Ecohydrology & Hydrobiology 26 (2026) 100783

Contents lists available at ScienceDirect

Ecohydrology & Hydrobiology

journal homepage: www.elsevier.com/locate/ecohyd

Macrophyte–fish associations in a tropical reservoir: the role of aquatic vegetation in structuring fish assemblages☆

Francisco Gerson Araújo [a,*], Robinson Luiz Campos Machado Pitelli [b], Robinson Antonio Pitelli [b], Antônio Manoel Matta dos Santos Lameirão [c], Felipe Pinheiro da Cruz [c], Rinaldo José da Silva Rocha [c], Rafaela de Sousa Gomes Gonçalves [a], Gustavo Henrique Soares Guedes [a]

[a] *Laboratório de Ecologia de Peixes, Departamento de Biologia Animal, Universidade Federal Rural do Rio de Janeiro, 23897-000, Seropédica, Rio de Janeiro State, Brazil*
[b] *Ecosafe Agricultura e Meio Ambiente SS Ltda., 856 Rua Monteiro Lobato St., Jaboticabal, 14870-410, SP, Brazil*
[c] *LIGHT Energia S.A., 168 Marechal Floriano Avenue, Rio de Janeiro, 20080-002, RJ, Brazil*

ARTICLE INFO

Keywords:
Fish-macrophyte interactions
Eutrophication
Fish community structure
Tropical reservoirs

ABSTRACT

Aquatic macrophytes are key structural components of freshwater ecosystems and strongly influence fish assemblages by modifying habitat structure, resource availability, and refuge conditions. This study examined how spatial and seasonal environmental variation shapes macrophyte assemblages and how vegetation structure relates to fish assemblages along a longitudinal gradient (upper, middle, lower zones) and across hydrological seasons (dry and wet) in a eutrophic tropical reservoir in southeastern Brazil. We hypothesized that (1) spatial and seasonal gradients structure macrophyte composition; (2) macrophyte richness and abundance influence fish richness and abundance; and (3) species-specific associations occur between macrophytes and fishes. Macrophyte assemblages followed a longitudinal pattern, with higher richness in the rocky upper zone and greater colonization in the deeper lower zone, with no significant seasonal variation, partially supporting H1. Fish assemblages varied spatially and seasonally, with higher richness and abundance in the lower zone during the wet season, associated with higher temperature and turbidity and lower dissolved oxygen. Macrophyte richness did not affect fish richness, whereas greater macrophyte colonization was associated with lower fish abundance, partially supporting H2. Species-specific associations supported H3: *Panicum rivulare* was associated with *Hoplias malabaricus* (both seasons) and *Poecilia vivipara* (dry season) in the upper zone, while *Polygonum lapathifolium* was associated with *Loricariichthys castaneus* (both seasons), *Rineloricaria paraibensis* (wet season), and *Hypostomus affinis* (middle zone, both seasons). Our findings suggest that maintaining intermediate and structurally heterogeneous macrophyte cover through selective control, rather than complete removal, is essential for sustaining fish assemblages in tropical reservoirs. Effective management should incorporate both longitudinal reservoir gradients and seasonal hydrological dynamics into adaptive monitoring and conservation programs.

☆ Acknowledgements

We thank Wagner Uehara, Victoria de Jesus Souza, Leonardo de Almeida Freitas, and Dandhara Carvalho Rossi (Laboratory of Fish Ecology, UFRRJ) for assistance during fieldwork. This work was funded by ANEEL/LIGHT/FUNEP Research & Development (R&D) Project (Contracts 1.0358/2022 and 4500515435, Project FUNEP #4735), entitled *"Development of Environmental Indicators to Assess the Influence of Aquatic Macrophyte Management in the Santana Reservoir.* Fish were collected under license from IBAMA/ICMBio (authorization no. 10707) and in accordance with the Ethics Council for Animal Use (CEUA/ICBS/UFRRJ; protocol no. 12,179).

* Corresponding author.
E-mail addresses: gerson@ufrrj.br (F.G. Araújo), rlpitelli@ecosafe.agr.br (R.L.C.M. Pitelli), rapitelli@ecosafe.agr.br (R.A. Pitelli), antonio.lameirao@light.com.br (A.M.M.S. Lameirão), felipe.cruz@light.com.br (F.P. Cruz), rinaldo.rocha@light.com.br (R.J.S. Rocha), rafaeladsg@hotmail.com (R.S.G. Gonçalves), gustavohsg@outlook.com (G.H.S. Guedes).

https://doi.org/10.1016/j.ecohyd.2026.100783
Received 6 April 2026; Received in revised form 13 June 2026; Accepted 25 June 2026
Available online 8 July 2026

1. Introduction

Reservoirs are complex anthropogenic ecosystems in which ecological patterns arise from interactions among longitudinal gradients, seasonal hydrological dynamics, and human-driven environmental filters (Straskraba and Tundisi, 1999; Agostinho et al., 2016; Alkhadher et al., 2025). Structured along upstream-downstream gradients, these systems exhibit marked temporal variability linked to hydrological seasonality, characterized in southeastern Brazil by a warm, wet period and a cooler, dry season, which plays a key role in shaping fish assemblages through environmental filtering, habitat availability, and resource distribution (Thornton, 1990; Terra et al., 2010; Peres-Neto et al., 2012; Wanjari et al., 2025).

Aquatic macrophytes are central to habitat architecture in tropical reservoirs, mediating trophic interactions, nutrient cycling, and providing refuge and spawning sites for fish (Dibble et al., 2006; Thomaz et al., 2008; Jeppesen et al., 2012). By increasing structural heterogeneity, macrophytes can enhance fish diversity and abundance, particularly in littoral zones, while promoting species-specific associations between particular fish and macrophyte species (Warfe and Barmuta, 2006; Thomaz and Cunha, 2010). However, hydrological regulation and nutrient enrichment may reshape macrophyte communities and fish assemblages by altering connectivity and disturbance regimes, with excessive macrophyte proliferation potentially reducing habitat accessibility and creating hypoxic microhabitats that constrain fish occupancy and movement (Carpenter et al., 1998; Silva-Pereto et al., 2014; Agostinho et al., 2016; Arantes et al., 2019).

Environmental drivers of macrophyte assemblages vary along latitudinal and longitudinal gradients, reflecting differences in temperature, nutrient dynamics, hydrology, sediment type, and depth that ultimately influence fish community composition. In tropical reservoirs, warmer conditions and moderate nutrient inputs can promote macrophyte biomass and habitat complexity, enhancing refuge and nursery areas for fish (Lacoul and Freedman, 2006; Thomaz et al., 2008; Jeppesen et al., 2012). Along the riverine-lacustrine gradient, declining flow and sediment load, coupled with increasing water transparency and depth, drive shifts in vegetation forms that influence habitat heterogeneity, connectivity, and trophic interactions among fish species (Thornton, 1990; Strand and Weisner, 2001; Mehner et al., 2005; Agostinho et al., 2007; Guedes and Araújo, 2022; Quirino et al., 2023).

Hydrological seasonality further regulates physicochemical properties such as temperature, turbidity, conductivity, and dissolved oxygen, affecting primary productivity and macrophyte growth (Shafiq et al., 2014; Silva-Pereto et al., 2014; Jargal et al., 2021). Although these changes can influence fish metabolism and reproductive dynamics, community structure is often more strongly shaped by habitat attributes such as depth, sediment type, and macrophyte cover, which provide refuge and feeding and spawning sites that buffer environmental variability (Dibble et al., 2006; Warfe and Barmuta, 2006; Agostinho et al., 2007; Thomaz and Cunha, 2010).

