



Complex homes, complex lives: how macrophyte structural complexity shapes taxonomic and functional diversity in periphytic ciliate communities

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Abstract Freshwater ecosystems, although representing less than 1% of Earth's surface, are biodiversity hot spots whose supports ecosystem functions. In these systems, environmental heterogeneity, driven by habitat structural complexity, is recognized as a key factor shaping community structure. This study evaluated how structural complexity of four aquatic macrophytes influences the taxonomic and functional attributes of periphytic ciliate communities. Macrophytes were categorized using the macrophyte complexity index: *Nymphaea amazonum*, *Cabomba furcata* and *Egeria najas* (intermediate), and *Utricularia foliosa* (most complex). Richness and density tended to be higher in the most complex macrophytes, although significant differences emerged between the least and most complex species. For functional metrics, only

functional richness showed differentiation among plants, increasing along the complexity gradient. Both taxonomic and functional composition varied among ciliate communities in different macrophytes, notably between the least and most complex species. RLQ analysis revealed segregation among macrophytes, with specific traits associated with particular plants. However, the weak differences found between the least and intermediate complexity suggest that increasing structural complexity does not necessarily mean an increase in overall heterogeneity. Instead, fine-scale microhabitat features (interstitial spaces, roughness and protrusions) appear to play a key role.

Keywords Diversity · Habitat structure · Environmental filtering · Microhabitats · Protozoa

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Introduction

Understanding the factors that shape and maintain biodiversity is essential, since biodiversity plays a central role in sustaining ecological processes, maintaining ecosystem balance, and ensuring the provision of key ecosystem services to human societies (Lynch et al., 2023). Freshwater ecosystems, although representing only about 1% of the Earth's surface, sustain disproportionately high biodiversity due to a combination of ecological and evolutionary processes (Heino, 2011). The natural fragmentation of these environments promotes strong population isolation

and speciation of individuals (Balian et al., 2008), while high environmental heterogeneity and hydrological dynamism expand niche diversity and favor species coexistence (Ward et al., 1999; Huber et al., 2020; Liu et al., 2021).

However, the structuring of diversity is not only related to regional scales; local scales, such as microhabitats within aquatic ecosystems, also influence local diversity (Sousa et al., 2025). Thus, aquatic plants, such as macrophytes, create a three-dimensional physical matrix that modifies hydrodynamics, sedimentation, light, and nutrient availability, in addition to increasing habitat complexity and the number of microhabitats available for colonization (Thomaz & Cunha, 2010; Sousa et al., 2025). Studies have demonstrated, both experimentally and in natural environments, that areas with different macrophyte species support greater richness, abundance, and functional diversity of aquatic invertebrates, corroborating the idea that macrophytes are important local drivers of biodiversity patterns, from microorganisms to large vertebrates (Vieira et al., 2007; Thomaz et al., 2025).

Microbial communities play a pivotal role in aquatic ecosystems, as they are actively involved in nutrient cycling and energy transfer, thus functioning as key organisms in these processes (Kaur et al., 2021; Garner et al., 2022). In this context, habitat structural complexity can be a key factor in understanding how diversity is organized within aquatic environments (Huang et al., 2020; Yang et al., 2020). The unique spatial structure provided by aquatic plants (macrophytes) plays a crucial role in the growth and survival of numerous freshwater organisms (Dibble & Thomaz, 2009). This structural complexity also supports microbial assemblages, as demonstrated in some studies (Gu et al., 2021; Liu et al., 2021; Li et al., 2023).

Among microbial organisms, ciliate protists are unicellular eukaryotes that regulate energy and nutrient fluxes within biogeochemical cycles and play essential roles in food web dynamics (Sherr et al., 1986). Owing to their short life cycles and high sensitivity to environmental changes, ciliates are also recognized as valuable bioindicators of water quality (Segovia et al., 2016; Budziak & Fyda, 2024). In freshwater aquatic environments, ciliate protozoans are widely distributed in all compartments, including pelagic, benthic and littoral ones, where they can be

found attached to aquatic macrophytes, which provide structural support, shelter, and resources at multiple scales (Thomaz & Cunha, 2010; Tokeshi & Arakaki, 2012; Kovalenko et al., 2012; Miranda et al., 2022), thereby favoring the coexistence of species with distinct ecological functions.

Reviews on habitat complexity in aquatic systems show that this complexity is multifaceted, involving diversity, size, and abundance of organisms within a community. As a result, the effects of complexity depend strongly on the body size and lifestyle of the organisms occupying the habitat (Tokeshi & Arakaki, 2012; Kovalenko et al., 2012). For fish, studies conducted in Neotropical floodplains and reservoirs indicate that denser and more voluminous macrophyte beds, characterized by higher stem and leaf density, increase species richness, morphological diversity, and abundance, particularly of juveniles, as these habitats serve as spawning sites (Montoya-Ospina et al., 2020; Cardozo et al., 2021; Hinz et al., 2023; Thomaz et al., 2025). Dense macrophytes provide a three-dimensional environment that functions as a refuge from visual predators and expands the area available for feeding (Sánchez-Botero & Araújo-Lima, 2001; Sánchez-Botero et al., 2007; Thomaz & Cunha, 2010). For aquatic macroinvertebrate communities, complexity is often defined at the intermediate scale (such as scales measured in centimeters) associated with plant architecture, such as leaf arrangement and root density or length. Macrophytes with more subdivided structures and greater surface area tend to sustain higher macroinvertebrate richness and abundance due to the increased availability of microhabitats, which serve both as substrate for periphyton and as attachment sites for different groups (Thomaz, 2023; Mayer-Pinto et al., 2024).

In contrast, for small-bodied organisms such as microcrustaceans and protozoans, macrophyte structural complexity operates at the millimeter scale (or even smaller). In these cases, leaves and roots act as microrefuges, forming a structurally complex microhabitat characterized by high microscopic roughness and steep gradients of food, nutrients, oxygen, and light (Vieira et al., 2007; Miranda et al., 2022). Submerged macrophytes with higher development of periphytic and epiphytic organisms tend to harbor more diverse ciliate communities with higher abundances compared to open-water areas or less structured vegetation (Yu et al., 2022). Small invertebrate

communities may also rely on denser and more structurally complex habitats for functions similar to those of larger organisms (Warfe & Barmuta, 2006). From a functional perspective, similar patterns may occur, as more complex habitats promote greater niche diversity and ecological interactions (Meerhoff & de los Ángeles González-Sagrario, 2022). Thus, variations in macrophyte structure may modulate the functional traits within ciliate protozoan communities, which exhibit distinct taxonomic and functional diversity (Perrin & Dorrel, 2024).

In this sense, the integration of taxonomic (species identity and the variance of its attributes) and functional diversity (the variety of roles or functions organisms perform in an ecosystem) provides valuable insights into community dynamics, allowing the evaluation of different patterns of richness and abundance of organisms (Barnett et al., 2007; Escalas et al., 2019; Bevilacqua et al., 2021). A functional approach is especially helpful when environmental heterogeneity influences not only which species are present, but also how they contribute to overall ecosystem functioning (Barnett et al., 2007; Hébert et al., 2017). Within this framework, functional diversity indices have been proposed to describe different patterns of trait distribution inside communities (Mason et al., 2005). Among these metrics, functional richness (FRic) represents the amount of functional space occupied by species in a community, representing the range of different strategies present. Functional evenness (FEve) shows how uniform the distribution of species is and their abundances across functional space. On the other hand, functional divergence (FDiv) measures how abundance is concentrated toward the extremes of trait distributions (considering functional characteristics), indicating a certain degree of specialization or niche partitioning for a given species/or trait (Mason et al., 2005; Villéger et al., 2008; Mouchet et al., 2010). Additionally, functional dispersion (FDis) exhibits the mean distance of species, relative to the community centroid in trait space, weighted by their abundances (Laliberté & Legendre, 2010). Another useful metric is the community-weighted mean (CWM) which can capture the average trait value in the community, weighted by species abundances, reflecting the dominant functional strategies, rather than the overall structural pattern of trait distribution inside the functional space (Garnier et al., 2004).

Therefore, the use of complementary diversity metrics can help elucidate how ciliate communities are structured across habitats with different levels of complexity, and how these patterns may reflect ecosystem functioning, stability, and resilience. However, although the structural complexity of macrophytes is known to influence habitat heterogeneity and species coexistence, its effects on the taxonomic and functional dimensions of microbial communities remain insufficiently explored (Zingel & Nöges, 2008). In this context, the present study aimed to investigate the influence of aquatic macrophyte structural complexity on the taxonomic (richness, density and composition) and functional structure (based on the functional indices: functional richness, evenness, divergence, dispersion, and community-weighted mean traits and functional composition) of ciliate protozoan communities associated with these plants. We formulated and tested the following predictions: i) taxonomic richness and density of ciliate communities will vary among macrophytes with different structural complexities, with higher values expected in more complex plants; ii) functional diversity indices (FRic, FEve, FDiv, FDis) will also differ among macrophyte species according to their structural complexity, indicating trait filtering by more complex macrophytes; iii) taxonomic and functional composition of ciliate communities will differ between macrophytes of higher and lower structural complexity.

