, 2023).

From an ecological standpoint, the complex harbors 202 bird species (34 migratory) and 51 fish species (11 migratory), as well as threatened species such as the northern screamer (*Chauna chavaria*) and 17 plant species with some degree of threat. Its most ecologically important sectors include the confluence with the Cesar River, due to its role in hydrosedimentological exchange and connectivity with the Magdalena River, and the littoral margins with floating and rooted vegetation, which provide habitat and refuge for aquatic fauna (Schmidt-Mumm and Janauer, 2014; Ramsar, 2023).

2.3. Population and sampling periods

Macrophyte species recorded in the La Zapatosa Wetland constituted the study population. Sampling was conducted during two contrasting periods, corresponding to the rainy season (14 October 2023) and the dry season (13 April 2024), with one sampling campaign in each season, in order to analyze temporal variations associated with carbon storage.

2.4. Sampling design and sampling points

Based on a prior assessment of the environmental and ecological conditions of the ecosystem, together with field safety conditions and accessibility, three sampling stations were defined and georeferenced using geographic coordinates: E1, Chiriguaná (9°22'06.5" N; 73°37'38.1" W); E2, Chimichagua (9°14'36.4" N; 73°48'20.5" W); and E3, Cesar River confluence (9°12'27.6" N; 73°43'56.4" W). These sampling points were located in areas influenced by the municipalities of Chiriguaná and Chimichagua, as well as in a sector characterized by hydrological connectivity between the wetland and the Cesar River, a key zone for hydrosedimentological exchange processes.

Under these criteria, the three stations were selected to cover contrasting environmental conditions of the wetland: (i) Chiriguaná, a sector receiving domestic wastewater discharges from the municipality and runoff from agricultural and livestock activities; (ii) Chimichagua, a sector adjacent to the main municipal town; and (iii) the Cesar River confluence, a water inflow–outflow zone where hydrosedimentological exchange occurs (ONF Andina, 2013). Their location also considered river access, field safety conditions, and the presence of macrophyte belts. Finally, since the water surface exceeds 35,000 ha, the stations are not intended to represent the entire complex, but rather to characterize vegetated littoral strips subject to three different conditions of anthropogenic pressure and hydrological connectivity; therefore, the results should be interpreted at the scale of the sectors evaluated.

Data collection on aquatic macrophytes was carried out using a sampling scheme based on transects perpendicular to the shore. For this purpose, two transects approximately 25 m long were established at each station and in each season, crossing the macrophyte belt from near the shore toward the open water. Each transect consisted of five 1 m² quadrats spaced 5 m apart. These five quadrats were the replicates of each transect, so that ten quadrats were evaluated per station in each season (60 quadrats in total over the two campaigns). Each quadrat was subdivided into 25 subquadrats of 0.04 m², in which the percentage of occupation of each species was recorded to estimate vegetation cover and characterize its spatial distribution. Thus, the quadrats provided subsamples within each transect and covered the different life forms present (floating, rooted emergent, and rooted submerged). Taxonomic identification was conducted directly in the field through consultation of specialized literature, following the criteria established in the *Manual of Basic Methods for Sampling and Analysis in Plant Ecology* (Mostacedo and Fredericksen, 2000). In addition, one sample per species was collected in each quadrat, including the aerial and root parts and avoiding sediment residues. Samples were stored

in labeled paper bags, kept at a temperature that prevented decomposition, and transported to the environmental laboratory of the Universidad Popular del Cesar, following the Protocol for sampling and laboratory analysis of macrophytes in rivers (España, 2015).

2.5. Biomass and carbon content estimation

In each 1 m² quadrat, the entire biomass of each species present was harvested, including aerial and root structures, according to the Protocol for sampling and laboratory analysis of macrophytes in rivers (España, 2015). In the laboratory, each sample was washed to remove adhering sediment, drained to remove surface water, and separated into an aerial fraction (stems and leaves) and a root fraction. The total fresh weight of each fraction (Pt) was recorded, and a subsample was weighed fresh (Ph) and oven-dried at 60°C to constant weight (minimum 24 h) to obtain the dry weight (Ps), following the procedure applied to macrophytes by Maldonado-Jiménez and Aparicio-Saavedra (2021). With these values, the moisture content on a wet basis (Equation 1) and the dry biomass per unit area (Equation 2) were calculated:

$$CH\ (\%)\ =\ \frac{P_h - P_s}{P_h} \times 100 \quad (1)$$

$$B\ =\ \frac{P_t \times \left(1 - \frac{CH}{100}\right)}{A} \quad (2)$$

Where CH is the moisture content (%), Ph the wet weight of the subsample (g), Ps its dry weight (g), Pt the total fresh weight of the fraction harvested in the quadrat (g), A the quadrat area (1 m²), and B the dry biomass per unit area (g m^{-2}).