Relationships between fish richness, abundance, and macrophyte cover in tropical reservoirs are therefore complex and often nonlinear. Intermediate levels of macrophyte colonization can enhance diversity by increasing habitat heterogeneity and providing refuge, spawning substrates, and feeding grounds, whereas excessive growth may limit movement and reduce habitat accessibility (Miranda and Hodges, 2000; Xie et al., 2005). Littoral habitat availability, regulated by depth gradients, shoreline slope, and macrophyte distribution, thus acts as a key environmental filter shaping fish assemblage composition, connectivity, and functional traits (Franco et al., 2024; Prado et al., 2024).

The Santana Reservoir, located in Rio de Janeiro State within the Paraíba do Sul River basin, was formed by damming the Piraí River and receives pumped water from the Paraíba do Sul River, reversing the natural flow for approximately 20 km. The reservoir is eutrophic and strongly influenced by urban, industrial, and agricultural inputs, which have promoted extensive proliferation of submerged and floating macrophytes along its margins (Camara et al., 2024). Despite its importance within a major hydropower complex, interactions between aquatic biota and environmental conditions in the reservoir remain poorly understood.

This study aimed to: (i) characterize spatial and temporal variation in limnological conditions and habitat structure; (ii) describe the composition and distribution of aquatic macrophyte and fish communities; and (iii) evaluate how macrophyte colonization and composition influence fish assemblage structure along spatial gradients and seasonal hydrological variation (dry and wet periods). We tested the following hypotheses: H1: Seasonal and spatial environmental variation influences macrophyte composition and colonization; H2: Macrophyte richness and abundance influence fish assemblage richness and abundance; H3: Species-specific associations occur between macrophytes and fish, reflecting differential habitat use mediated by vegetation structure. Together, these analyses provide a mechanistic understanding of the processes structuring fish assemblages in tropical reservoirs and support effective management and conservation.

2. Material and methods

2.1. Study area

The Santana Reservoir, built in 1945, lies at 361–363 m above sea level (22°31′50″S, 43°49′15″W; Fig. 1) is part of Light's hydropower generation complex in Rio de Janeiro State, Brazil, encompassing the municipalities of Piraí, Santanésia, and Barra do Piraí. Formed by a dam on the Piraí River approximately 11 km upstream from its confluence with the Paraíba do Sul River (PSR), the reservoir exhibits a unique hydrological configuration. Water pumped from the Paraíba do Sul River is introduced near the dam, reversing the natural flow of the Piraí River for approximately 20 km upstream. At the upper limit of this reach, water is pumped again to supply another reservoir located 35 m above Santana Reservoir. In addition to this pumped inflow from the PSR, the system receives water from the lower reach of the Piraí River, the system's original source, and from small tributaries within this section of the Piraí River basin, which was impounded to form the Santana Reservoir. (Pitelli et al., 2025). The drainage basin covers 82.5 km^2, with a surface area of 6.1 km^2, storage volume of 19.9 Mm^3, mean depth of 3.3 m, and maximum depth of 12 m (Mattos et al., 2022). The reservoir is eutrophic and has a short water residence time (~1 day) (Camara et al., 2024). The regional climate is seasonal tropical with a dry winter and wet summer (Aw), according to the Köppen–Geiger classification (Kottek et al., 2006). Average rainfall ranges from approximately 500 mm during winter to 1500–2500 mm during summer, while air temperatures ranges from 15 to 31 °C.

Based on its longitudinal environmental gradients and hydrological configuration, the Santana Reservoir can be divided into three distinct zones (Fig. 1). The Upper zone (22°32′S, 43°49′W), located immediately upstream of the dam, exhibits shallow depth (< 2 m), lentic conditions, sandy substrate, and intense presence of submerged macrophytes, reflecting the direct influence of reservoir operations. The Middle zone (22°33′S, 43°49′W), situated in the central portion of the reservoir between the Santana dam and the Vigário Pumping Station, is characterized by shallow water (< 3 m), seasonal flow conditions, and occurrence of floating macrophytes. The Lower zone (22°36′S, 43°52′W), the most distal portion from the dam, is characterized by dense macrophyte stands, clay and sandy substrate, and a higher degree of anthropogenic influence. This longitudinal zonation is consistent with the riverine–lacustrine gradient widely described for tropical reservoirs (Thornton, 1990; Agostinho et al., 2007), and reflects the unique hydrological configuration of the Santana system, in which pumped inflow from the Paraíba do Sul River reverses the natural flow of the Piraí River for approximately 20 km (Fig. 1).

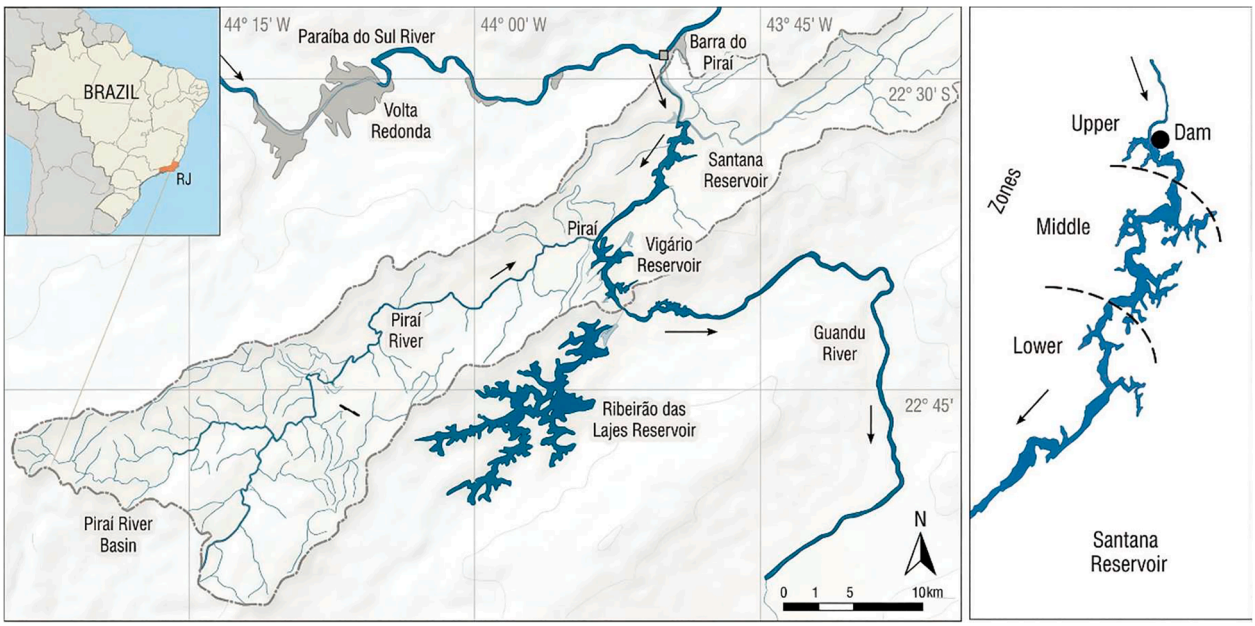

Fig. 1. Map of the Santana Reservoir showing the three sampling zones (Lower, Middle, and Upper) for biotic and abiotic data collection.

2.2. Biotic and abiotic samplings

Simultaneous sampling of fish assemblages, aquatic macrophytes, physical and chemical water parameters, and structural habitat components was carried out at three sites along the longitudinal axis of the Santana Reservoir to ensure representative coverage of spatial variation and habitat diversity.