Materials and methods

Study area

The sampling of ciliate protozoan communities was conducted in Lagoa das Garças, a lagoon located in the Upper Paraná River floodplain, Paraná, Neotropical region, Brazil (22°45'S; 53°20'W). The Lagoa das Garças is characterized by an average water temperature of 26 °C, mean pH of approximately 7.11 (neutral characteristics), mean depth of approximately 2.0 m, water level ranges from 80 cm during low water periods to 4 m during high water periods, length of 2,128.1 m, total surface area of 14.1 ha, and a perimeter of 4,338.2 m. Its margins are predominantly covered by grasses, and the surrounding landscape is composed of multiple strata of riparian vegetation (Bortolini et al., 2014).

The lake exhibits a markedly elongated and narrow morphology, with a high length-to-width ratio and a predominantly linear axis. Its margins are relatively well-defined, with slight sinuosity along its length, and the water body is laterally constrained by dense riparian vegetation bordering both margins along most of its extension. The system is extensively colonized by aquatic macrophytes, which form multiple monospecific stands distributed along the longitudinal axis of the lake.

Classification of macrophyte structural complexity

According to Dibble & Thomaz (2006), the structural complexity of macrophytes is related to their plant architecture, defined by the quantity and arrangement of their morphological structures. Thus, species with greater branching and abundance of leaflets exhibit higher levels of complexity compared to those with less branched structures. Accordingly, we defined the following complexity levels among the selected aquatic macrophytes: i) *Nymphaea amazonum* Mart. & Zucc. (1832); ii) *Cabomba furcata* Schult. (1830); iii) *Egeria najas* Gardener (1842); iv) *Utricularia foliosa* L. (1753).

As a measure of this complexity, the index proposed by Dibble & Thomaz (2006) was used, according to the formula:

$$MCI_i = \frac{FH_i}{HC_i} + \frac{FV_i}{VC_i}$$

where FH_i is the frequency of horizontal interstices; HC_i is the average length of horizontal interstices; FV_i is the frequency of vertical interstices; VC_i is the average length of vertical interstices.

For each macrophyte sample, horizontal and vertical interstices were quantified using a reference area of 1 cm². This means that the smallest features measured correspond to interstices occurring within this 1 cm² unit. The frequencies and average lengths obtained at this resolution were then incorporated to calculate the MCI index. Frequencies (FH_i and FV_i) were obtained as counts of interstices within each 1 cm² reference area (integer values). Average interstice lengths (HC_i and VC_i) were measured from scanned images calibrated with a reference scale in Image-Pro Express and recorded in centimeters. Thus, the measurement resolution of FH_i and FV_i is one interstice,

whereas HC_i and VC_i inherit the measurement resolution of the calibrated image-based procedure.

Sampling and laboratory analysis

Sampling was carried out over three consecutive days. During the sampling event, two samples of the upper 15 cm of the submersed macrophytes (*U. foliosa*, *C. furcata*, *E. najas*, and *N. amazonum*) were randomly collected on both sides of the boat, so that 6 samples of each macrophyte species were obtained in single and monospecific patches, considerably distant from each other. These patches were distributed across the lake. The collected macrophytes were placed in plastic bags, stored in coolers, and transported to the laboratory for further processing.

The ciliate community samples were obtained by scraping and washing the different macrophyte species with the final volume established as 100 mL per sample. Quantitative analyses of ciliate communities were performed in vivo (Madoni, 2005) immediately after collection to prevent cell loss and morphological changes resulting from fixation (Pfister et al., 1999). Using single-channel pipettes (Eppendorf), aliquots of 100 µL were analyzed on glass slides under a conventional optical microscope (Olympus BX51), totaling 1 mL per sample. Additionally, to record the occurrence of rare species, a qualitative analysis was performed using 1 mL of the concentrated sample in a Sedgewick-Rafter chamber. At magnifications of 100x, 400x, and 1000x, ciliates were identified and counted at the lowest taxonomic level possible, based on specialized literature (Foissner et al., 1999). Richness was expressed as the total number of species observed in each sample and density in cells.cm⁻² of macrophyte area.

To ensure reproducibility of the area-based density estimates, density was calculated in two steps. First, the total number of individuals in each processed sample was estimated from the counted subsample according the formula:

$$N_{sample} = n \times \frac{V_{count}}{V} \times DF$$

where n is the total number of individuals counted in the analyzed subsample volume; V_{final} is the standardized final volume after scraping and washing (100 mL); V_{count} is the total volume counted

(1 mL); DF is the additional dilution factor applied prior to counting (if no dilution was used, DF=1).

For the second step, the ciliates density per unit macrophyte area was obtained according to the formula:

$$Dcm^2 = \frac{A}{N} sample$$

where A is the macrophyte area (cm²) corresponding to the processed plant fragment.

Macrophyte dimensions (stem diameter and total leaf area) were quantified from scanned images using Image-Pro Express software. The area (A) was treated as a projected one-sided area derived from scanned images. This projected area was used as the denominator for expressing densities as cells.cm⁻², and the use of the upper 15 cm of the submerged portion for all macrophytes standardized the sampled plant portion across contrasting morphologies.

Functional traits were selected to represent variation in the ecological niche of species and to understand community structuring across habitats. Accordingly, different functional traits of protist species were classified, including numerical traits (e.g., length) and categorical traits (e.g., nutrition, habitat, encystment, defense, attachment ability, shape, and trophic guild). To avoid ambiguity between similarly named traits, we treated nutrition and trophic guild as complementary but conceptually distinct attributes. Nutrition describes the feeding mode and prey-size spectrum (i.e., how food is acquired and the typical size range of prey), whereas trophic guild describes the dominant resource type (i.e., what is consumed). Trait assignments followed published species descriptions and trait compilations; when multiple feeding

behaviors were reported, we assigned categories based on the dominant feeding strategy/resource most consistently reported for the taxon, and we classified broadly generalist taxa as omnivorous. Both categorical and numerical traits were defined based on the literature (Weisse, 2017; Meira et al., 2021; Oliveira et al., 2024) (Table 1). Traits were assigned at the level of identified morphospecies, in accordance with taxonomic and ecological descriptions reported in the literature.

Data analysis

To test prediction I, aiming to determine whether there were differences in taxonomic richness and density of the community, nonparametric statistical methods were employed due to violations of the assumptions of normality and homoscedasticity (Zar, 2010). Each macrophyte species was represented by six independent replicates (n=6 per species; total=24 samples). Thus, the Kruskal–Wallis test, a nonparametric alternative to one-way analysis of variance, was used (one-way ANOVA), to verify the existence of significant differences between the groups (Kruskal & Wallis, 1952). *P*-values ≤ 0.05 were considered significant. In cases of significance, Dunn's post hoc test was performed to identify which specific pairs of groups differed significantly (Dunn, 1964). Dunn's test is particularly suitable for samples of unequal sizes and maintains control over the family-wise error rate in multiple comparisons (Dinno, 2015), considering values of *P* ≤ 0.05 as significant.

To test prediction II, functional diversity metrics were calculated to assess both the range and the

Table 1 List of functional traits used, according to Weisse (2017), Meira et al. (2021), and Oliveira et al. (2024)

Traits	Type
Nutrition	Nano/microinterceptor, pico-filter, mixotrophic and nanofilter
Trophic guild	Bacterivorous, algivorous, omnivorous and predatory
Length	20 to 435 µm
Habitat	Periphytic and benthic, pelagic, Epibiont, anaerobic
Encystment	Yes or No
Defense mechanism	No defense, toxicyst, trichocyst, mucocyst and pigmentocyst
Attachment ability	Attach or not attach
Shape	Elipsoid, lance-shaped, Oviform, Coniform, cylinder-shaped, Fusiform, Scutiform, Lageniform, Pyriform, Trumpet-shaped, Obconiform

distribution of functional traits within macrophyte communities across different habitat complexity levels. We quantified functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDisp) for each sampling unit, based on the multidimensional trait space occupied by the ciliate community. Trait data were assembled for all species recorded in the samples, including both numerical and categorical traits. Prior to analysis, categorical traits were converted to factors, and the numerical trait (length) was standardized to zero mean and unit variance. Functional diversity indices were computed in R using the “dbFD” function (*FD* package). Because the trait dataset combined categorical and numerical variables, species functional dissimilarities were calculated using Gower distance (Gower, 1966), as implemented in “dbFD” for mixed-type traits (`stand.x=TRUE`). The input data consisted of (i) a site-by-species presence-absence matrix (i.e., incidence data; 4 macrophyte species with six replicates each, totaling 24 sampling units) and (ii) a species-by-trait matrix (Villéger et al., 2008). FRic, FEve, Fdiv, and FDisp were then derived from the functional space defined by species traits and their incidence within each sampling unit.