Next, organic matter was determined by loss on ignition: a subsample of dried and ground material (up to 5 g) was ashed in a muffle furnace at 650°C for 3 h, and the organic matter content (OM) was obtained as the difference between the dry weight and the ash weight (Equation 3), so that the estimated carbon was free of the mineral fraction (Paredes-García *et al.*, 2021). Organic carbon was then estimated by applying a carbon fraction of 0.45 to the organic matter (Equation 4). This value is consistent with the mean carbon content reported for plant tissues at the global scale, which ranges from 45.0 to 47.9% depending on the organ and is lower in herbaceous than in woody plants (Ma *et al.*, 2018). Finally, carbon was expressed as CO_2 using the ratio between the molecular masses of CO_2 and C (44/12 = 3.67), per unit mass (Equation 5) and per unit area (Equation 6):

$$MO\ (\%)\ =\ \frac{P_s - P_c}{P_s} \times 100 \quad (3)$$

$$C\ (\%)\ =\ MO\ (\%)\ \times\ 0{,}45 \quad (4)$$

$$CO_2\ (g\ kg^{-1})\ =\ \frac{C\ (\%)}{100} \times 3{,}67 \times 1000 \quad (5)$$

$$CO_2\ (g\ m^{-2})\ =\ B \times \frac{C\ (\%)}{100} \times 3{,}67 \quad (6)$$

Where Pc is the ash weight (g). Results were expressed by species, structure (aerial and root), station, and season.

It is important to note that these values correspond to the carbon contained in the standing biomass at the time of each sampling (stock), and not to rates of primary productivity or net carbon assimilation, whose estimation requires repeated measurements over time (Mitsch and Mander, 2018). Accordingly, in this study the terms carbon "fixation" or "capture" refer to the carbon contained in macrophyte biomass at the time of sampling.

2.6. Water physicochemical variables

At each station and in each season, temperature (SM 2550), dissolved oxygen (SM 4500-O), pH, electrical conductivity (SM 2510 B), and salinity (SM 2520) were measured in situ in the water column with a multiparameter meter calibrated before each use; transparency was determined with a Secchi disk and depth with a graduated rod. Repeated readings were taken at each station and are reported as maximum and minimum values and standard deviation. Turbidity (SM 2130 B, nephelometric), total phosphorus (SM 4500-P B,E, photometric), and total nitrogen (EN 12260:2003, UV-VIS spectrophotometry) were determined in grab samples collected in plastic containers and preserved for transport to the laboratory.

2.7. Statistical analysis

Statistical analysis was performed using R software, applying multivariate analysis methods. Data were organized into a matrix in which macrophyte species were treated as units of analysis, and biomass and stored carbon variables were used as descriptors.

Prior to the multivariate analysis, normality of residuals was verified with the Shapiro–Wilk test; differences in biomass between stations and structures (aerial and root), and in physicochemical variables between stations and seasons, were evaluated by analysis of variance (ANOVA), with mean comparisons using Duncan's test ($\alpha = 0.05$).

To reduce data dimensionality and evaluate relationships between species and variables, a Principal Component Analysis (PCA) based on the correlation matrix was applied. Prior to analysis, variables were standardized to eliminate the effect of differences in measurement scales.

PCA is an ordination technique that transforms a set of correlated variables into a smaller number of orthogonal (uncorrelated) components that retain most o

f the original variance (Jolliffe and Cadima, 2016). It was chosen because it allows biotic and physicochemical variables measured on different scales to be synthesized simultaneously, removes redundancy among correlated variables, and represents in a biplot the position of the samples and the contribution of each variable, which facilitates the identification of environmental and functional gradients without requiring a prior response model. Its limitations include the assumption of linear relationships among variables, sensitivity to outliers and to measurement scale (hence the prior standardization), and the fact that components are combinations of variables whose ecological interpretation is not always straightforward; moreover, it is an exploratory method that does not allow causal inference (Jolliffe and Cadima, 2016). This technique has been widely used in vegetation studies, for example, to discriminate tree species from hyperspectral data (Pandey *et al.*, 2014) and to relate macrophyte groups to environmental variables in lake ecosystems after data standardization and verification of suitability with Bartlett's test of sphericity and the Kaiser–Meyer–Olkin criterion (Różańska-Boczula and Sender, 2025).

Two PCAs were performed. The first (Figure 3) used moisture percentage, organic matter, minerals, organic carbon, biomass, CO_2 equivalent, cover, and CO_2 per unit area as descriptors, with the samples of each species as observations. The second (Figure 4) integrated macrophyte cover, biomass, and richness with water physicochemical variables (electrical conductivity, turbidity, pH, temperature, dissolved oxygen, and transparency). In both cases, variables were standardized to zero mean and unit variance (z-scores), so that the PCA was computed on the Pearson correlation matrix; components were obtained by eigenvalue decomposition, the first two were retained based on their percentage of explained variance, and the contribution of each variable was interpreted from its loadings, considering those with the highest absolute values as relevant (Jolliffe and Cadima, 2016).

The PCA was conducted using specialized R packages (RStudio, version 2024.04.2), and results were visualized through a correlation biplot that simultaneously represented observations and variables. The final plot included species grouping and dispersion ellipses,

facilitating the exploration of the multivariate structure of the data.

