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The complexity of aquatic macrophytes and environmental variables as a filter of functional traits of aquatic invertebrates from a subtropical stream in southern Brazil

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Abstract. Aquatic macrophytes play a key role in structuring aquatic ecosystems due to their varying degrees of structural complexity and perform diverse functions for different organisms (e.g., refuge and food resources). Environmental variables can serve as filters by selecting organisms with characteristics adapted for establishment in these environments. The aquatic invertebrate community is the most frequent and abundant biotic component associated with these plants. In this study, we investigated whether macrophyte complexity and environmental variables affect the richness, abundance and functional traits of the aquatic invertebrate community across different seasons in a subtropical stream. We collected different species of macrophytes in the fall and spring of 2021 and defined the degree of structural complexity —low (C1), medium (C2) and high (C3)— based on biotype and plant biomass. We washed the plants under running water and identified the organisms at the lowest possible taxonomic level. Five functional characteristics were defined: size, life stage, reproduction, body shape and eating habits. We determined the richness, abundance, frequency of occurrence, density and frequency of functional traits of invertebrates, and calculated the Shannon-Weiner index, Simpson dominance and evenness. A total of 1650 individuals were recorded in the fall and 1228 in the spring. The lowest diversity, equitability and dominance were observed for C1 in autumn and for C3 in spring. Autumn showed a greater number of categories of functional traits than spring. The flow and width of the stream showed greater amounts of correlations with the functional traits. The different degrees of macrophyte complexities influence the metrics and functional traits; however, environmental variables act primarily on them.

[Keywords: aquatic invertebrates, functional traits, subtropical sand stream, macrophyte architecture]

Resumen. La complejidad de las macrófitas acuáticas y las variables ambientales como filtro de los rasgos funcionales de los invertebrados acuáticos en un arroyo subtropical del sur de Brasil. Las macrófitas acuáticas actúan en la estructuración de los ecosistemas acuáticos debido a sus diferentes grados de complejidad estructural, y realizan distintas funciones para diferentes organismos (e.g., refugio y recursos alimenticios). Las variables ambientales pueden actuar como filtros al seleccionar organismos con características adaptadas para su establecimiento en estos lugares. La comunidad de invertebrados acuáticos es el elemento biótico asociado más frecuente y abundante a estas plantas. En este estudio investigamos si la complejidad de las macrófitas y las variables ambientales influyen en la riqueza, la abundancia y los rasgos funcionales de la comunidad de invertebrados acuáticos en diferentes estaciones del año en un arroyo subtropical. Recolectamos diferentes especies de macrófitas en el otoño y la primavera de 2021 y definimos el grado de complejidad estructural —bajo (C1), medio (C2) y alto (C3)— en función del biotipo y la biomasa vegetal. Lavamos las plantas con agua corriente e identificamos los organismos en el nivel taxonómico más bajo posible. Se definieron cinco características funcionales: tamaño, etapa de vida, reproducción, forma corporal y hábitos alimentarios. Determinamos la riqueza, abundancia, frecuencia de ocurrencia, densidad y frecuencia de los rasgos funcionales de los invertebrados y calculamos el índice de Shannon-Weiner, la dominancia de Simpson y la uniformidad. Encontramos 1650 individuos en otoño y 1228 en primavera. Observamos la menor diversidad, equidad y dominancia de invertebrados para C1 en otoño y para C3 en primavera. El otoño presentó un mayor número de categorías de rasgos funcionales que la primavera. El caudal y el ancho del arroyo mostraron mayores correlaciones con los rasgos funcionales. Los diferentes grados de complejidad de las macrófitas influyen en las métricas y rasgos funcionales; sin embargo, las variables ambientales actúan principalmente sobre ellos.

[Palabras clave: invertebrados acuáticos, rasgos funcionales, arroyo de arena subtropical, arquitectura macrófita]

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Introduction

Aquatic macrophytes influence the structuring of ecosystems through ecological processes and the functional traits of their associated organisms (Thomaz and Cunha 2010). These plants support diverse habitats that can be colonised by mammals, fish, amphibians and aquatic invertebrates (Brito et al. 2021). In addition, they provide substrates for reproduction and refuge from predators (Quirino et al. 2021) and are important food resources due to their high biomass production (Tomaz and Cunha 2010). The complexity of macrophytes has proved to be an important tool for ecological assessment of aquatic systems (Wolters et al. 2018; Poi et al. 2021; Son et al. 2021) however, studies in subtropical streams are still scarce. The complexity of aquatic macrophytes can be assessed through leaves, stems, petioles, roots, biomass (Nascimento-Filho et al. 2021), or even their biological form. Some researchers demonstrated that macrophytes with a greater degree of complexity and higher plant biomass are associated with greater densities of aquatic invertebrate communities (Growder and Cooper 1982; Ferreiro et al. 2011; Wolters et al. 2018; Nascimento Filho et al. 2021).