To characterize the functional density of trait categories within each sampling unit, we calculated community-weighted means (CWM; Garnier et al., 2004) for each trait using the same presence-absence weighting. For categorical traits, the species-by-trait matrix was transformed into binary dummy variables (one-hot encoding), allowing estimation of the proportional representation of each category per sample. CWMs for categorical traits were obtained by multiplying the site-by-species matrix by the dummy trait matrix and standardizing by total species incidence in each sampling unit. For the numerical trait (length), CWM values represent the mean trait value weighted by species occurrences (Garnier et al., 2004; Villéger et al., 2008). These calculations were implemented with custom R scripts using base R and the “model.matrix” function for dummy coding. Differences in functional richness (FRic) among habitat complexity levels were evaluated using one-way analysis of variance (ANOVA), followed by TukeyHSD post hoc tests ($p \leq 0.05$). ANOVA assumptions were checked, where residual normality was verified with the Shapiro–Wilk test and homoscedasticity was assessed

using Levene test; both assumptions were met for FRic.

We assessed the relationship between habitat complexity with richness, density and each functional diversity metric using simple linear regression models (ordinary least squares). For each attribute (richness, density and functional indices), we fitted models of the form $\text{attribute} \sim \text{complexity}$ and evaluated model performance using the Pearson correlation coefficient (R) and the coefficient of determination (R^2). Statistical significance was determined from the t-test associated with the slope parameter (i.e., the effect of complexity), and P -values were extracted from the regression summary. Regression lines and 95% confidence intervals were visualized with the “geom_smooth” function by method “lm.”

Finally, to test prediction III, regarding the community composition among different macrophyte species, the taxonomic attribute was assessed using presence and absence data through permutational analysis of variance (PERMANOVA) (Vicente-Gonzalez & Vicente-Villardón, 2021), considering the “Jaccard” dissimilarity matrix with 999 permutations and a significance threshold of $P \leq 0.05$. We used a multivariate dispersion homogeneity test (PERMDISP) as a prerequisite for PERMANOVA. For graphical visualization, a principal coordinates analysis (PCoA) was performed. For functional traits composition (using the CWM values), differences in overall functional structure between complexity levels were further assessed using PERMANOVA, based on “Bray–Curtis” dissimilarity of the trait proportion matrices, and a PCoA (using the CWM values) for graphical demonstration. The trait distance matrix was ordinated within “dbFD,” retaining axes according to the default criterion ($m = \text{"max"}$) and applying the default correction for negative eigenvalues ($\text{corr} = \text{"sqrt"}$).

To investigate how ciliate functional traits and species composition respond to macrophyte structural complexity, we used the integrated RLQ analysis approach. This analysis enabled simultaneous examination of the relationships between macrophyte structural complexity, community species composition, and their respective functional traits. The “L” matrix (ciliate species by macrophyte species) was represented by the presence–absence of the ciliate morphospecies in each sampling unit. The “R” matrix consisted of structural complexity with four ordered levels, corresponding to each

of the macrophyte habitat complexity. The "Q" matrix (species by traits) included ciliate functional traits encoded as factors. Thus, RLQ analysis was applied, aiming to integrate the three matrices and explore the relationships between structural complexity, species composition, and functional traits. We used two principal axes and tested the global significance of the analysis through a Monte Carlo permutation test with 9,999 permutations, considering P -values ≤ 0.05 as significant. Complementing the RLQ, a fourth-corner analysis was employed to test specific associations between functional traits and the habitat complexity gradient through species composition. We applied the same permutation model used in the RLQ, with 9,999 permutations, using the FDR procedure for multiple comparison correction, through the adjusted P -values ($P \leq 0.05$ as significant).

All statistical analyses and graphics were performed using R 4.4.2 environment (R Core Team, 2024), coupled with RStudio (Posit), and utilizing the *vegan* (Oksanen et al., 2019), *ggplot2* (Wickham, 2016), *tidyverse* (Wickham et al., 2019), *ape* (Paradis et al., 2019), *ade4* (Dray & Siberchicot, 2017), and *ggforce* (Pedersen, 2020) packages.

Results

When calculating the complexity of macrophytes, following the MCI index proposed by Dibble & Thomaz (2006), the mean values registered for each macrophyte species were: *N. amazonum* = 1.2; *C. furcata* = 5.16; *E. najas* = 5.54; *U. foliosa* = 7.67 (Fig. 1).

For the protist community, over the course of the study, 56 ciliate morphospecies were recorded (see Supplementary Material 1). Among the 9 taxonomic groups found, the ones with the highest number of species, in all macrophyte species, were Hypotrichida, representing from 24.3 to 31.0% of total species number, followed by Peritrichida (13.5% to 23.1%). Gymnostomatida and Nassulida had lower contributions throughout the study (Fig. 2). *U. foliosa* supported higher richness of ciliates, with 45 registered, followed by *C. furcata*, with 38 morphospecies, *E. najas* with 33 morphospecies and *N. amazonum* (macrophyte with minor habitat complexity) supported 28 ciliate morphospecies. Similarly, regarding density, *U. foliosa* showed the highest values, with a maximum of 872 ind.cm⁻², followed by *E. najas* (707 ind.cm⁻²), *C. furcata* (550 ind.cm⁻²), and *N. amazonum* (147 ind.cm⁻²).

Kruskal–Wallis tests revealed significant differences in ciliate species richness and density among macrophyte species (Fig. 3; $H(3) = 13.5$, $P = 0.003$ for richness; $H(3) = 7.8$, $P = 0.050$ for density). Dunn's

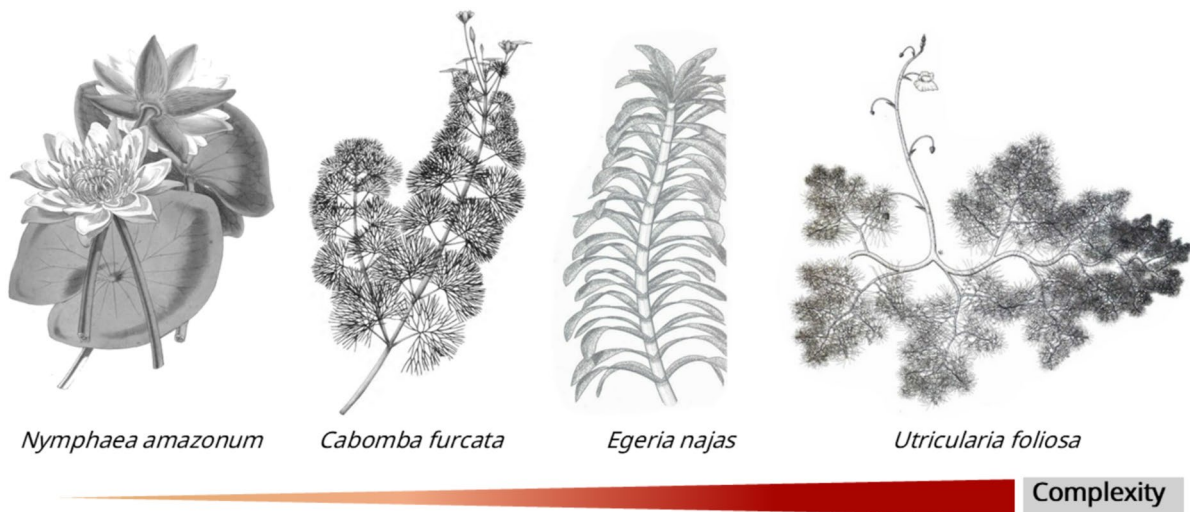


Fig. 1 Selected and sampled macrophyte species according to structural complexity. The schematic images of each plant were provided by Aline Rosado