3. RESULTS AND DISCUSSION

3.1. Macrophyte identification

The floristic composition of macrophytes in the La Zapatosa Wetland is presented in the taxonomic tree shown in Figure 2:

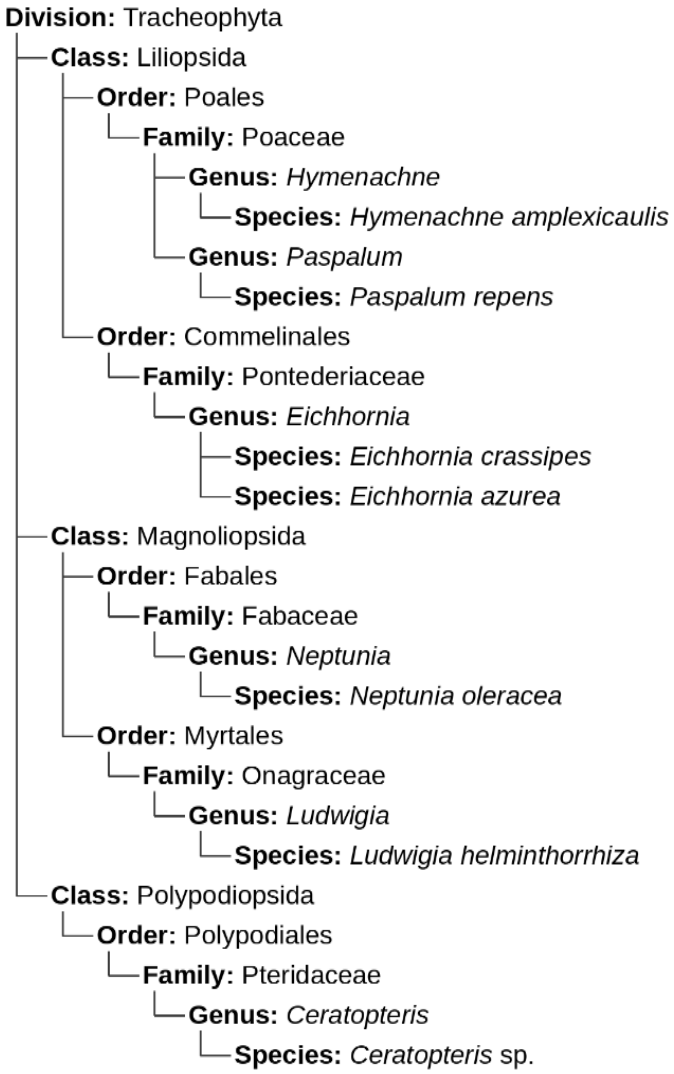


Figure 2. Hierarchical taxonomic diagram (division, class, order, family, genus, and species) of the aquatic macrophytes recorded at three stations of the La Zapatosa Wetland during the rainy (October 2023) and dry (April 2024) seasons; six genera and five families of the division Tracheophyta were identified.
Source: prepared by the author based on data from the master's research project (Moscote Vides, 2024).

The taxonomic analysis of macrophytes present in the La Zapatosa Wetland identified a total of six genera and five families, belonging to the division Tracheophyta and distributed across the classes Liliopsida, Magnoliopsida, and Polypodiopsida. These results indicate a diverse floristic composition, characteristic of continental aquatic ecosystems with high environmental heterogeneity.

3.2. Presence–absence matrix

The analysis of the presence–absence matrix revealed temporal changes in macrophyte composition and species richness (S) across the sampling sites. During the rainy season, the Chiriguaná station exhibited the highest diversity, with five species, while three species were recorded at both the Cesar River confluence and Chimichagua. During the dry season, a general decrease in richness was observed, with three species in Chiriguaná and two species at both the Cesar River confluence and Chimichagua (Table 1).

Table 1. Presence–absence matrix and species richness (S) of macrophytes at three sampling sites during the rainy (R) and dry (D) seasons.

Species	Chiriguaná (R)	Chiriguaná (D)	Cesar R. confluence (R)	Cesar R. confluence (D)	Chimichagua (R)	Chimichagua (D)
Eichhornia crassipes	✓	✓	✓	✓	—	—
Eichhornia azurea	—	—	—	—	✓	—
Ludwigia helminthorrhiza	✓	—	✓	—	—	—
Neptunia oleracea	✓	✓	✓	—	✓	✓
Hymenachne amplexicaulis	✓	✓	—	✓	✓	—
Ceratopteris sp.	✓	—	—	—	—	—
Paspalum repens	—	—	—	—	—	✓
Species richness (S)	**5**	**3**	**3**	**2**	**3**	**2**

Note: (R) = rainy season; (D) = dry season. Prepared by the author based on data from the master's research project (Moscote Vides, 2024).

The changes observed in macrophyte richness and composition between the rainy and dry seasons in this study, evidenced by higher species richness during the rainy season in Chiriguaná (5 species) compared to the dry season (3 species), may be associated with variations in water depth, which acts as a determining factor in structuring plant assemblages. This pattern is consistent with findings reported in a floodplain in Santo Tomás during the flooding period of the Magdalena River (northern Colombia), where spatial and temporal variations in macrophyte assemblages were closely related to the hydrological regime (Pozo-García *et al.*, 2022). In that study, richness, cover, and diversity increased during periods of flooding and high water levels, whereas during the dry period, richness and abundance decreased due to reduced water levels. Likewise, in that wetland *Neptunia oleracea*, together with *Ludwigia helminthorrhiza*, was positively associated with nitrate concentrations, coliform bacteria, and water transparency, whereas *Eichhornia crassipes* showed high phenotypic plasticity and tolerance to both water-level variations and organic enrichment (Pozo-García *et al.*, 2022). These species were also present in the present study. Overall, these results reinforce the concept that hydrological dynamics act as an ecological filter regulating species composition, dominance, and the potential for plant biomass accumulation in tropical wetlands.