Standardized protocols were applied to sample (i) fish, (ii) aquatic macrophytes, (iii) physical and chemical water parameters, and (iv) habitat characteristics at the Santana Reservoir between August 2023 and September 2025. Sampling followed a quarterly design, totaling nine independent sampling campaigns conducted across both the wet (November–March) and dry (July–September) seasons. Sampling was carried out in three zones along the longitudinal gradient of the reservoir (upper, middle, and lower zones; Fig. 1). The total sampling effort comprised 24 sampling units, corresponding to all zone–campaign combinations, except for three campaigns in which the lower zone was not sampled (in March 2024, October 2024, and March 2025) due to operational and environmental constraints that prevented access to this area.

Macrophyte communities were surveyed using boat-based assessments. Aquatic macrophyte density was assessed along the reservoir margins within a 10-m-wide strip extending along the shoreline at each sampling site. Macrophyte taxa were identified and cover rank was determined at each transect site using a modified Braun-Blanquet ranking system (Braun-Blanquet, 1932; Poore, 1955): (i) high density (score = 100), species dominant and structuring the landscape of the sampling area; (ii) medium density (score = 50), species occurring in substantial numbers but not defining site physiognomy; (iii) low density (score = 25), species present but requiring visual effort to detect; and (iv) very low density (score = 12), species observed only sporadically or represented by fragments (for taxa reproducing via fragmentation) (Pitelli et al., 2008,2009). Although semi-quantitative methods are inherently subject to observer subjectivity, all field assessments were conducted by the same trained team throughout the study period, following standardized criteria for score assignment, supporting its suitability for comparative analyses. Species identification followed specialized taxonomic literature, including Kismann and Groth (1997), Pott and Pott (2000), Lorenzi (2008), and Pitelli et al. (2023).

Fish communities were sampled using both passive and active gears. At each site, six monofilament gillnets (35 × 2.8 m) with mesh sizes ranging from 15 to 140 mm between opposite knots were deployed: two ≤30 mm (small mesh), two 30–60 mm (medium mesh), and two 60–140 mm (large mesh). Nets were set at dusk, when fish activity is typically higher (Guedes and Araújo, 2022), and retrieved at dawn, operating for approximately 13 h. In addition, ten dip-net hauls and ten cast net throws were conducted at each site along marginal vegetation and macrophyte stands to target small bodied juveniles and species of the order Cyprinodontiformes (Araújo et al., 2024). Captured fish were identified to species level and quantified *in situ*. Live specimens were released after measurement, whereas individuals that died during handling were fixed in 10% formalin, preserved in labeled containers, and subsequently catalogued in the ichthyological collection of the Fish Ecology Laboratory, Universidade Federal Rural do Rio de Janeiro (LEP-UFRRJ) (Araújo and Guedes, 2025).

Physical and chemical water parameters were measured using a multiparameter probe (Hanna HI98194), which recorded water temperature (°C), dissolved oxygen (mg L^{-1}), oxidation–reduction potential (mV), pH, electrical conductivity (mS cm^{-1}), turbidity (FNU), and total dissolved solids (mg L^{-1}). Each variable was measured six times at each site, with three replicates during gillnet deployment and three during retrieval. Water transparency (m) was assessed using a Secchi disk at both deployment and retrieval.

Habitat characterization was conducted using a scoring protocol ranging from 0 to 4, based on the relative coverage of each habitat component, following these criteria: 0 = absence of coverage, 1 = low coverage, 2 = moderate coverage, 3 = high coverage, and 4 = complete coverage. The environmental habitat descriptors evaluated included: (i) instream structure (presence of branches, leaf litter, woody debris, roots, and bank slope); (ii) riparian cover (grasses, shrubs, and trees); and (iii) substrate composition (clay, sand, or rock). Habitat components were estimated within an area of approximately 200 m^2 (20 m in length × 10 m in width), encompassing a 5 m aquatic zone (from the waterline toward the reservoir) and a 5 m terrestrial zone (from the waterline outward), following Guedes et al. (2020) and Ferreira et al. (2021). Water depth was measured at an equidistant point between opposite margins using a Speedtech SM-5 digital depth sounder, with centimeter precision.

2.3. Data analysis

2.3.1. Environmental variables

Spatial and seasonal differences in each environmental variable (water physicochemical parameters and habitat conditions) were tested using a two-way analysis of variance (ANOVA), with zone (upper, middle, and lower) and season (dry and wet) as fixed factors. ANOVA was selected because it is appropriate for testing differences in continuous univariate variables among categorical groups and their interactions. The interaction between zone and season was also evaluated. When significant effects were detected ($p < 0.05$), Tukey's post hoc test was applied to identify pairwise differences among factor levels.

Multivariate analyses followed the framework proposed by Clarke (1993) and Anderson et al. (2008), widely adopted in ecological studies evaluating spatial and temporal variation in community structure. Differences in each set of environmental conditions (*i.e.*, depth; water physical and chemical variables; substrate composition; instream structure; and riparian cover) were assessed using a Permutational Multivariate Analysis of Variance (PERMANOVA) based on a Euclidean distance matrix. The model included two fixed factors: zone (three levels: upper, middle, and lower) and season (two levels: dry and wet). When significant effects were detected, pairwise comparisons were conducted to identify differences among factor levels.

To examine spatial and seasonal patterns in the selected environmental variables (physicochemical and habitat), *i.e.*, those that showed significant differences among zones and/or seasons according to ANOVA, a Principal Component Analysis (PCA) was performed. PCA was employed as an ordination technique to reduce the dimensionality of the environmental dataset and to identify the main axes of variation, facilitating the visualization of gradients among zones and seasons (Legendre and Legendre, 1998). Prior to the analysis, all environmental variables were normalized (mean-centered and scaled to unit standard deviation) to remove the effects of differing measurement scales. The first two PCA axes were then plotted to summarize the main environmental gradients and to visualize patterns of variation among zones and seasons.

2.3.2. Biotic variables

The structure of fish and macrophyte communities was compared among reservoir zones and hydrological seasons. Prior to analysis, abundance data were log (x + 1) transformed to reduce the influence of dominant species. Differences in community structure were tested using a Permutational Multivariate Analysis of Variance (PERMANOVA) based on a Bray-Curtis similarity matrix, with zone (upper, middle, and lower) and season (dry and wet) as fixed factors. Bray-Curtis similarity was used because it is widely recommended for ecological community data due to its sensitivity to species abundances and reduced influence of joint absences. When significant effects were detected, pairwise comparisons were performed to identify differences among factor levels. Patterns of community composition were further explored using non-metric multidimensional scaling (nMDS), an ordination technique used to graphical visualize high-dimensional data by representing it in a lower-dimensional space, preserving the rank order of dissimilarities between samples (Clarke, 1993). A Similarity Percentage Analysis (SIMPER) was used to identify the species contributing most to within-group similarity (Clarke, 1993), considering the combinations of zone (upper, middle, and lower) and season (dry and wet).

The relationship between fish assemblage structure and aquatic macrophyte composition was assessed using distance-based redundancy analysis (dbRDA). The dbRDA was chosen because it allows the direct ordination of a multivariate response matrix (fish assemblages) against a set of explanatory variables (macrophyte composition), operating on any dissimilarity measure and thus being suitable for species abundance data (McArdle and Anderson, 2001). Macrophyte and fish data matrices included only the species that contributed most to dissimilarities among reservoir zones and seasons, as identified by SIMPER analysis. This selection reduced the influence of rare species and emphasized the main ecological patterns linking fish and macrophytes. The dbRDA was then used to evaluate how variation in macrophyte composition explains fish assemblage structure along the reservoir's seasonal and longitudinal gradient.