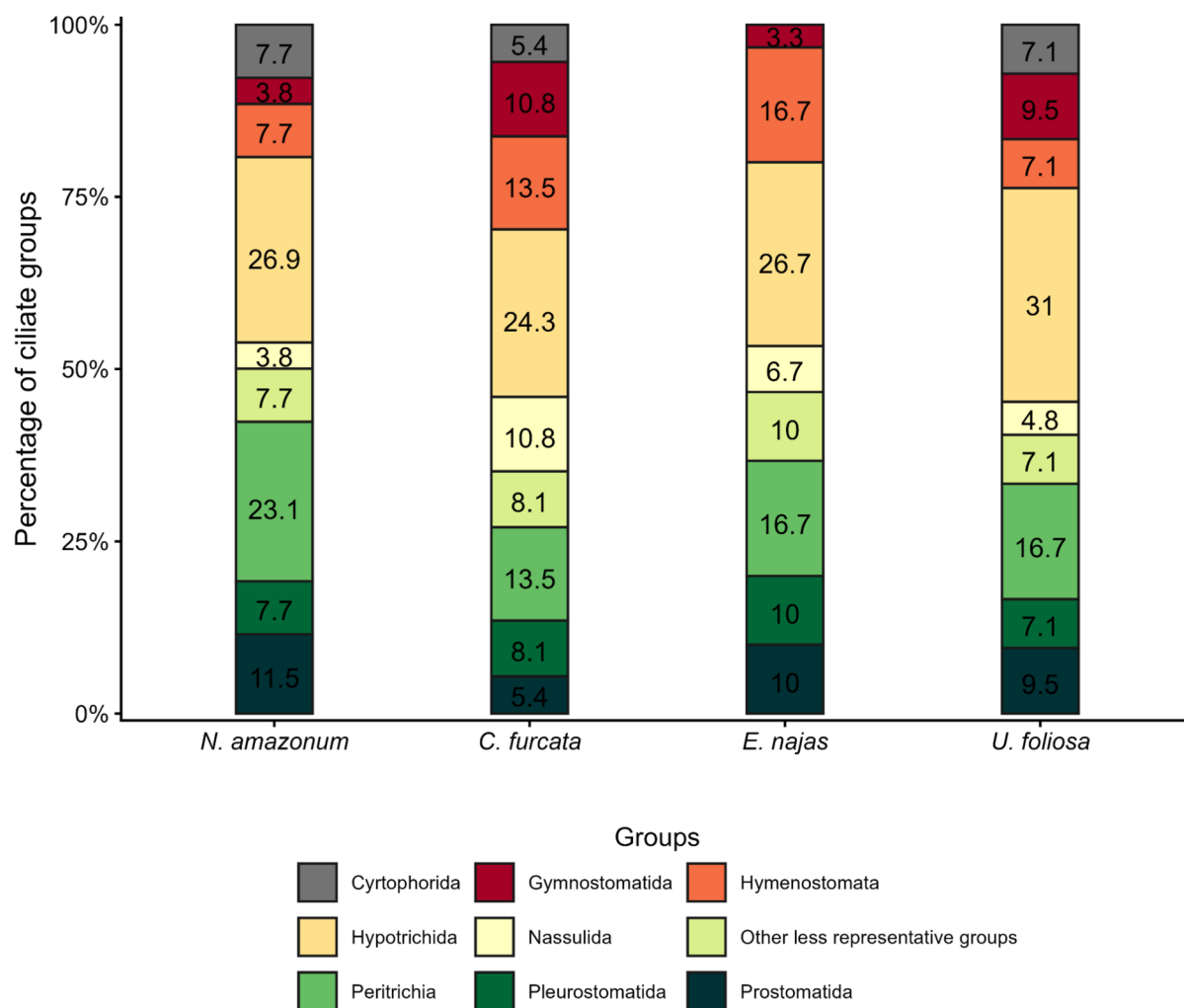


Fig. 2 Richness of taxonomic groups of ciliates in different macrophytes with distinct structural complexity gradient (from least complex *N. amazonum* to most complex *U. foliosa*).

Other less representative groups = Heterotrichida, Odontostomatida and Oligotrichida

post hoc test identified a significant difference only between *N. amazonum* and *U. foliosa*, both for richness ($Z = -3.6$; $P = 0.001$) and density ($Z = -2.4$; $P = 0.049$), with higher values of these attributes for the macrophyte species with greater complexity (Fig. 3). Linear regression indicated a positive relationship between habitat complexity and ciliate richness, with richness increasing as complexity increased (Fig. 3C; $R^2 = 0.65$; $P < 0.001$). For density, a positive association with complexity was also observed (Fig. 3D; $R^2 = 0.21$; $P = 0.03$).

Permutational analysis of variance (PERMANOVA) revealed significant differences in

species composition associated with different aquatic macrophytes (Fig. 4; $F = 1.6$; $R^2 = 0.1$; $P = 0.010$). The model, which explained approximately 19.4% of the total variation in community composition, indicates that macrophyte species influence community structure.

Subsequent pairwise comparisons identified specific significant differences between structural complexities. Significant differences in community composition were observed between *E. najas* and *U. foliosa* ($P = 0.030$) as well as between *N. amazonum* and *U. foliosa* ($P = 0.030$). In contrast, no significant differences in community composition were

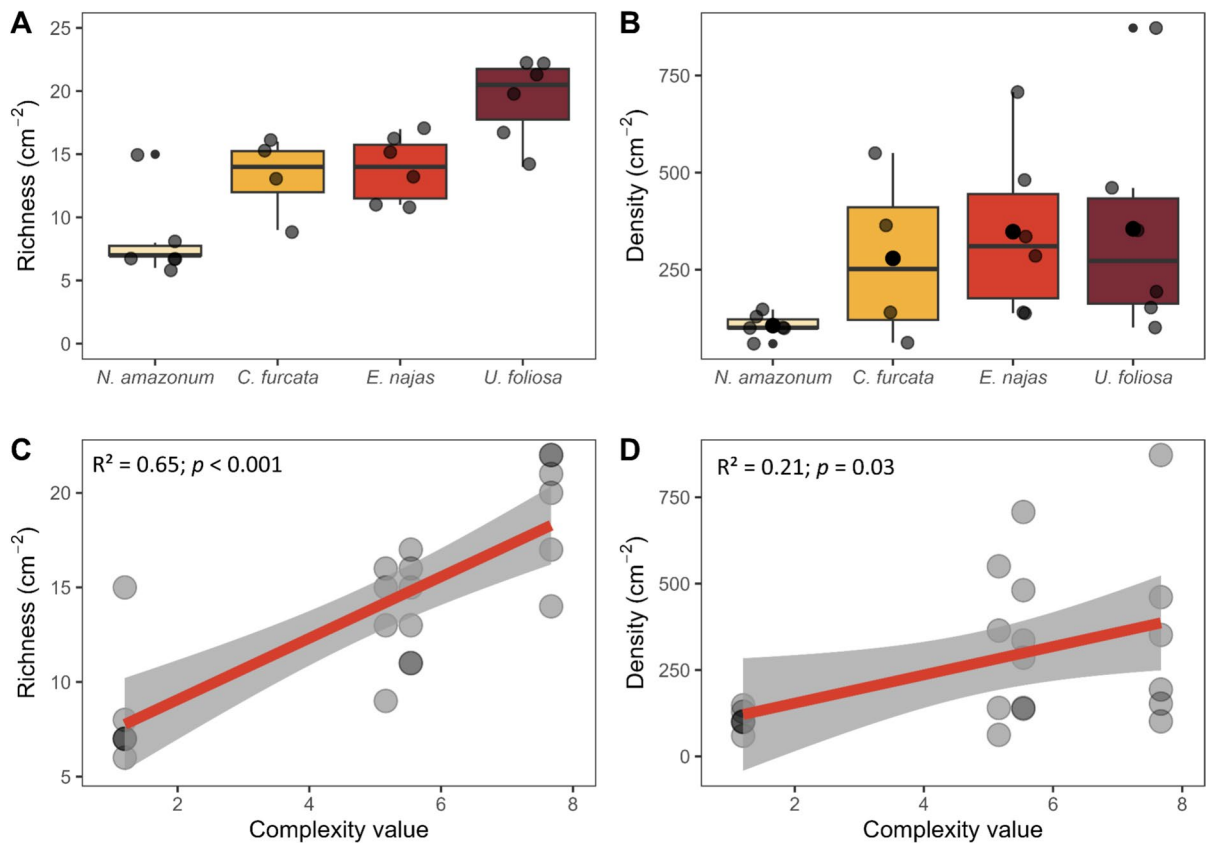


Fig. 3 Species richness (A and C) and density (B and D) of the ciliate community associated with different species of aquatic macrophytes. The central line in the graphics denotes the median values. The box plots represent, respectively, the