Complementarily, the information presented in the presence–absence table shows that species richness was also higher during the rainy season across the three sampled locations, decreasing during the dry phase. This pattern is consistent with that documented for the La

Zapatosa wetland complex by Schmidt-Mumm and Janauer (2014), who reported that free-floating and rooted macrophytes increase their development during rising water levels and reduce their presence as flooding recedes. Table 1 shows this same behavior: floating species such as *Eichhornia crassipes* and *Neptunia oleracea* are associated with higher water levels, whereas rooted species exhibit more variable occurrences depending on substrate availability during the dry season. These findings support the view that hydrological dynamics are a key structuring factor of plant assemblages, regulating both species presence and the extent of their populations within the system.

3.3. Percentage cover and seasonal variation of aquatic macrophytes

To synthetically present the spatial and seasonal variation of aquatic macrophytes, percentage cover values by species were compiled for the areas of influence of Chiriguaná, Chimichagua, and the Cesar River confluence. The data were organized in a compact format that integrates, for each site, both rainy and dry seasons within a single cell, facilitating direct comparison of changes in cover between hydrological periods (Table 2).

Table 2. Percentage cover (%) of each macrophyte species at the Chiriguaná, Chimichagua, and Cesar River confluence stations (La Zapatosa Wetland) in the rainy (R, October 2023) and dry (D, April 2024) seasons.

Species	Chiriguaná (R/D)	Chimichagua (R/D)	Cesar River confluence (R/D)
Paspalum repens	0 / 0	0 / 22	0 / 0
Eichhornia azurea	0 / 0	37 / 0	0 / 0
Ceratopteris sp.	2 / 0	0 / 0	0 / 0
Hymenachne amplexicaulis	9 / 0.08	2 / 0	32 / 19
Neptunia oleracea	63 / 0.48	8 / 10	2 / 0
Ludwigia helminthorrhiza	20 / 0	0 / 0	7 / 0
Eichhornia crassipes	2 / 6.67	0 / 0	21 / 2

R: rainy season; D: dry season. Values expressed as percentage cover. Prepared by the author based on data from the master's research project (Moscote Vides, 2024).

The seasonal variation observed in macrophyte cover across the three sampling sites in the La Zapatosa Wetland reflects a pattern widely documented in tropical wetlands, where the hydrological regime—particularly flood pulses and water recession periods—acts as the primary driver of vegetation structure. Studies in Neotropical wetlands have shown that water level fluctuations function as ecological filters that reorganize species dominance and expansion, favoring floating and emergent macrophytes during the rainy season and limiting their development during the dry season (Noleto *et al.*, 2019). This pattern is consistent with our findings: during the rainy season, floating species such as *Neptunia oleracea* and *Eichhornia azurea* reached their highest cover values, up to 63% in Chiriguaná and 37% in Chimichagua, respectively. In contrast, their presence decreased markedly during the dry season, when reduced water levels restrict the development of strictly aquatic hydrophytes and favor the persistence of species more tolerant to shallow conditions, such as *Hymenachne*

amplexicaulis, which maintains relatively high cover at the Cesar River confluence even during recession periods.

This pattern is not exclusive to La Zapatosa: in the Lower Sinú region, the highest abundance of hydrophytes is recorded during periods of rising water levels, whereas the dry season significantly reduces vegetation cover (Pérez-Vásquez *et al.*, 2015). Similarly, in wetlands of southeastern Bangladesh, macrophyte cover reaches its highest values during the rainy season (35–39%) and progressively declines during summer, winter, and autumn (Hossain *et al.*, 2024). The consistency across these systems demonstrates that macrophyte responses to hydrological regimes represent a recurrent pattern in tropical wetlands, regardless of geographic location.

The increase in cover during the rainy season suggests favorable conditions for macrophyte expansion, allowing certain species to dominate large areas of the water surface. The dominance of specific species indicates competitive and exclusion processes, where a few macrophytes achieve high cover and displace others. Additionally, these seasonal changes may influence ecosystem dynamics by altering light availability, habitat structure, and primary productivity, thereby affecting other biological components (Dembowska, 2015).

3.4. Multivariate ordination of macrophytes and their relationship with carbon storage variables

Continental wetlands play an essential role in carbon storage, both in living biomass and sediments, yet they remain less studied than coastal systems. Research conducted in the floating wetland of Lake Cuitzeo has shown that vegetation spatial structure, changes in cover, and the presence of dominant or invasive species directly influence the amount of carbon accumulated, reaching significant values in both aboveground biomass and the substrate (Paredes-García *et al.*, 2021). These findings highlight the importance of understanding how macrophyte composition and distribution modulate biogeochemical processes in inland wetlands. From this perspective, the multivariate analysis applied to the La Zapatosa Wetland allows for an integrated exploration of the relationship between plant community structure, water physicochemical conditions, and carbon storage, providing key insights for a continental ecosystem that, like other inland wetlands, has historically received less scientific attention.