Effects of macrophyte abundance (cover), richness, and environmental variables on fish abundance and species richness were analyzed using Generalized Linear Models (GLMs). This analysis provides a flexible framework for modeling ecological response variables, allowing us to assess the influence of environmental predictors and macrophyte structure on fish assemblages while accounting for the distributional properties of ecological data. GLMs were fitted using a negative binomial distribution for fish abundance and a Poisson distribution for species richness. The negative binomial distribution was used to account for overdispersion in abundance data, whereas the Poisson distribution was appropriate for species richness because the variance was approximately proportional to the mean. Spatial (zone: lower, middle, and upper) and temporal (season: dry and wet) factors were included in the models as categorical predictors. Additional fixed effects included habitat variables that differed among zones or seasons according to ANOVA, as well as the first principal component (PC1) of water physicochemical variables, used as a synthetic environmental predictor. Macrophyte structure was incorporated using the macrophyte colonization score in the fish abundance model and macrophyte species richness in the fish richness model. Predictor significance was assessed using Type II likelihood ratio tests (analysis of deviance), and model fit was evaluated using the Akaike Information Criterion (AIC). Model assumptions were examined through simulation-based residual diagnostics (DHARMa package), including tests for dispersion, zero inflation, and residual uniformity.

PERMANOVA, SIMPER, and nMDS analyses were performed using the PRIMER 6 + PERMANOVA statistical package (Anderson et al., 2008). PCA (function *prcomp*; package *stats*), and Generalized linear model (GLM) with negative binomial distribution were fitted using the function glm.nb (package MASS; Venables and Ripley, 2002). Model diagnostics were performed using simulation-based residual analyses implemented in the package DHARMa (Hartig, 2019). All analyses were conducted in R (R Core Team, 2025).

3. Results

3.1. Environmental variables

Physical and chemical water variables did not differ among zones (Pseudo-$F = 0.26$; $p = 0.90$; Tables S1–S3 Supplementary Material), but showed seasonal variation (Pseudo-$F = 5.14$; $p = 0.002$) in water temperature ($F = 89.35$; $p < 0.001$) and turbidity ($F = 4.86$; $p < 0.001$) with higher values in the wet seasons, and in dissolved oxygen ($F = 8.32$; $p < 0.001$), and oxidation–reduction potential (ORP) ($F = 5.28$; $p = 0.03$) with higher values in the dry seasons. Transparency, pH, conductivity, and total dissolved solids did not show significant differences among either zones or seasons (Table S3; Supplementary Material).

Water depth differed significantly among zones ($F = 13.42$; $p < 0.001$; Tables S1–S3; Supplementary Material), with lower values in the upper zone, compared to the middle and lower zones. No significant differences were detected in depth among seasons ($F = 0.07$; $p = 0.79$), nor for the interaction between season and zone ($F = 0.27$; $p = 0.74$). Habitat variables related to instream structure (woody debris, roots, leaf litter, bank slope, and branches) and riparian vegetation (grasses, shrubs, and trees) did not differ significantly among zones, seasons, or their interaction ($p > 0.05$ for all variables; Tables S1–S3; Supplementary Material). Regarding substrate composition, only the proportion of rocks differed significantly among zones ($F = 5.48$; $p = 0.01$), whereas mud and sand showed no spatial or seasonal variation (Tables S1-S3; Supplementary Material).

Seasonal variation was the main structuring pattern of

environmental conditions in the Santana Reservoir (Fig. 2), with the first two PCA axes explaining 65.09% of the total variation. Samples from the wet season were associated with higher temperature and turbidity, whereas samples from dry season were characterized by higher ORP and dissolved oxygen along Axis 1. Axis 2 was positively related to conductivity and transparency.

3.2. Aquatic macrophytes

A total of 29 aquatic macrophyte species, representing 18 families and 13 orders, were recorded (Table S4; Supplementary Material). Poaceae exhibited the highest species richness (five species), followed by Araceae (three species) and Pontederiaceae (three species). The highest richness was recorded in the upper zone (26 species) (Table S4; Supplementary Material). Species richness in the middle and lower zones was 21 and 22 species, respectively. The highest cumulative macrophyte colonization score was recorded in the middle zone (34,847), followed by the upper (25,177) and lower zones (14,340). Among all species, *Urochloa subquadripara* (Trin.) R.D. Webster exhibited the highest spatial dominance in the Santana Reservoir, reaching a total colonization score of 15,036 and occurring at high abundance across all zones and seasons. Other abundant macrophytes included *Panicum rivulare, Typha dominguensis, Colocasia esculenta, Pistia stratiotes, Eichhornia azurea*, and *Polygonum lapathifolium*.

PERMANOVA based on macrophyte colonization abundance revealed significant differences among zones (Pseudo-F = 3.41; p = 0.002), whereas no significant differences were detected between seasons (Pseudo-F = 1.55; p = 0.21) or for the zone × season interaction (Pseudo-F = 0.52; p = 0.88). Pairwise comparisons showed that the middle zone (highest abundance) differed from the upper zone (t = 1.98; p = 0.001), which in turn differed from the lower zone (lowest abundance; t = 1.64; p = 0.02). Spatial differences in community structure were indicated by the nMDS ordination plot, which showed distinct sample groupings among zones (Fig. 3A; stress = 0.21). Samples from the upper zone formed a distinct cluster, clearly separated from those of the middle and lower zones. In contrast, samples from the middle and lower zones partially overlapped. No clear seasonal pattern was observed between the dry and wet seasons.

SIMPER analysis revealed consistently high within-group similarity, ranging from 74.72% to 86.32% (Table 1). Community structure was characterized by the recurrent dominance of a limited set of spatially structured species. *Urochloa subquadripara* was dominant across all zones and seasons. *Panicum rivulare* was typical of the upper zone throughout the year, whereas *Polygonum lapathifolium* was characteristic of the middle and lower zones year-round. *Typha dominguensis* was typical of the upper zone throughout the year and of the middle zone during the dry season, while *Salvinia auriculata* was representative only of the lower zone in the dry season (Table 1).

3.3. Ichthyofauna

A total of 1146 individuals were sampled, with the lowest abundance observed in the upper zone (222 individuals), while the middle and lower zones exhibited similarly higher abundances (453 and 471 individuals, respectively). Fish richness and abundance were always higher in the wet season (Table S5). Fish richness showed small variations among zones, with the highest number of species recorded in the middle (22 species) and lower zones (21 species) during the wet season, and lower values in the middle zone during the dry season. Higher abundances were recorded in the middle and lower zones, whereas lower abundances occurred in the upper zone (Table S5). Temporal variation in catch structure was evident across hydrological seasons, with higher richness and abundance values observed during the wet season. In the upper zone, abundance increased from 52 individuals in the dry season to 170 in the wet season. In the middle zone, catches rose from 63 individuals in the dry season to 390 in the wet season. Similarly, the lower zone showed higher abundance in the wet season (269 individuals) compared to the dry season (202 individuals).