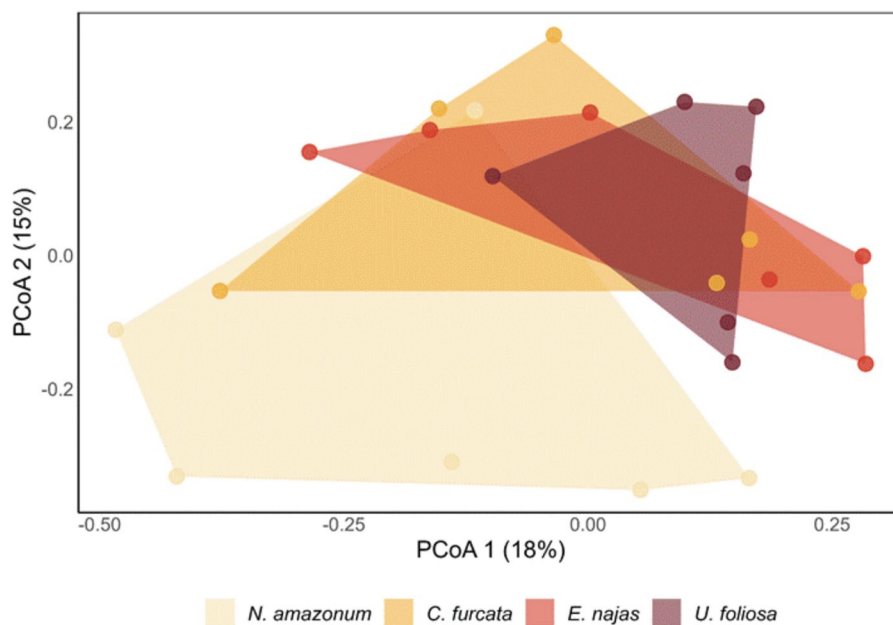
observed between *C. furcata* and the other species ($P > 0.05$).

Functional richness (FRic) also varied consistently among macrophyte species (Fig. 5A). The lowest FRic values were observed in communities established in *N. amazonum*, while *U. foliosa* and *C. furcata* exhibited the highest functional richness of ciliate communities. ANOVA indicated a significant effect of macrophyte species on FRic ($F=8.3$, $P<0.001$), with post hoc tests confirming that *U. foliosa* and *C. furcata* communities had significantly greater functional richness compared to *N. amazonum*. The ciliate community in *E. najas* displayed intermediate FRic values, not significantly different from the other groups. On the other hand, functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis) of the ciliate community did not differ significantly among macrophyte

species (Fig. 5B to D; ANOVA $P>0.05$). Linear regressions showed that habitat complexity explained a substantial portion of the variation for FRic, with a significant positive relationship (Fig. 5E; $R^2=0.56$; $P<0.001$). In contrast, there was no evidence of a relationship between complexity and FEve (Fig. 5F; $R^2=0.08$; $P=0.157$) nor with FDiv (Fig. 5G; $R^2=0.05$; $P=0.278$). For FDis, a positive trend was observed, but also not significant (Fig. 5H; $R^2=0.15$; $P=0.06$).

The mean density of traits, based on CWM, revealed distinct patterns among macrophyte species (Fig. 6A to H). The length trait of ciliates varied among macrophyte species (Fig. 6A), with higher mean trait values in *U. foliosa* and lower values in *N. amazonum*. Regarding the presence of defense structures (Fig. 6B), a predominance of ciliates lacking defense structures was observed across all

Fig. 4 Principal Coordinates Analysis (PcoA) for taxonomic species composition between macrophyte species. Axis 1 explained 18% of the community variation, while Axis 2 explained 15% of this variation, thus totaling 33% of the total explanation



macrophyte species; however, among all analyzed types, the toxicyst defense structure was the most representative, especially in *E. najas*. A decrease in the presence of ciliates containing mucocyst and pigmentocyst structures was also observed from the least complex to the most complex macrophyte. Regarding the nutrition trait (Fig. 6C), an increase in the nano/microinterceptor type and a decrease in pico-filter were observed from the least complex to the most complex macrophyte.

Regarding the CWM for habitat types (Fig. 6D), a predominance of periphytic and benthic organisms was noted across all macrophyte species. Furthermore, the absence of organisms exclusively belonging to the periphytic trait was observed for *E. najas*. Regarding encystment ability (Fig. 6E), and attachment ability (Fig. 6F), most protists lacked these characteristics. The ciliate shape type showed high variation among macrophyte species; for this trait, the most representative type was Oviform, followed by ellipsoid, with both exhibiting opposite trends: Oviform increased from the least complex to the most complex macrophyte, while ellipsoid showed an inverse pattern. Finally, the trophic guild trait (Fig. 6I) displayed a similar CWM distribution pattern among macrophyte species, with a predominance of omnivorous Ciliates.

Based on the PERMANOVA, there were significant differences in functional composition among the four habitat complexity levels ($R^2=0.2$, $F=1.8$, $P=0.016$). The graphical representation (PCoA; Fig. 7) and pairwise comparisons revealed differentiation in the functional composition of the ciliate community between *C. furcata* and *U. foliosa*, $P=0.037$; *E. najas* and *N. amazonum*, $P=0.005$, and *N. amazonum* and *U. foliosa* ($P=0.001$). Graphically, *N. amazonum* occupied a markedly broader functional trait space compared to the other macrophyte species.

To understand the relationship between habitat complexity, taxonomic composition, and their respective functional traits, the RLQ analysis revealed that the structural complexity of macrophytes leads to changes in the functional composition of the ciliate community (Fig. 8). The RLQ model, considering the strength of the co-structure of the analysis, was 25.8%, with the first two axes explaining a total of 95.6% of the co-structure between functional traits and the different complexities (RLQ1=53.2%; RLQ2=42.4%). The Monte Carlo permutation test indicated that the functional traits–habitat complexity association is significant (model 2: Std.Obs=2.3; $P=0.021$; model 4: Std.Obs=2.5; $P=0.010$).

Thus, a clear segregation of macrophyte species was observed along the axes, associated with different

functional traits of the ciliate species. Ciliate species with periphytic habit, along with attachment ability, pico-filter feeding mode, and protists with conical, oviform, and trumpet-shaped body forms, were associated with *N. amazonum*. For *C. furcata*, algivorous and predatory protists, with nanofilter feeding capability, fusiform, pyriform, and obconiform body shapes, were more associated with this plant. In *E. najas*, cylindrical and lanceolate-bodied protists, with mixotrophic tendencies and pelagic habit, were observed. Finally, in *U. foliosa*, the highest complexity macrophyte was associated with organisms having lageniform, scutiform, and ellipsoid body shapes, linked to the numerical trait of length, encystment capability, and periphytic and benthic habits (Fig. 8).

Complementing the RLQ, the fourth-corner analysis showed that only shape was significantly related to the macrophyte complexity gradient ($\chi^2=40.6$; Std. Obs=3.4; $p_{\text{adj}}=0.026$). The other functional traits did not show a significant association with habitat complexity ($p_{\text{adj}} > 0.5$).

Discussion

Community taxonomic patterns and macrophyte complexity

We observed dominance of Hypotrichida and Peritrichia across all macrophyte species. These groups are frequently associated with a periphytic lifestyle (Pauleto et al., 2009; Buosi et al., 2011; Velho et al., 2013). Peritrichids are preferentially sessile, meaning that they are capable of attaching to a substrate, while Hypotrichids, with their flattened bodies, larger size, and modified ciliature (cirri) for locomotion and anchoring on surfaces, may be using macrophytes as shelter and substrate (Reut et al., 2021; Jiang et al., 2025). Thus, the morphological characteristics of aquatic macrophytes, such as their stem and leaf structures, can influence the attributes of communities that use these plants as habitats (Pereira et al., 2010).

In this study, the higher average richness of ciliates recorded in the most complex plants suggests that greater structural complexity expands the diversity of microhabitats and opportunities for niche partitioning (Dibble & Thomaz, 2006; Thomaz et al., 2008). However, significant differences were only observed

between *U. foliosa* and *N. amazonum*, even though *C. furcata* and *E. najas* exhibited considerably higher complexity compared to *Nymphaea*.

Functional indices as a sensitive indicator of environmental filtering

We found that structurally complex macrophyte species exhibited significantly higher functional richness (FRic) compared to the least complex species (*N. amazonum*), with intermediate values observed in *E. najas*. This supports the idea that habitat complexity promotes niche differentiation and selects for different traits, allowing the coexistence of species with divergent functional characteristics (Heck & Crowder, 1991; Tokeshi & Arakaki, 2012; Kovalenko et al., 2012). This index appears to be a relevant measure for evaluating community responses, often considered an indicator of the ecological strategies present in a community and linked to ecosystem multifunctionality (Cadotte et al., 2011).