Aquatic invertebrates constitute the main group of organisms that can be used to assess the ecological conditions of lotic systems (Magomguia et al. 2016), due to their wide distribution, richness and abundance (Santana et al. 2021); use as bioindicators (Callisto et al. 2002; Schiller et al. 2017), and relationships with ecosystem productivity (Weyl and Coetzee 2013). The functional traits of invertebrates (e.g., body size, eating habits, life stage, body shape and mode of reproduction) are used by several authors to develop studies focused on the ecological conditions of these environments (Tachet et al. 2002; Castro et al. 2018; Sodré and Bozelli 2019; Conceição et al. 2020). It is recognized in the literature that environmental characteristics and water quality are fundamental components that shape invertebrate communities in continental aquatic environments (Leunda et al. 2009). Another determining variable on assemblages is the change in precipitation patterns, which causes effects of decreasing the richness and abundance of organisms (Kim et al. 2018). In turn, functional traits have consistent and robust patterns for understanding local conditions (Edegbene et al. 2024).

Functional trait categorization is an approach used to describe the structure of communities in aquatic systems (Gomes et al. 2019; Serra et al. 2019). Invertebrates with certain functional traits may be sensitive to environmental variations (Schmera et al. 2017) and therefore allow researchers to understand ecosystem processes (Diaz and Cabido 2001). The use of functional traits can be combined with phylogenetic diversity for biomonitoring purposes (Saito et al. 2015). Functional feeding groups allow researchers to understand the distribution of energy use within aquatic ecosystems (Silva et al. 2008). In addition, the evaluation of functional characteristics of the Chironomidae family has been employed to evaluate the anthropogenic impacts on reservoirs (Gomes et al. 2018).

In this study, we evaluated the community of invertebrates associated with aquatic macrophytes and their relationships with environmental variables in a subtropical stream located in the coastal plain of southern Brazil. The aim of this study was to determine whether macrophyte complexity and environmental variables can influence the diversity, richness, abundance, equitability and functional traits of aquatic invertebrates in two seasons. Our hypothesis is that aquatic macrophytes with a higher degree of complexity in the autumn season present higher values of richness, abundance and diversity of functional traits than in the spring season, and the functional traits evaluated will have some kind of correlation with the environmental variables.

Materials and Methods

Study area

The municipality of Rio Grande is located in the southern portion of the Coastal Plain of Rio Grande do Sul, forming part of the coastal sandy morphic unit (Albertoni et al. 2007). The coastal plain, which was formed recently, originated from constant sea level transgressions and regressions (Buchmann et al. 2009) and currently encompasses rich aquatic ecosystems (Vieira and Rangel 1988). The portion of the plain where the Rio Grande is inserted has a low altitude (Trindade et al. 2010), which facilitates the development and establishment of plant species in lotic systems (Vieira and Rangel 1988).

We carried out two samplings in a stream that is approximately 6 km long, located in a peripheral urban region (32°04′35′′ S - 52°15′08′′ W) and known regionally as Cabeças Stream

(Figure 1). This type of water body has hydrological dynamics that are weather dependent (Albertoni and Palma-Silva 2010). The first sampling took place in May 2021, and the second, in September 2021. The month of May is characterized as the autumn weather season in the region and had an accumulated precipitation volume of 25.2 mm (Table 1). The month of September is marked by spring, and accumulated rainfall totaled 172.8 mm (Table 1).

Environmental variables. We measured the environmental variables with a multiparameter probe, with 15 measurements for each collection period. We also collected three water samples (500 mL each) in each period to determine the concentrations of total nitrogen, total phosphorus and chlorophyla-*a* (Mackereth et al. 1978; Valderrama 1981; Baumgarten et al. 1996). We measured the width (m), depth (m), and flow (m/s) of the stream with five measurements at each period along the stream. The climate in the region is humid subtropical according to the Köppen classification, with an average annual temperature between 17 and 19 °C and annual rainfall between 1200 and 1500 mm (Alvares et al. 2013).

Sampling and Biological Processing. We sampled three types of aquatic macrophytes along the stream according to their occurrence. These macrophytes were the most abundant and presented different biological forms and morphological characteristics. The species determined were: *Stuckenia pectinata* (L.) Börner, *Ludwigia hexapetala* (Hook. and Arn.), and *Eichhornia azurea* (Sw.) Kunth. We collected each macrophyte from a stream site (Figure 1). Sampling in spring was influenced by a rainy period in the region. To collect plants, a 300 µm mesh sampler with an area of 0.07 m² was used; we considered the plant material retained within this area to be a sample. In each collection, we performed three reps for each macrophyte species. We collected roots and photosynthetic parts from each macrophyte species and stored them in plastic bags in thermal boxes with ice.