Fish assemblage composition varied both spatially among zones (Pseudo-F = 2.21; p = 0.006) and temporally between seasons (Pseudo-F

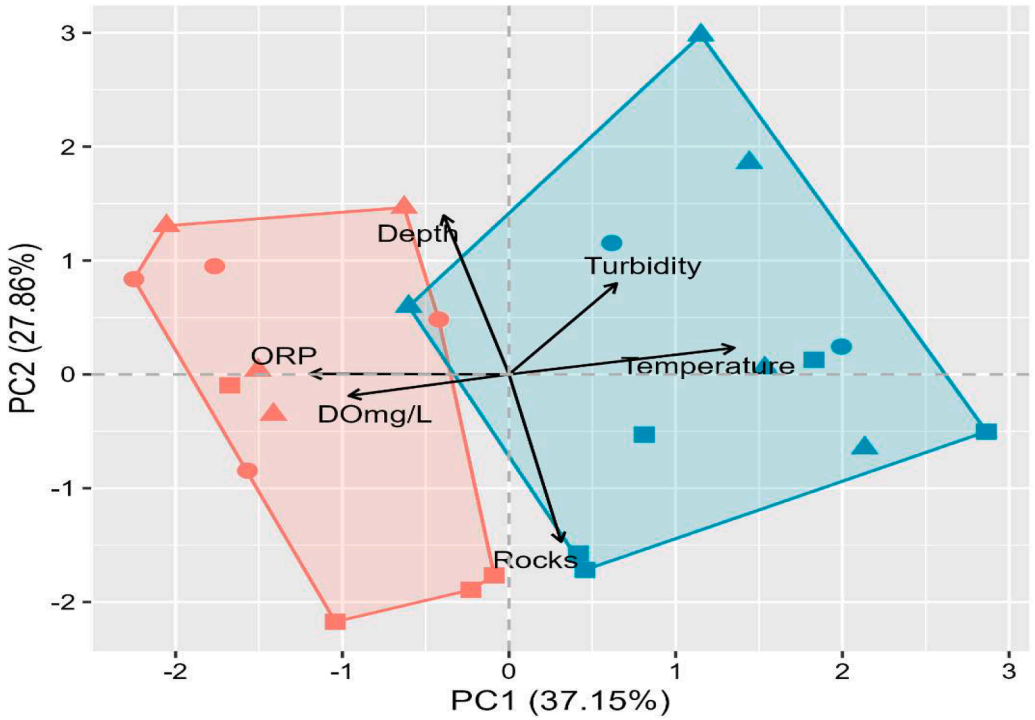

Fig. 2. Principal Component Analysis (PCA) ordination on selected physical and chemical water variables across sampling seasons and zones. Colors indicate sampling seasons (green = wet; red = dry), and symbols represent zones (squares = upper, triangles = middle, circles = lower). ORP, Oxid-Reduction Potential. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

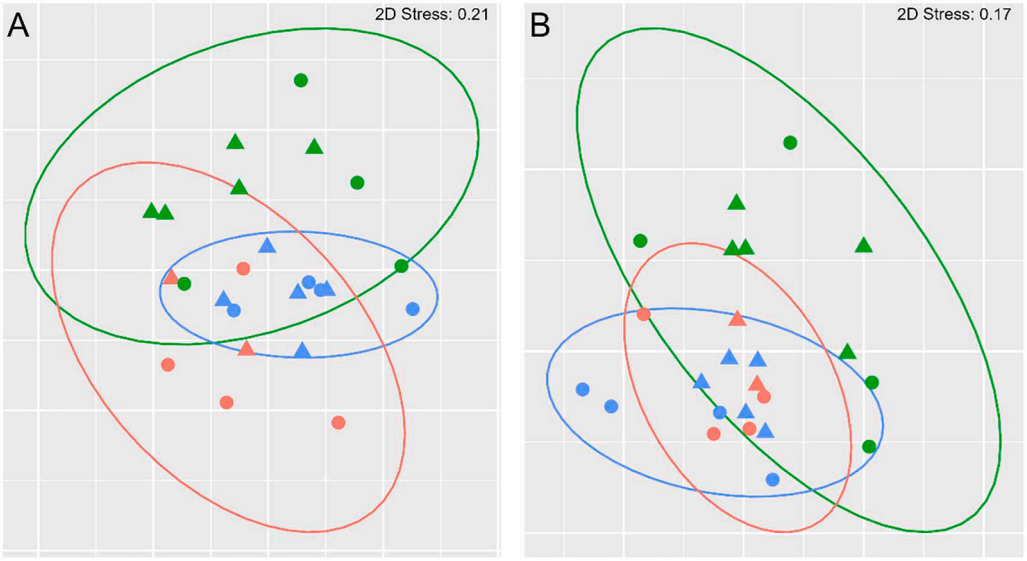

Fig. 3. Non-metric multidimensional scaling (nMDS) ordination of macrophyte composition (A) and fish assemblages (B). Colors indicate sampling zones (upper, green; middle, blue; lower, red), and symbols represent seasons (dry, circles; wet, triangles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

Table 1
Average within-group similarity (%) of aquatic macrophyte assemblages in the upper, middle, and lower zones of the Santana Reservoir during the dry and wet seasons, based on SIMPER analysis.

Species	Upper		Middle		Lower	
	Dry (74.72)	Wet (81.12)	Dry (83.52)	Wet (86.32)	Dry (80.32)	Wet (84.5)
Urochloa subquadripara	11.13	9.91	10.25	9.92	11.59	9.96
Panicum rivulare	10.38	9.25				
Typha dominguensis	9.83	9.01	9.23			
Colocasia esculenta	9.87	9.21			10.32	9.63
Polygonum lapathifolium			9.51	8.84	10.6	8.91
Salvinia auriculata					9.92	

= 2.13; $p = 0.03$), but no significant zone × season interaction was observed (Pseudo-$F = 0.71$; $p = 0.79$). Pairwise comparisons showed that the upper zone differed from the middle ($t = 1.81$; $p = 0.002$) and lower zones ($t = 1.50$; $p = 0.03$).

The nMDS ordination plots revealed spatial and seasonal structuring of fish assemblages, highlighting differences among reservoir zones and between seasons (Fig. 3B). Samples from the upper zone formed a well-defined cluster, positioned mainly in the lower portion of the ordination space, indicating a species composition distinct from that of the middle and lower zones. In contrast, samples from the middle and lower zones showed partial overlap. Seasonal separation between the dry and wet periods was also evident, with samples occupying different regions of the ordination space irrespective of zone, supporting the significant effects of zone and season detected by PERMANOVA.

The SIMPER analysis revealed differences in assemblage composition among zones and seasons, with intragroup similarity values ranging from 5.99% to 62.73% (Table 2). In the Upper zone during the dry season, intragroup similarity was low and mainly driven by *Poecilia vivipara* (Bloch and Schneider, 1801) in the dry season, which contributed 69.90% of group similarity and *Hoplias malabaricus* (both seasons), In the wet season, similarity increased to 62.73% and was distributed among *Geophagus brasiliensis* (Quoy and Gaimard, 1824) (24.34%), *Psalidodon parahybae* (Eigenmann, 1908) (16.09%), and *Astyanax lacustris* (Lütken 1875) (14.42%),

The Middle and Lower zones showed moderate intragroup similarity, which increased from the dry to the wet season. In the Middle zone, similarity rose from 21.13% in the dry season to 43.10% in the wet season. During the dry season, similarity was mainly driven by

Table 2
Average within-group similarity (%) of ichthyofauna in the upper, middle, and lower zones of the Santana Reservoir, during the dry and wet seasons, based on SIMPER analysis.

Species	Upper		Middle		Lower	
	Dry (5.99)	Wet (33.01)	Dry (21.13)	Wet (43.10)	Dry (30.8)	Wet (50.12)
Psalidodon parahybae		16.09				
Hoplias malabaricus	30.10	10.78			15.23	
Astyanax lacustris		14.42				
Poecilia vivipara	69.9					
Geophagus brasiliensis		24.34				
Crenicichla lacustris		13.22				15.62
Hypostomus affinis			42.93	11.39		
Loricariichthys castaneus			19.85	44.79	64.84	30.56
Rineloricaria paraibensis				13.03		12.92
Hoplosternum littorale			20.35			

Hypostomus affinis (42.93%), followed by *Hoplosternum littorale* (20.35%) and *Loricariichthys castaneus* (19.85%), whereas in the wet

season *Loricariichthys castaneus* became the main contributor (44.79%), followed by *Rineloricaria paraibensis* Mejia & Buckup 2024 (13.03%) and *Hypostomus affinis* (11.39%). A similar seasonal increase was observed in the Lower zone, where similarity rose from 30.80% in the dry season to 50.12% in the wet season, being dominated by *Loricariichthys castaneus* (64.84%), and by *Loricariichthys castaneus* (30.56%), and *Rineloricaria paraibensis* (12.92%) in the wet season.