Despite the notably differences in FRic, no significant variation was detected in functional evenness (FEve), functional divergence (FDiv), or functional dispersion (FDisp) among the macrophyte types. This suggests that although more complex habitats support a greater richness of functional traits, the relative distribution of these traits and their respective occupancy in functional space within the community may remain stable (Villéger et al., 2008; Mouillot et al., 2013). This pattern may reflect the simultaneous action of habitat filtering and trait similarity, balancing the combination and divergence of functional traits across different habitat types (Götzenberger et al., 2012; Spasojevic & Suding, 2012).

In addition to the functional indices, the functional ordination explicitly revealed that ciliate assemblages associated with *N. amazonum* occupied a notably broader functional trait space compared to the other macrophyte species. Rather than showing functional expansion with increasing structural complexity, the simplest macrophyte supported the widest dispersion of trait combinations, whereas communities associated with more complex macrophytes were functionally coupled. This pattern suggests that low-complexity habitats may allow the coexistence of species with contrasting ecological strategies, while increasing macrophyte complexity promotes stronger trait-based

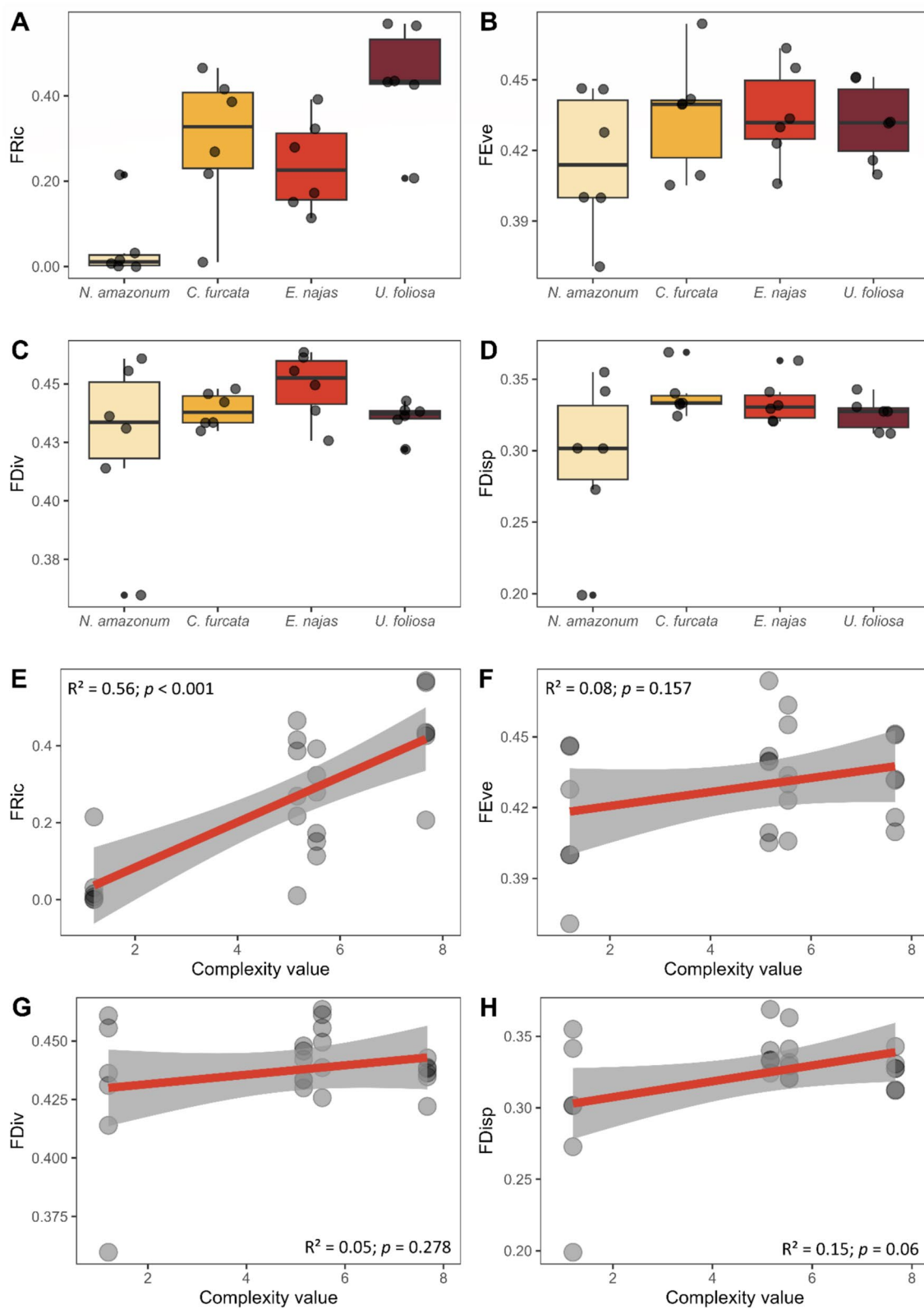


Fig. 5 Functional richness (FRic) (A and E), functional evenness (FEve) (B and F), functional divergence (FDiv) (C and G) and functional dispersion (FDis) (D and H) across different macrophyte species. The central line in the graphics denotes the median values. The box plots represent, respectively, the interquartile interval of standard deviation, and the small black points above or below indicate outliers in the observations. For the linear regressions, these indicate trends adjusted by regression, accompanied by 95% confidence intervals (shaded areas)

environmental filtering (Jiang et al., 2025), leading to functional convergence and niche filtering.

Furthermore, changes in specific traits through FRic, while FEve, FDiv, and FDis remained stable, appear consistent with the existence of functional replacement among organisms in each habitat complexity (Mayer-Pinto et al., 2024), suggesting that not all components of functional diversity respond similarly to complexity and that gains in potential functions can occur without major changes in the degree of redundancy or the distribution of abundances in trait space.

Trait filtering mechanisms along the complexity gradient

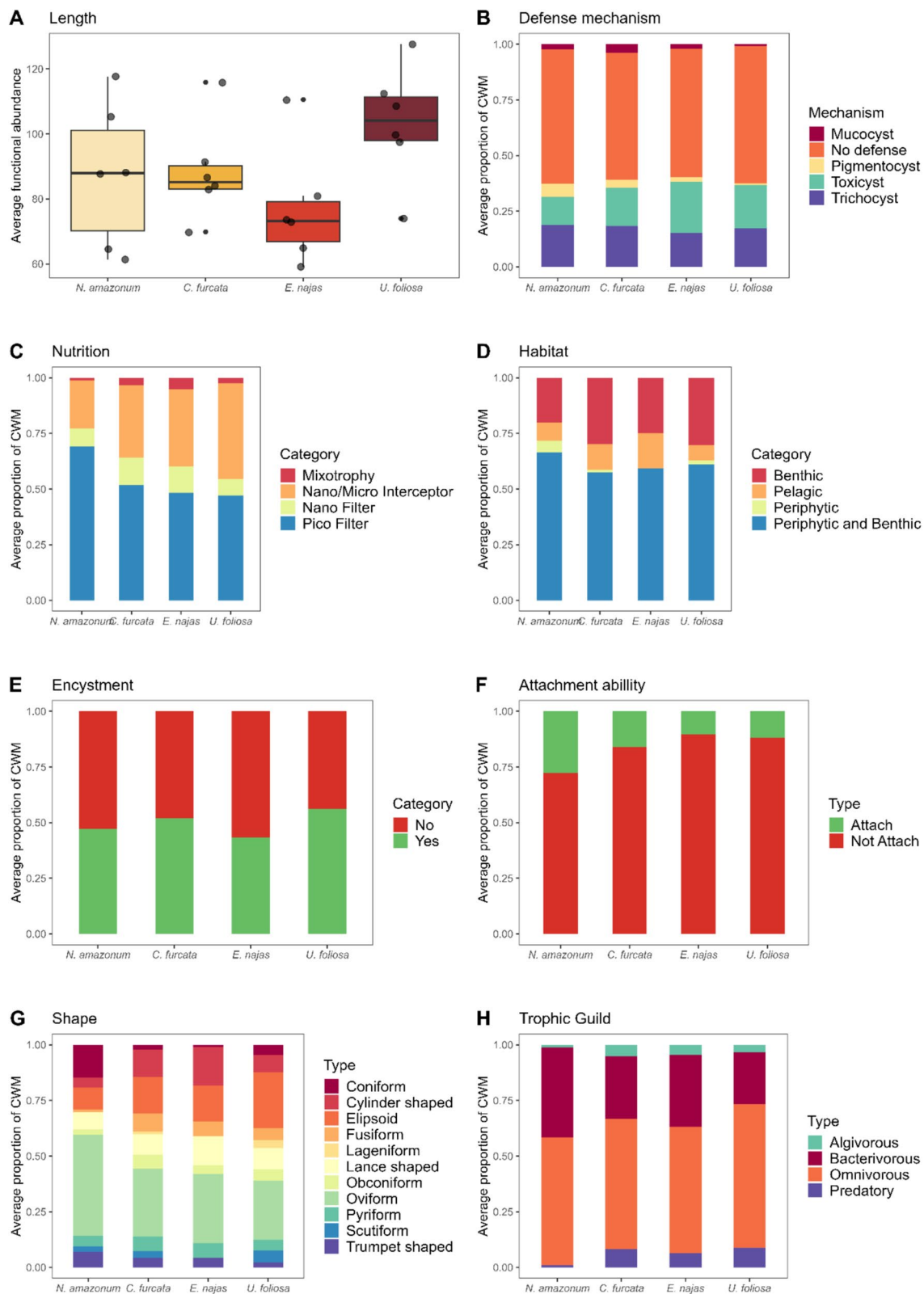
Regarding trait abundance, measured through community-weighted means (CWM), the mean trait value was significantly higher for *U. foliosa* and *C. furcata*, reinforcing the idea that more complex macrophytes support functionally more diverse communities (Thomaz & Cunha, 2010; Vadeboncoeur et al., 2014). The proportional composition of certain categorical traits also changed along the complexity gradient: For example, the higher proportion of species exhibiting toxicyst defense mechanisms in more complex macrophytes may indicate selective advantages in structurally complex environments, possibly linked to higher predation pressure or greater ability for interspecific competition (Weisse et al., 2016). Thus, changes in habitat structure not only affect the species present in the environment but also the ecological functions they perform. This functional alteration modifies essential processes, such as nutrient cycling and energy flow, resulting in changes in ecosystem dynamics (Thomaz et al., 2008; Laliberté & Legendre, 2010; Gagic et al., 2015).