The PCA (Figure 3) allowed the identification of functional patterns among the evaluated macrophytes in terms of stored carbon. The first two components explained 67.5% of the total variance (PC1: 46.3%; PC2: 21.2%). PC1 represented a gradient associated with tissue quality: negative values were related to higher organic carbon content and biomass, and positive values to higher moisture content. PC2 separated spatial expansion (cover, positive values) from carbon stored per unit area (CO_2 m^{-2}, negative values). Within this multivariate space, *Neptunia oleracea* was positioned mainly toward negative PC1, with tissues of higher organic carbon content, and showed a wide dispersion along PC2, indicating variable cover and carbon per m^2. *Hymenachne amplexicaulis* had several samples on negative PC2, associated with higher carbon stored per unit area. *Eichhornia crassipes* was located toward positive PC1, with moister tissues and lower organic carbon content, as were the isolated observations of *Paspalum repens* and *Ceratopteris* sp., while *Ludwigia helminthorrhiza* exhibited the greatest plasticity, occupying a broad range along PC1 without extreme values of carbon per unit area. Overall, the PCA reveals a trade-off between spatial expansion and carbon stored per square meter, and highlights that tissue chemical quality modulates carbon content beyond total biomass.

These results are consistent with those reported by Harpenslager *et al.* (2022), who demonstrated that the availability or removal of macrophytes directly influences the capacity of lacustrine systems to fix carbon, linking vegetation loss to reduced carbon input via photosynthesis and altering short-term accumulation dynamics. Accordingly, spatial structure (cover) and tissue quality (organic carbon content) emerge as key attributes explaining differences in stored carbon among species, reinforcing the importance of conserving aquatic

vegetation as a fundamental component of the carbon balance in the La Zapatosa Wetland.

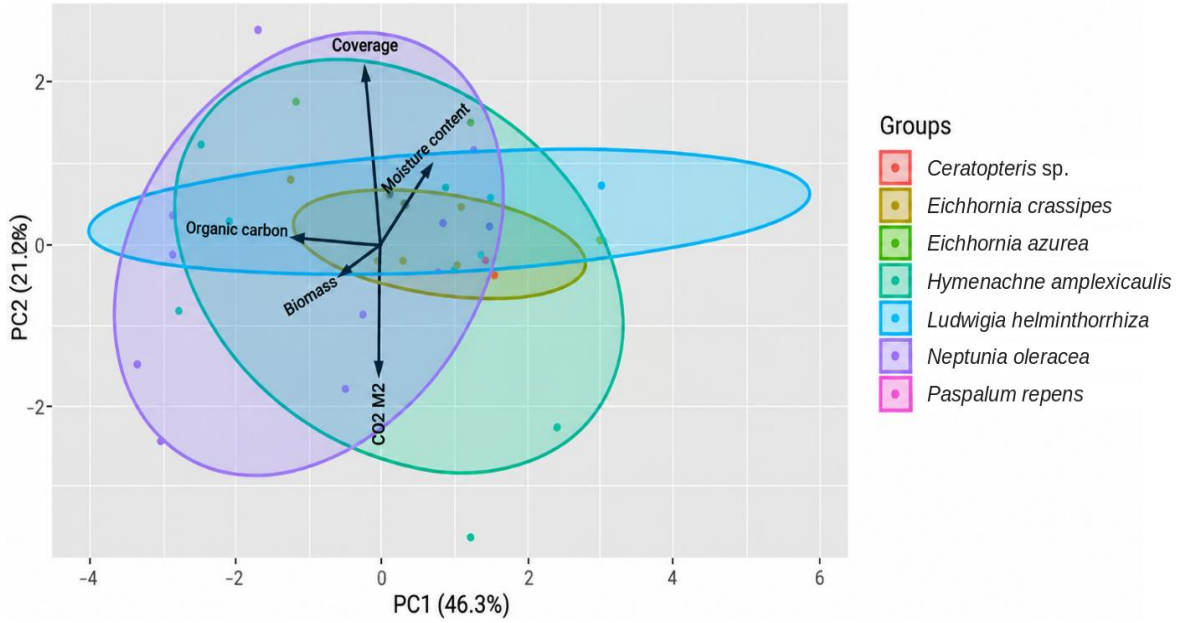


Figure 3. Correlation biplot of the Principal Component Analysis (PCA) of macrophyte samples from the La Zapatosa Wetland based on cover, biomass, moisture content, organic carbon, and CO_2 stored per square meter. PC1 and PC2 explain 46.3% and 21.2% of the total variance, respectively; points represent individual samples, ellipses group the samples of each species, and arrows indicate the direction and magnitude of the contribution (loadings) of each variable. Coverage: cover (%); Moisture content: moisture content (%); Organic carbon: organic carbon (%); Biomass: dry biomass (g m^{-2}); CO2 M2: CO_2 equivalent stored per square meter (g m^{-2}).
Source: Moscote Vides (2024).

At a broader ecosystem scale, these findings align with the role of wetlands in the biogeochemical carbon cycle, as they facilitate the incorporation of atmospheric CO_2 through the photosynthetic activity of flooded vegetation and promote its storage in biomass and waterlogged soils. This function positions wetlands as strategic components in climate change mitigation due to their capacity to retain carbon and support natural regulatory processes (García-Murcia *et al.*, 2024).