3.4. Relationships between fish and macrophytes

The dbRDA ordination revealed consistent associations between fish assemblages and aquatic macrophytes across reservoir zones (Fig. 4). The first axis explained 39.6% of the fitted variation (14.3% of the total variation) and represented the main gradient in fish assemblage composition, while the second axis accounted for 29.6% of the fitted variation (10.7% of the total variation). Together, these axes indicate that a substantial proportion of the variation in fish assemblage structure was explained by the presence and spatial distribution of macrophytes.

The dbRDA1 axis primarily separated samples along the reservoir's longitudinal gradient. Samples from the upper zone (green) were positioned at positive axis scores and were associated with higher contributions of *Panicum rivulare* and *Astyanax lacustris*. In contrast, samples from the middle (blue) and lower (red) zones showed greater overlap in multivariate space and were associated with species such as *Salvinia auriculata, Psalidodon parahybae*, and *Hoplosternum littorale* (Hancock, 1828). Fish assemblage structure was primarily linked to the presence of a specific subset of aquatic macrophyte species, suggesting that certain plant taxa play a key role in shaping local community patterns. In particular, *Polygonum lapathifolium* was consistently associated with the siluriforms *Hypostomus affinis, Rineloricaria nigricauda*, and *Loricariichthys castaneus* in the middle and lower zones. *Salvinia auriculata* was associated with *Psalidodon parahybae*, whereas *Typha dominguensis* was linked to *Poecilia vivipara* in the upper zone.

According to the GLM results, fish abundance was significantly lower in the upper zone ($\beta = -1.44$, p = <0.001) than in the lower zone (Table 3). The wet season had a significant positive effect on fish abundance ($\beta = 1.72$; $p < 0.001$) (Table 3). Macrophyte colonization was negatively associated with fish abundance ($\beta = -0.37$; $p = 0.02$), whereas rock cover was positively associated with abundance ($\beta = 0.36$; $p = 0.01$) (Table 3; Fig. 5). In contrast, depth ($\beta = 0.048$; $p = 0.79$) and PCA1 ($\beta = 0.19$; $p = 0.17$) were not significant predictors (Table 3). Fish species richness was primarily influenced by hydrological seasonality, with significantly higher richness during the wet season ($\beta = 1.15$; $p < 0.001$) (Table 3), indicating a strong effect of seasonal hydrological dynamics on local assemblage structure. The upper zone ($\beta = -0.72$; $p = 0.014$) also exhibited significantly lower richness compared to the lower zone (Table 3). Macrophyte richness ($\beta = -0.11$; $p = 0.18$), depth ($\beta = -0.09$; $p = 0.46$), and PCA1 ($\beta = 0.13$; $p = 0.18$) were not significant predictors (Table 3; Fig. 5). The significance of predictors was confirmed using Type II likelihood ratio tests (Tables S6, Figure S1; Supplementary

Table 3
Generalized linear models (GLMs) evaluating 1) the effects of macrophyte colonization, season, depth and PC1 on fish abundance; and 2) the effects of macrophyte richness, season, depth and PC1 on fish species richness. Significance: ***$p < 0.001$; *$p < 0.05$; n.s, $p > 0.05$.

Variable	Estimate (β)	Standard Error	z value	*p*-value
Fish abundance				
Intercept	3.22	0.32	9.88	<0.001
Zone (Middle)	−0.07	0.36	−0.18	0.85n.s.
Zone (Upper)	−1.44	0.41	−3.50	**0.001****
Period (Wet)	1.72	0.41	4.20	**<0.001*****
Depth	0.048	0.19	0.26	0.79n.s.
Rocks	0.36	0.14	2.56	**0.01***
PCA1	0.19	0.13	1.37	0.17n.s.
Macrophyte colonization	−0.37	0.15	−2.27	**0.02***
Fish richness				
Intercept	1.74	0.21	8.120	<0.001***
Zone (Middle)	−0.31	0.19	−1.66	0.09n.s.
Zone (Upper)	−0.72	0.29	−2.43	**0.01****
Period (Wet)	1.15	0.29	4.00	**<0.001*****
Depth	−0.09	0.13	−0.74	0.46n.s.
Rocks	0.08	0.09	0.92	0.36n.s.
PCA1	0.13	0.09	1.35	0.18n.s.
Macrophyte richness	−0.11	0.08	−1.34	0.18n.s.

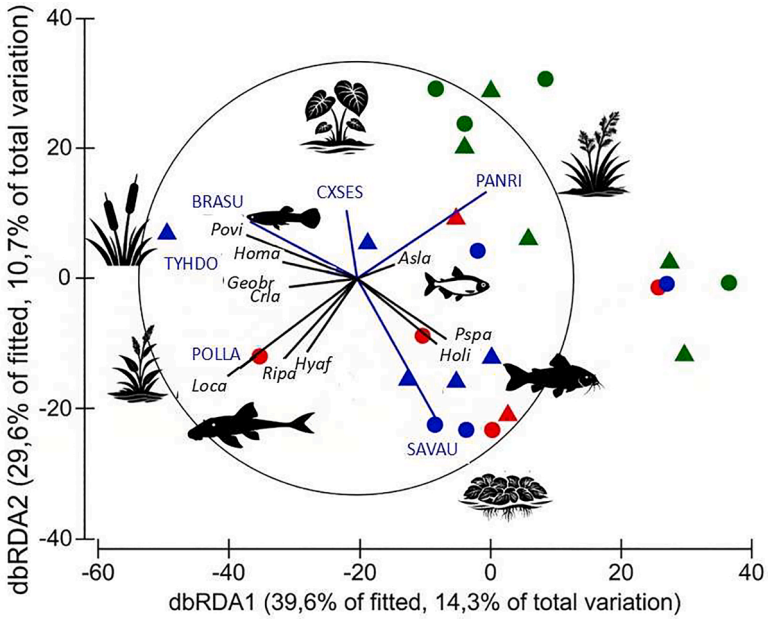

Fig. 4. Ordination diagram from distance-based redundancy analysis (dbRDA) of macrophyte and fish assemblages in the Santana Reservoir. Colors indicate sampling zones (upper, green; middle, blue; lower, red), whereas symbols represent hydrological seasons (dry, circles; wet, triangles). Full macrophyte species names are provided in Table S4, and full fish species names are provided in Table S5 of the Supplementary Information. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