The changes in functional composition observed along the complexity gradient of aquatic macrophytes also align with the perspective that habitat complexity

acts as a mechanism for trophic decoupling and stabilization of biotic interactions. Structurally complex habitats could increase predator–prey system persistence by providing refuges that reduce resource overexploitation and compartmentalize the food web (reviewed in Kovalenko et al., 2012). In our case, the increase in FRic and the reorganization of traits such as defense, nutrition, and body shape in more complex macrophytes suggest that these plants create conditions for the coexistence of distinct trophic guilds (e.g., interceptors vs. filter feeders, omnivores vs. predators), while favoring trait combinations that maximize refuge use and the exploitation of microgradients of resources (Song et al., 2023). This functional rearrangement is consistent with the idea that physical complexity not only increases local diversity but can also modulate energy and matter flows, altering microbial consumption rates, nutrient cycling, and the coupling of present organisms (Laliberté & Legendre, 2010; Gagic et al., 2015; Mayer-Pinto et al., 2024).

Our results are in line with earlier evidence that the geometric organization of habitat space is a primary determinant of community structure and functioning. Khailov et al. (2001) demonstrated quantitative relationships between organism densities and geometric parameters such as surface complexity, spatial heterogeneity, and the size distribution of pores and interstices, indicating that biological patterns can emerge directly from how space is configured, such as demonstrated by Khailov & Yurchenko (1997) for small polychaete worms (from 2 to 5 mm). In our case, this principle appears to extend to microscopic scales (in this case, the microscopic scale is the size of the ciliated protists that utilize this complex architecture): fine-scale geometric attributes of macrophytes (e.g., interstitial spaces, branching architecture, and surface roughness) likely operate as key ecological filters, favoring specific ciliate morphologies and functional strategies. Accordingly, habitat complexity should not be treated as a single, unidimensional property, but rather as a hierarchical arrangement of geometric features acting across multiple spatial scales, which helps explain why different structural proxies may capture distinct components of community variation.

Thus, the significant association between ciliate functional traits and the macrophyte complexity gradient suggests that trait composition is not randomly distributed among habitats (Song et al., 2023). In *N.*



◀Fig. 6 (A) Mean community weighted trait value (Length). The central line in the graphics denotes the median values. The bars represent, respectively, the interquartile interval of standard deviation, and the small black points above or below indicate outliers in the observations; (B–H) Proportional representation of trait categories (CWM) for each macrophyte stand. Bars show average composition; colors indicate trait categories

amazonum, the least complex macrophyte, traits such as periphytic habit, strong attachment capacity, pico-filter feeding, and coniform/oviform/trumpet body shapes were predominant. This pattern likely reflects the simple architecture of *N. amazonum*, which provides few microhabitats and limited structural heterogeneity. As a result, it predominantly selects for species capable of attaching to smooth stems and efficiently filtering small suspended particles (e.g., *Vorticella*, *Epistylis*) (Risse-Buhl et al., 2009; Jiang et al., 2025). An explanation for this involves hydrodynamic exposure. Macrophyte stands can attenuate local water velocity, and this effect typically increases with plant architectural complexity, generating sheltered microzones within the roots and stems (Doods & Biggs, 2002). Under comparatively less complex architectures, epiphytic organisms may detach. Thus, traits related to strong attachment can be selectively favored, particularly for periphytic ciliates that rely on stable positioning to feed and persist on substrate surfaces (Arnon et al., 2007). In this sense, the association of *N. amazonum* with attachment ability and pico-filter feeding may reflect not only lower microhabitat diversity, but also a more exposure-prone plant surface where attachment confers a key performance advantage.

With increasing structural complexity in *C. furcata*, there was a marked contribution of algivorous and predatory habits, as well as the emergence of additional body shapes such as fusiform, pyriform, and obconiform forms. Nano-filter and nano/micro-interceptor feeding strategies also became more common. This shift in functional composition likely reflects the higher number of branches and greater surface area provided by *C. furcata*, which expand the diversity of available niches and resources (Thomaz et al., 2008; Dibble & Pelicice, 2010; Poi et al., 2021).

Increased complexity is known to support more specialized and functionally diverse groups among different communities (Friedman et al., 2020; Oleinski et al., 2025), as observed here for ciliates. In *E. najas*, which exhibits even greater structural

heterogeneity, traits such as cylindrical and lanceolated body shapes were frequent, along with a notably increase in mixotrophy and pelagic life habits. Yet, this suggests that *E. najas* can support species capable of alternating between benthic and pelagic feeding modes, likely due to its complex three-dimensional architecture and dense foliage, which enhance light availability pockets, organic matter retention, and resource heterogeneity (Leão et al., 2021). In contrast, for the most structurally complex macrophyte, *U. foliosa*, the traits most strongly associated with this habitat were related to body shape, especially lageniform, scutiform, and ellipsoid forms. Additionally, *U. foliosa* supported larger protist species with benthic and periphytic habits. This pattern suggests that its highly branched and dense architecture creates a wide array of stable microhabitats, allowing the establishment of larger and more specialized ciliates (Reut et al., 2021; dos Santos et al., 2022). The three-dimensional structure of *U. foliosa* likely enhances substrate availability, biofilm accumulation, and the formation of microzones with reduced water flow (Gastauer et al., 2021), all of which favor species capable of exploring complex surfaces and maintaining attachment even in intricate spaces.

Study limitations and scale considerations

Although the structural complexity of macrophytes was directly quantified in this study using the macrophyte complexity index (MCI; Dibble & Thomaz, 2006), some limitations related to scale and underlying mechanisms need to be addressed, especially when interpreting the observed patterns. First, the index was calculated based on the frequency and average length of horizontal and vertical interstices using a reference area measured at the centimeter scale, therefore capturing mesoscale architectural features of plant structure and integrating interstitial distribution and spacing at the centimeter scale. However, in our dataset, ciliates ranged from approximately 20 μm to 435 μm in body length, meaning that most ciliate species might interact with structural features occurring at submillimeter or microscopic scales, which were not explicitly quantified here. Thus, while the MCI effectively represents plant architecture among species, it may not fully capture the finest-scale roughness, microcavities, or surface irregularities that possibly impact the structure of

Fig. 7 Principal Coordinates Analysis (PCoA) for functional species composition between macrophyte species. Axis 1 explained 30% of the community variation, while Axis 2 explained 17% of this variation, thus totaling 47% of the total explanation