In this context, the functional patterns identified in the PCA are also consistent with experimental evidence showing that macrophyte life form and architecture determine how each species contributes to the carbon cycle. Liu *et al.* (2026) reported that floating macrophytes—such as *Neptunia oleracea*—are characterized by extensive cover and high biomass accumulation, whereas emergent species exhibit higher carbon fixation rates per unit area, and submerged species are more closely associated with water quality improvement processes. This functional differentiation is consistent with the PCA results, where floating species are oriented toward high cover values, while emergent or amphibious species, such as *Hymenachne amplexicaulis*, align with higher carbon stored per unit area. Recent experimental findings further support this pattern: Diao *et al.* (2026) demonstrated that ecosystems dominated by canopy-forming submerged macrophytes exhibit significantly lower CO_2 and CO_2eq fluxes compared to those dominated by bottom-dwelling species, due to differences in spatial occupation and photosynthetic capacity associated with aboveground biomass. In such systems, the higher growth rates and biomass of canopy-forming species enhance CO_2 and nutrient uptake, whereas in communities dominated by bottom macrophytes, variables such as alkalinity and pH emerge as key factors regulating CH_4 fluxes. In this regard, both the PCA and experimental evidence indicate that macrophyte architecture and life form are critical

determinants of carbon storage and greenhouse gas balance, underscoring the importance of considering functional traits when interpreting the role of these communities in tropical wetlands.

However, higher carbon stored in aquatic vegetation does not necessarily imply a more favorable net climate balance. Studies conducted in coastal wetlands have shown that efficient CO_2 uptake may coexist with partial returns of fixed carbon to the atmosphere in the form of CH_4 and N_2O, revealing a decoupling between photosynthetic fixation and net greenhouse gas balance. Hsieh *et al.* (2021) documented marked diurnal and seasonal variations in GHG emissions, where photosynthesis reduced CO_2 emissions during the day, while CH_4 and N_2O emissions followed opposite patterns influenced by temperature and other environmental factors. Although this study was conducted in an estuarine wetland, the underlying physiological and microbial mechanisms are applicable to continental wetlands such as La Zapatosa, particularly in systems with high plant productivity and organic matter availability.

From this perspective, the gradient observed in the PCA between carbon stored per unit area and spatial expansion reflects functional trade-offs inherent to macrophyte architecture, highlighting the need to interpret stored carbon within a broader ecosystem context. While higher biomass promotes carbon storage, it may also increase the availability of labile organic compounds that serve as substrates for methane production. Additionally, environmental factors such as water temperature can modulate the intensity of these processes, creating scenarios in which high plant biomass coexists with significant greenhouse gas emissions (Chingangbam and Khoiyangbam, 2023).

Finally, several studies have shown that, although wetlands may exhibit significant GHG emissions, the high plant productivity and carbon accumulation associated with macrophyte-dominated communities allow freshwater wetlands to function as net carbon sinks when considered over longer time scales. Within this framework, differences in architecture, cover, and biomass allocation among plant life forms directly modulate carbon fluxes and reservoirs, which is consistent with the functional gradients revealed by multivariate ordination (Marín-Muñiz and Hernández, 2020).

3.5. Multivariate analysis of the relationship between macrophytes, environmental variables, and carbon storage in the La Zapatosa Wetland

Multivariate analysis is a fundamental tool for understanding the complex interactions among macrophyte communities, water physicochemical variables, and carbon storage potential in tropical wetlands. Given the high environmental heterogeneity of these systems and the nonlinear relationships among their components, PCA made it possible to synthesize the joint variability of the variables and to identify the main ecological gradients of the evaluated sectors of La Zapatosa, detecting associations between species and environmental conditions that are not evident through univariate analyses.

The physicochemical variables differed markedly between seasons. Electrical conductivity ranged from 162 to 230 µS cm^{-1} in the rainy season and from 322 to 489 µS cm^{-1} in the dry season, with significant differences between seasons ($F = 238.27$; $p < 0.001$) and stations ($F = 21.97$; $p < 0.001$). pH ranged from 5.89 to 7.12 in the rainy season and from 5.74 to 9.17 in the dry season (season: $F = 16.64$, $p = 0.003$; station: $F = 9.26$, $p = 0.007$); dissolved oxygen, from 5.9 to 8.41 mg L^{-1} in the rainy season and from 7.09 to 8.0 mg L^{-1} in the dry season (station: $p = 0.016$; season: $p = 0.046$); and water temperature, from 31.5 to 34.1°C in the rainy season and from 29.7 to 39.1°C in the dry season, with differences between stations ($p = 0.042$). Turbidity (26.2–271 NTU in the rainy season and 62–496 NTU in the dry season) and Secchi transparency (0.05–0.45 m) showed high spatial variability. The increase in conductivity and pH during the dry season is consistent with the concentration of ions associated with the reduction in water volume.

The Principal Component Analysis (PCA) revealed clear associations among water physicochemical variables, macrophyte community structure, and carbon storage potential in the La Zapatosa Wetland. The first two components jointly explained 65.7% of the total variance (PC1: 37.0%; PC2: 28.7%), adequately representing the main environmental gradients of the system.