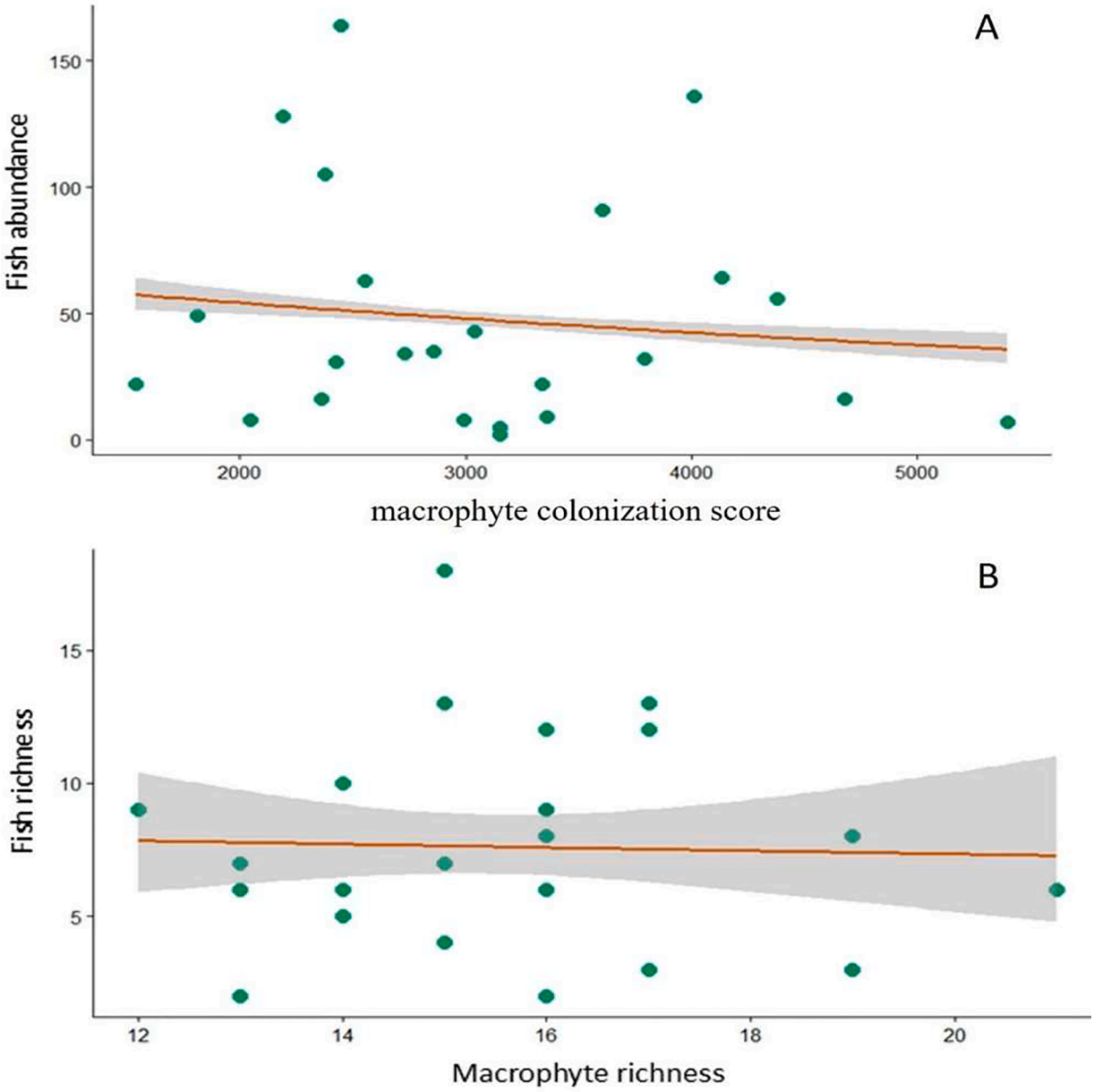

Fig. 5. Relationships between structural attributes of aquatic macrophytes and the fish community. (A) Macrophyte abundance (colonization) *vs.* fish abundance and (B) macrophyte richness *vs.* fish species richness, as estimated by GLMs. Points represent observed values; the solid line indicates model predictions, and the shaded area represents the 95% confidence interval.

Material). Fish abundance tends to decrease with higher macrophyte colonization rates, whereas species richness does not appear to be affected by macrophyte richness (Fig. 5).

4. Discussion

4.1. Environmental variables

Environmental variation in the Santana Reservoir was driven primarily by seasonal rather than longitudinal processes, indicating that climatic forcing exerts stronger control over limnological dynamics than spatial heterogeneity along the reservoir axis. Such dominance of hydrological seasonality is widely reported in tropical reservoirs, where rainfall-driven changes in runoff and water residence time regulate water column conditions (Thornton, 1990; Araújo et al., 2011; Alkhadher et al., 2025).

Higher temperature and turbidity during the wet season likely result from enhanced runoff and allochthonous inputs associated with rainfall, which increase suspended particles and reduce water clarity (Quevedo-Castro et al., 2019). In contrast, higher dissolved oxygen and oxidation–reduction potential during the dry season suggests more stable water column conditions and greater atmospheric reaeration under lower turbidity (Bellanger et al., 2004; Luo et al., 2024). In contrast to these seasonal effects, several chemical variables (pH, conductivity, transparency, and total dissolved solids) remained relatively stable across zones and seasons, suggesting a high degree of chemical homogeneity throughout the reservoir. This pattern is typical of lentic systems, where mixing processes buffer localized inputs and promote spatial uniformity of dissolved constituents (Thornton, 1990; Winton et al., 2019).

Spatial differences were primarily associated with geomorphological features along the reservoir gradient. The shallower conditions observed in the upper zone reflect the fluvial character typical of upstream reservoir sections, whereas deeper downstream areas exhibit more

lacustrine conditions due to reduced flow near the dam (Carneiro and Bini, 2020). Similarly, the higher proportion of rocky substrate in the upper zone likely reflects stronger flow energy capable of retaining coarse materials while transporting finer sediments downstream (Agostinho et al., 2016; Carneiro and Bini, 2020). Consistent with these interpretations, PCA results indicate that hydrological seasonality represents the main axis of environmental variation in the system, with potential implications for habitat structure and resource availability for aquatic biota (Tundisi et al., 2008; Winton et al., 2019).

4.2. Longitudinal structuring of macrophytes

Aquatic macrophyte distribution in the Santana Reservoir was primarily structured along the longitudinal gradient, with significant differences among zones but no seasonal effect. This pattern reflects the environmental heterogeneity typical of reservoirs, where transitions from riverine to lacustrine conditions modify hydrodynamics, sediment characteristics, nutrient availability, and water transparency, creating distinct habitat conditions that favor different macrophyte species and life forms. Consequently, reservoir zonation appears to exert stronger influence on macrophyte assemblages than short-term temporal variation (Thomaz and Cunha, 2010; Bornette and Puijalon, 2011; Fares et al., 2025).

Species richness was highest in the upper zone, likely associated with greater environmental heterogeneity and residual fluvial characteristics, whereas the middle and upper zone showed the highest macrophyte colonization, consistent with stable lentic conditions that favor dominant, stand-forming taxa (Thomaz et al., 2025). Community composition was dominated by widely distributed and ecologically tolerant species, particularly *Urochloa subquadripara*, which occurred abundantly across all zones and seasons. Other taxa showed more restricted distributions, with *Panicum rivulare, Typha dominguensis*, and *Colocasia esculenta* mainly associated with the upper zone, while *Polygonum lapathifolium* and *Salvinia auriculata* were more frequent in the middle and lower zones.

In eutrophic systems, dense stands of species such as *Urochloa subquadripara* and *Salvinia auriculata* can reduce light penetration, alter predator-prey interactions, and modify local physicochemical conditions through organic matter accumulation (Saulino and Trivinho-Strixino, 2017; Quirino et al., 2022; Tasker et al., 2022; Duque et al., 2023). When biomass thresholds are exceeded, structural complexity may shift from facilitating to limiting habitat conditions (Lopes et al., 2015; Quirino et al., 2023), potentially reducing fish abundance (Miranda and Hodges, 2000; Xie et al., 2001; Grenouillet et al., 2002; Hermes-Silva and Zaniboni-Filho, 2012). Moreover, anthropogenic pressures may promote invasive proliferation or native species loss, posing additional challenges for freshwater ecosystem management (Madzivanzira et al., 2023).