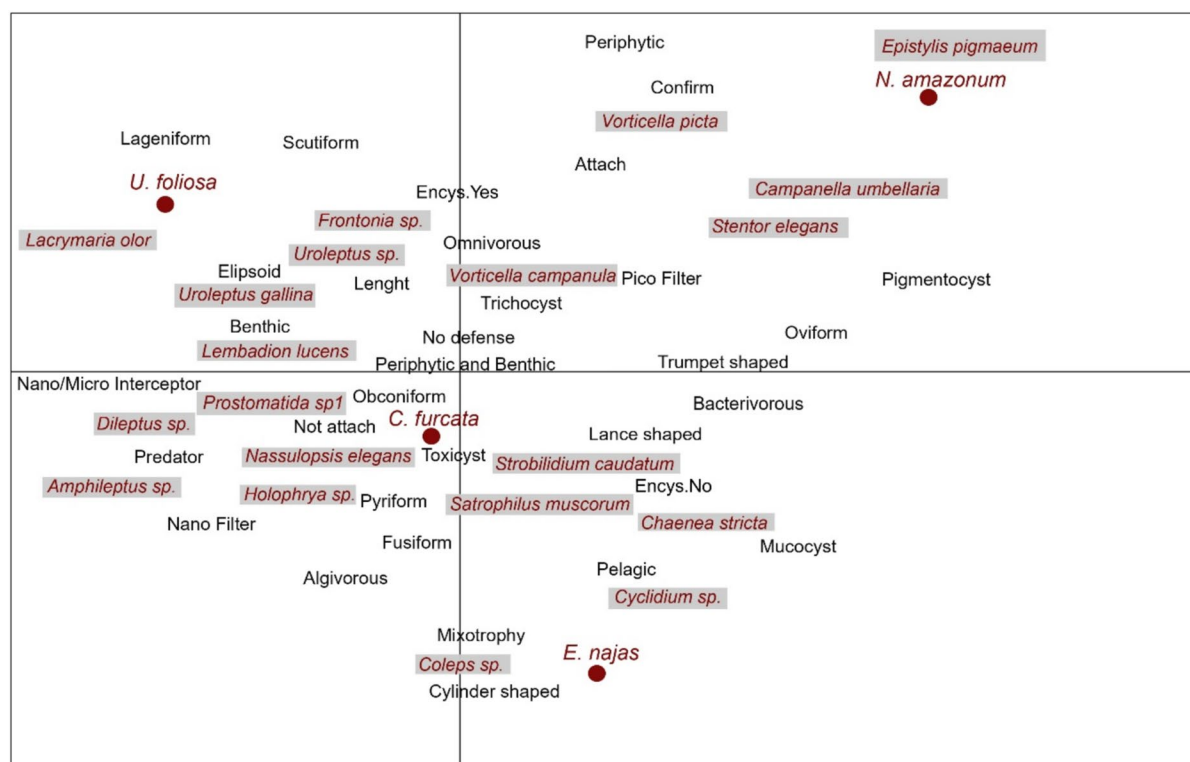
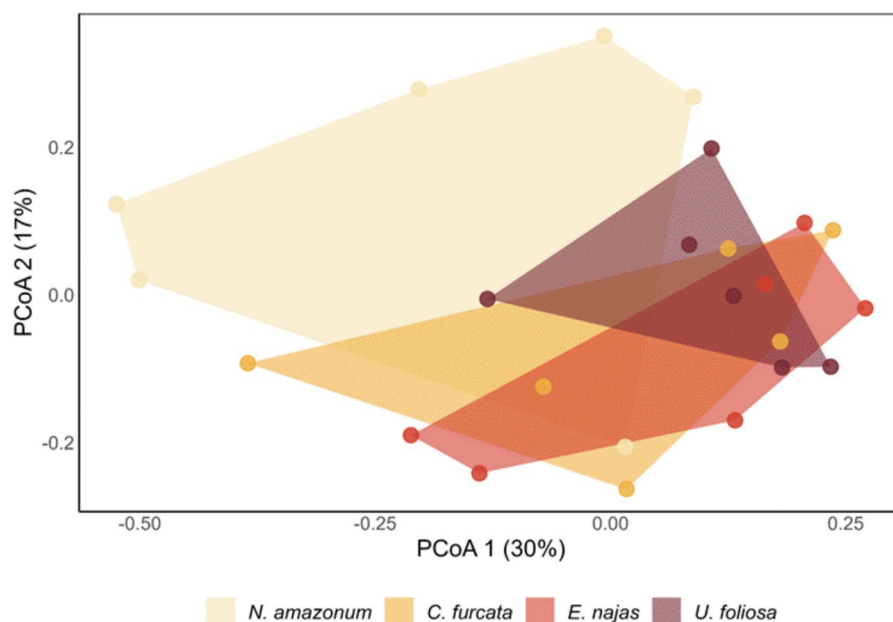


Fig. 8 R-mode linked to Q-mode (RLQ) biplot showing relationships between macrophyte species and ciliate traits. In each quadrant, the five species more related to the macrophyte species were presented. Macrophyte species are presented in red. Ciliate species are highlighted in grey boxes. The RLQ model,

considering the strength of the co-structure of the analysis, explained a total of 95.60% of the co-structure of functional traits with different macrophyte complexities (RLQ1=53.20%; RLQ2=42.40%)

microbial microhabitats (Vieira et al., 2007; Miranda et al., 2022).

Secondly, submerged macrophytes frequently host periphytic and epiphytic assemblages that themselves create complex three-dimensional matrices (Yu et al., 2022). Previous studies indicate that periphyton development can strongly influence ciliate richness and abundance (Yu et al., 2022). However, in the present study, periphytic biomass and the overall characteristics of this fraction were not directly measured. Consequently, we cannot determine whether the detected taxonomic and functional patterns are driven primarily by macrophyte architecture itself or indirectly mediated through differences in periphyton accumulation among plant species. In this sense, macrophyte structural complexity might operate both as a direct physical driver and as an indirect facilitator of biofilm development, which could represent an important factor for the development of many periphytic ciliate species.

Additionally, our functional analyses were based on presence–absence data. Therefore, abundance-weighted functional metrics might reveal additional patterns not captured here. In this context, the non-significant relationships observed for the other functional indices (FEve, FDiv, FDis) along the complexity gradient may reflect limitations inherent to presence–absence data, and these indices might respond differently if abundance information were incorporated (Xiong et al., 2018; Faquim et al., 2021; Valente-Neto et al., 2025). It is also important to note that this study was conducted in a single lagoon and during a single sampling season, which limits the general observed relationships across broader spatial and temporal scales. Macrophyte structural complexity was the main explanatory gradient investigated, and species identity may also have influenced the detected patterns. Because complexity and macrophyte species identity were not experimentally disentangled in the present design, their relative contributions cannot be fully separated.

Finally, while geometric and fractal approaches have been proposed for habitat–organism matching (Dibble & Thomaz, 2009; Loke & Chisholm, 2022), our study did not directly quantify fractal dimension or multi-scale surface topology beyond the MCI framework. Taken together, these considerations do not undermine the observed associations between macrophyte structural complexity and ciliate

community structure. Instead, they highlight that habitat complexity might operate across multiple spatial scales and in interaction with other biotic and methodological factors. Considering this, future studies should address the integration of plant architectural metrics, fine-scale surface characterization, periphyton quantification, and broader spatial and temporal replication, which would help clarify the relative importance of direct structural filtering versus indirect biofilm-mediated effects.

Conclusion

In this study, we demonstrate that the structural complexity of macrophytes plays a key role in shaping the richness, abundance, and composition in both taxonomic and functional diversity of freshwater ciliate communities. Functional attributes were more sensitive to changes in habitat structure than taxonomic metrics, reinforcing the value of trait-based approaches in detecting ecological responses. These findings support the broader ecological expectation that structurally complex habitats promote higher diversity by providing additional resources and niche opportunities.

Although structural complexity serves as a useful predictor of periphytic ciliate diversity, our results indicate that this variable should not be treated as a single efficient metric. Instead, the ecological filtering observed likely emerges from finer components of habitat architecture, such as microhabitat features, interstitial roughness, and the presence of cavities and protrusions, which can offer different types of attachment sites, refuges, and feeding zones for organisms with different sizes, shapes, and other functional traits. Future studies should consider that these small-scale structural features and their relationship with the taxonomic and functional components of a community to determine which dimensions of complexity most strongly influence community assembly and ecosystem functioning.

Overall, our study advances ecological understanding by using protists as a response group to clarify how habitat complexity influences both taxonomic and functional dimensions of diversity. It also highlights the importance of conserving aquatic environments that support structurally diverse macrophyte assemblages, as alterations in plant morphology or

composition may cascade to microbial communities, affecting nutrient cycling, energy flow, and the ecological functioning of freshwater ecosystems.

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Data availability The data are available on the Open Science Framework platform <https://osf.io/cku96/overview>.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article. The authors declare they have no financial interests.

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