PC1 (Figure 4) described a gradient of plant biomass and dominance, influenced by conductivity, turbidity, and macrophyte cover—variables closely associated with biomass accumulation and stored carbon. In contrast, PC2 was determined by temperature, pH, and water transparency, factors that regulate photosynthetic efficiency and species distribution.

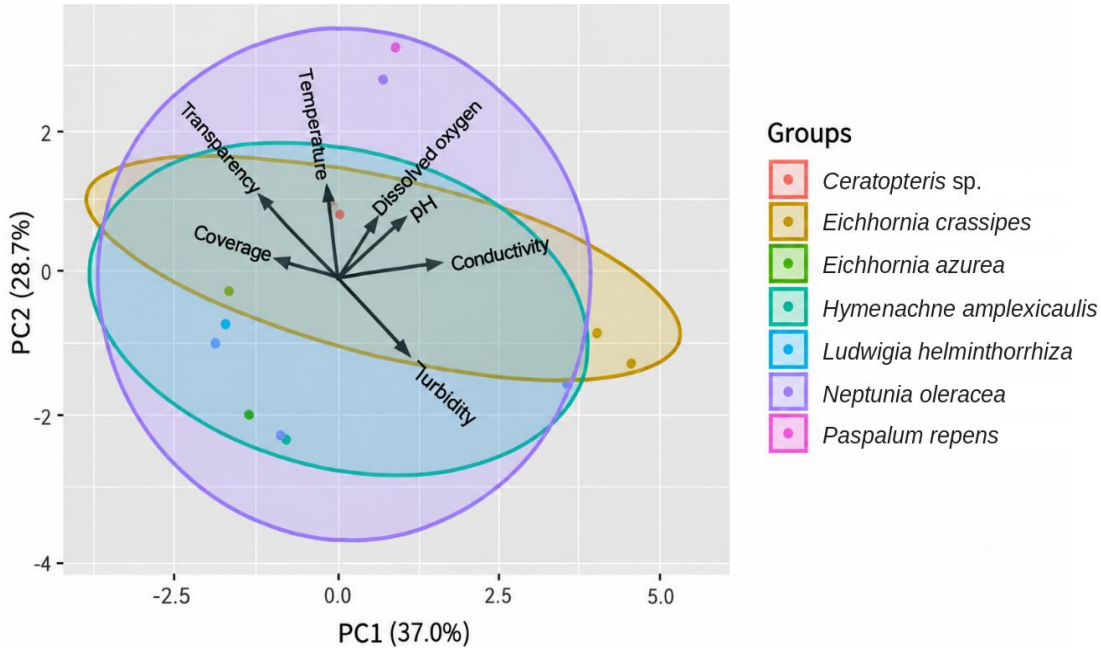


Figure 4. Correlation biplot of the Principal Component Analysis (PCA) relating macrophyte cover, biomass, and richness to water physicochemical variables (electrical conductivity, turbidity, pH, temperature, dissolved oxygen, and Secchi transparency) at three stations of the La Zapatosa Wetland during the rainy and dry seasons. PC1 and PC2 explain 37.0% and 28.7% of the total variance, respectively; ellipses group the observations of each species.
Source: Moscote Vides (2024).

Eichhornia crassipes and *Eichhornia azurea* were associated with high values of conductivity, turbidity, and cover, indicating their affinity for eutrophic environments and a high carbon content in their biomass at the time of sampling, although potentially of low stability due to their rapid turnover and decomposition. *Hymenachne amplexicaulis* occupied an intermediate position, standing out for its contribution to carbon storage in both aboveground biomass and sediments. In contrast, *Ceratopteris* sp. and *Ludwigia helminthorrhiza* were linked to clearer, less turbid sectors, associated with more homogeneous carbon storage among samples but lower total biomass. *Neptunia oleracea* exhibited a wide dispersion, reflecting high ecological plasticity and a variable contribution to carbon storage depending on environmental conditions. In this regard, water physicochemical variables directly influence biomass and species' richness, and the composition of aquatic plants may shift according to specific environmental conditions, reinforcing the relationship between physicochemical conditions and biodiversity (Botero-Álvarez *et al.*, 2020).

Complementarily, recent studies have shown that the factors regulating macrophyte structure and performance vary significantly across hydrological seasons. Meng *et al.* (2023) found that during the flooding season, water depth, transparency, and nutrient availability are

the main determinants of biomass and distribution of submerged macrophytes, whereas in the dry season, depth becomes less relevant and carbon content in water and sediments plays a more prominent role in regulating these communities. This seasonal behavior is consistent with the dynamics observed in the La Zapatosa Wetland, where gradients of turbidity, transparency, and conductivity identified in the PCA reflect transitions between periods of high water input and phases of water level recession, modulating the functional structure of macrophytes and their contribution to carbon storage.

Consistent with the above, the results from the La Zapatosa Wetland indicate that water quality and trophic status directly condition the structure of macrophyte communities and their functional contribution to the ecosystem. Water physicochemical variables are key drivers of aquatic ecosystem dynamics, directly influencing the structure of biological communities and exhibiting marked spatial and temporal variability (Rameshkumar *et al.*, 2019). The PCA showed that gradients associated with eutrophication—represented by turbidity, conductivity, and vegetation cover—favor the dominance of floating macrophytes such as *Eichhornia crassipes* and *Eichhornia azurea*, whereas sectors with greater transparency and improved optical conditions are associated with species such as *Ceratopteris* sp. and *Ludwigia helminthorrhiza*. This pattern is consistent with findings in other lacustrine systems, where water quality and nutrient levels determine macrophyte diversity, cover, and ecological function in the littoral zone, reflecting the ecological status of the water body (Różańska-Boczula and Sender, 2025).