4.3. Spatial and seasonal structuring of fish assemblages

Fish assemblages in the Santana Reservoir were structured by the interaction between longitudinal habitat gradients and hydrological seasonality, a pattern widely reported in tropical reservoirs (Agostinho et al., 2007; Chea et al., 2020). The predominance of Siluriformes in the middle and lower zones suggests that impounded conditions favor benthic and detritivorous taxa, particularly in downstream areas where sedimentation and organic matter accumulation are greater. These conditions promote species associated with benthic feeding and structurally complex substrates that provide both food resources and refuge.

Lower richness and abundance in the upper zone likely reflect more restrictive riverine conditions, including higher flow variability and reduced habitat stability (Fernando and Holčík, 1991). In contrast, the transition toward lentic conditions in the middle and lower zones increases habitat heterogeneity and resource availability, supporting more diverse and abundant assemblages (Thornton, 1990; Agostinho et al., 2007). The spatial differences detected by PERMANOVA and nMDS are consistent with this longitudinal zonation, typically linked to gradients in depth, substrate, and productivity that drive species turnover.

Seasonal changes in assemblage composition further indicate the influence of hydrological dynamics, as rainfall-driven increases in connectivity and water level alter habitat availability and resource distribution (Lowe-McConnell, 1999). The higher intragroup similarity during the wet season suggests enhanced dispersal and partial assemblage homogenization associated with increased connectivity (Junk et al., 1989; Agostinho et al., 2004). Together, these results indicate that fish assemblage organization in the Santana Reservoir is primarily governed by the combined effects of spatial zonation and seasonal hydrological variability. This pattern is consistent with the strong influence of seasonal hydrology on fish assemblages associated with aquatic macrophytes in neotropical systems, where flooding pulses increase habitat availability and food resources (Cajado et al., 2025).

4.4. Aquatic macrophytes as structural drivers of fish assemblages

Macrophyte composition varied mainly along the longitudinal gradient, whereas fish assemblages showed both spatial (upper, middle, and lower zones) and seasonal (dry and wet periods) variation, partially supporting H1. This pattern indicates that while hydrological seasonality influences limnological conditions and fish abundance, macrophyte distribution is primarily structured by spatial habitat configuration.

Consistently, dbRDA and SIMPER results showed that a substantial portion of the variation in fish assemblage composition was explained by the spatial distribution of macrophytes across reservoir zones, including species-specific associations between fish and particular vegetation types, supporting H3. In the upper zone, marginal grasses such as *Panicum rivulare* were associated with *Poecilia vivipara and Hoplias malabaricus*, likely reflecting the use of allochthonous resources. In the middle and lower zones, the coexistence of *Salvinia auriculata* and *Polygonum lapathifolium* increased habitat complexity by stabilizing sediments and retaining organic matter (Carpenter and Lodge, 1986; Thomaz and Cunha, 2010), favoring benthic and detritivorous fishes such as *Hypostomus affinis, Loricariichthys castaneus*, and *Rineloricaria paraibensis*, which tolerate low dissolved oxygen (Killgore and Hoover, 2001). Vegetation such as *Colocasia esculenta, Urochloa subquadripara*, and *Typha dominguensis* was associated with ecologically plastic species (*Poecilia vivipara, Geophagus brasiliensis*), while ambush predators (*Hoplias malabaricus, Crenicichla lacustris*) likely benefited from increased structural cover (Petry et al., 2010). Structurally complex stands may therefore favor species with specific ecological traits, such as benthic association, ambush predation, or opportunistic feeding, reorganizing assemblage structure through habitat-mediated mechanisms (Thomaz and Cunha., 2010). GLM results indicate that fish assemblages were structured primarily by hydrological seasonality and, to a lesser extent, by spatial variability, whereas macrophytes and sediment type had only a minor influence on fish abundance compared with short-term physicochemical variability. Increasing macrophyte colonization was associated with reduced fish abundance, suggesting ecological thresholds in the benefits of structural complexity and partially supporting H2. Although aquatic vegetation generally increases habitat heterogeneity and refuge availability (Agostinho et al., 2007; Thomaz and Cunha, 2010), excessive dominance may restrict movement and alter species interactions. Fish richness was unrelated to macrophyte richness, indicating that the relationship predicted in H2 was not supported for species richness and reinforcing the view that vegetation primarily reorganizes fish abundance and spatial distribution rather than driving local species exclusion.

Although limnological conditions differed between hydrological periods, they did not significantly explain fish abundance or richness, suggesting that seasonality acts primarily through hydrologically driven habitat expansion rather than direct physiological filtering. Rising water

levels during the rainy season increase habitat availability and resource supply, allowing fishes to exploit newly inundated areas (Agostinho et al., 2004; Wei et al., 2023), while macrophyte composition remains relatively stable along the longitudinal gradient (Silva-Pereto et al., 2014).

5. Conclusions

Fish assemblage structure in the Santana Reservoir reflects the interaction between spatial habitat heterogeneity and seasonal hydrological dynamics. Macrophyte assemblages are primarily structured along the longitudinal gradient of the reservoir, and their spatial distribution mediates species-specific habitat use.

This spatial structuring partially translates into fish assemblage organization, as macrophyte identity and distribution explain a substantial portion of variation in fish community composition across reservoir zones, partially supporting Hypothesis 1. Macrophyte richness did not influence fish richness, and increasing macrophyte colonization was associated with reduced fish abundance, suggesting that dense vegetation may restrict habitat accessibility rather than enhance diversity or abundance, partially supporting Hypothesis 2. In contrast, Hypothesis 3 was supported, as several fish species were associated with particular macrophyte taxa, indicating that vegetation identity and structural complexity influence habitat use. Overall, aquatic macrophytes act as key structural elements shaping fish spatial distribution, while seasonal hydrology mainly modulates fish abundance through habitat expansion during high-water periods. These findings highlight the dual ecological role of aquatic macrophytes as drivers of habitat complexity that can enhance biodiversity under moderate cover, but also act as ecological filters when excessively abundant. Maintaining this balance is essential for reservoir management aimed at sustaining fish diversity while avoiding habitat homogenization and reduced community resilience.

From a management perspective, our results indicate that maintaining intermediate levels of macrophyte cover may be essential for preserving habitat heterogeneity and sustaining fish assemblages in tropical reservoirs. Excessive proliferation of dominant taxa, such as *Urochloa subquadripara* and *Salvinia auriculata*, may reduce habitat accessibility, restrict fish movement, and decrease local fish abundance. Therefore, management actions should prioritize the selective control of dense macrophyte stands rather than complete vegetation removal, thereby preserving structurally heterogeneous habitats that support specific fish–macrophyte associations. Furthermore, monitoring programs should incorporate the longitudinal gradient of the reservoir and seasonal hydrological dynamics, given that fish assemblages responded strongly to habitat expansion during the wet season and to spatial variation in vegetation structure. These findings provide an ecological basis for adaptive reservoir management strategies that reconcile macrophyte control with the conservation of biodiversity and aquatic habitat functionality. Future studies should incorporate functional trait approaches and longer time series to better resolve the mechanisms linking macrophyte structure and fish assemblages, and to assess the stability of these patterns under interannual hydrological variability.

CRediT authorship contribution statement

Francisco Gerson Araújo: Writing – review & editing, Visualization, Formal analysis, Data curation, Conceptualization. **Robinson Luiz Campos Machado Pitelli:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Robinson Antonio Pitelli:** Writing – review & editing, Investigation, Formal analysis. **Antônio Manoel Matta dos Santos Lameirão:** Supervision, Project administration. **Felipe Pinheiro da Cruz:** Supervision, Project administration. **Rinaldo José da Silva Rocha:** Supervision, Project administration. **Rafaela de Sousa Gomes Gonçalves:** Writing – review & editing, Methodology, Formal analysis. **Gustavo Henrique Soares Guedes:** Writing – review & editing, Methodology, Investigation, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecohyd.2026.100783.

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