The patterns observed in the La Zapatosa Wetland are consistent with recent studies highlighting the role of multiple environmental filters in structuring macrophyte communities, where the synergistic effects of nutrient enrichment and external physical disturbances determine both species composition and biomass distribution. In this context, nutrient enrichment, primarily associated with anthropogenic activities, drives shifts toward communities dominated by eutrophication-tolerant species, while physical disturbances such as wind-induced turbulence and water level fluctuations contribute to marked spatial heterogeneity, favoring the establishment of macrophytes in more protected microhabitats. Collectively, these factors operate in an integrated manner, with water physicochemical properties acting as the primary drivers of macrophyte dynamics, regardless of specific geographic context (Wang *et al.*, 2025).

From this perspective, the dynamics observed in the La Zapatosa Wetland can be interpreted as the result of hierarchical interactions among the hydrological regime, physicochemical limnology, and macrophyte community structure. These interactions do not operate unidirectionally but through feedback processes that generate pronounced spatial heterogeneity (Rivera-Cáceda *et al.*, 2026). As in other shallow wetlands, variability in the hydrological cycle and its effects on depth, mineralization, and nutrient loads condition macrophyte responses, while aquatic vegetation itself modulates local physicochemical conditions by influencing light availability, gas exchange, and organic matter accumulation processes. This interaction defines the wetland as an integrated system composed of functional patches with differentiated dynamics, allowing plant dominance, biomass distribution, and carbon storage to reflect both environmental gradients and the adaptive capacity of macrophytes to natural and anthropogenic disturbances.

3.6. Limitations and research perspectives

The results should be interpreted considering the scope of the design. First, the three stations represent littoral strips with contrasting conditions of anthropogenic pressure and hydrological connectivity, but not the entirety of a complex whose water surface exceeds 35,000 ha; therefore, carbon estimates should not be extrapolated to the whole wetland. Second, one campaign was carried out per season, so the values obtained describe the carbon stored in biomass at two moments of the hydrological cycle and not primary productivity or the net

carbon balance. Finally, CH_4 and CO_2 fluxes and sediment carbon were not measured, although they are key components of the role of wetlands as carbon sinks or sources (Hsieh *et al.*, 2021; Chingangbam and Khoiyangbam, 2023).

To overcome these limitations, it is recommended to: (i) increase the number of stations along the hydrological gradients of the complex, including open-water zones and the channels connecting with the Magdalena River; (ii) carry out monthly or bimonthly sampling covering the bimodal regime, with successive biomass harvests to estimate net primary productivity and actual carbon assimilation rates; (iii) simultaneously measure CH_4 and CO_2 fluxes and sediment organic carbon to estimate the net greenhouse gas balance (Mitsch and Mander, 2018; Harpenslager *et al.*, 2022); (iv) use satellite imagery, drones, and remote sensors to scale macrophyte cover and biomass to the entire wetland (Mohanty and Pandey, 2025); and (v) evaluate how climate variability and extreme events (droughts and floods) modify the capacity of macrophytes to store carbon. This information would help guide the conservation of species with higher carbon stored per unit area, such as *Neptunia oleracea* (78.5 g CO_2 m^{-2} at the Cesar River confluence) and *Hymenachne amplexicaulis* (56.2 g CO_2 m^{-2} in Chimichagua) in the rainy season (Moscote Vides, 2024), within the management plans of the Ramsar site.

4. CONCLUSIONS

Macrophytes in the three sectors evaluated in the La Zapatosa Wetland showed marked sensitivity to the hydrological regime, exhibiting greater species richness and cover during the rainy season, confirming that water depth is a key structuring factor in these wetlands. Seasonal variations led to differentiated functional responses among floating, emergent, and amphibious species, with *Neptunia oleracea*, *Eichhornia azurea*, and *Hymenachne amplexicaulis* standing out as dominant components depending on environmental conditions. Multivariate analysis revealed that carbon stored in biomass does not depend solely on biomass, but also on attributes such as tissue quality, architecture, and life form, which explain differences in stored carbon among species. Likewise, physicochemical variables such as electrical conductivity, turbidity, temperature, and pH influenced plant distribution and their carbon storage capacity, revealing environmental gradients that modulate biomass accumulation in the sectors evaluated. Overall, the results indicate that macrophytes in the evaluated sectors of La Zapatosa Wetland store relevant amounts of carbon in their biomass, particularly during periods of greater plant cover; extrapolation to the entire complex requires broader spatial and temporal sampling, and this process should be interpreted considering potential simultaneous emissions of gases such as methane. The conservation and restoration of macrophytes emerge as essential strategies to maintain the wetland's function as a carbon sink and to strengthen its resilience to climate change.

5. DATA AVAILABILITY STATEMENT

Data availability not informed.

6. ACKNOWLEDGMENTS

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