In the laboratory, we washed the macrophytes with running water over a 250 µm sieve and dried them in an oven (60 °C until a constant mass was reached) to determine the dry biomass. We defined the complexity of macrophytes as low (C1) for the submerged macrophyte *S. pectinata*; medium (C2) for the amphibious plant *L. hexapetala*, or high (C3) for *E. azurea*, a macrophyte with floating leaves (Figure 1). We defined the different grades by using the respective values of dry biomass, types of leaves and biological forms (Table 2).

Subsequently, we preserved the fauna retained in the mesh in 80% alcohol containing 'rose bengal' (for staining) and separated

Table 1. Accumulated precipitation (mm) in the different seasons of the year in the municipality of Rio Grande, RS, Brazil. Source: database of the National Institute of Meteorology (INMET).

Tabla 1. Precipitación acumulada (mm) en las diferentes estaciones del año en el municipio de Rio Grande, RS, Brasil. Fuente: base de datos del Instituto Nacional de Meteorología (INMET).

Season	Period	Month	Monthly accumulated precipitation (mm)
Autumn	20/mar	March	139.6
		April	40.4
		May	25.2
	21/jun	June	82.8
Spring	22/sep	September	172.8
		October	63.0
		November	49.6
	21/dec	December	18.2

Table 2. Categorization of different degree of complexity of aquatic macrophytes.

Tabla 2. Categorización de diferentes grados de complejidad de macrófitas acuáticas.

Collect		*Stuckenia pectinata*	*Ludwigia hexapetala*	*Eichhornia azurea*
	Degree of complexity	Low	Medium	High
	Biological form	Underwater	Amphibious	With foating leaf
	Leaf format	Long and narrow	Obovate	Rounded
	Identification code	C1	C2	C3
Autumn	Dry biomass (g/m²)	247.42 g/m²	492.57 g/m²	683.28 g/m²
Spring		59.71 g/m²	106.14 g/m²	343.71 g/m²

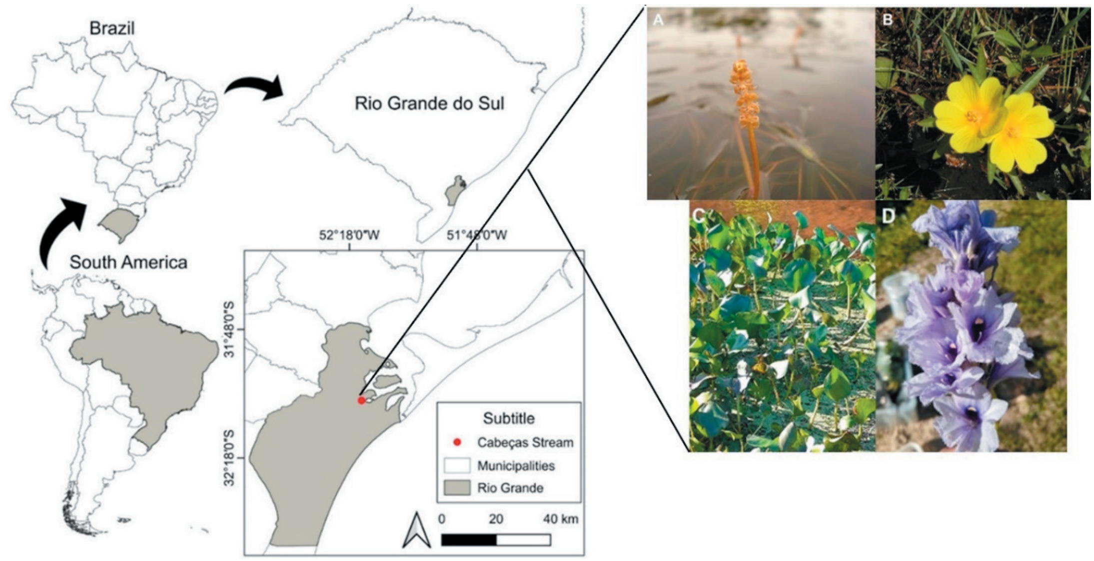

Figure 1. Location of Cabeças Stream in Rio Grande, Rio Grande do Sul, Brazil, and collected aquatic macrophytes. A) *Stuckenia pectinata*, low complexity. B) *Ludwigia hexapetala*, medium complexity. C) Photosynthetic part. D) Flower of *Eichhornia azurea*, high complexity. Pictures credits: Cláudio Trindade Trindade.

Figura 1. Ubicación del Arroyo Cabeças en Rio Grande, Rio Grande do Sul, Brasil, y macrófitas acuáticas recolectadas. A) *Stuckenia pectinata*, baja complejidad. B) *Ludwigia hexapetala*, complejidad media. C) Parte fotosintética. D) Flor de *Eichhornia azurea*, alta complejidad. Créditos de las fotografias: Cláudio Trindade Trindade.

them with the aid of a stereomicroscope. We counted and identified invertebrates at the lowest possible level based on the literature (Domínguez and Fernández 2009; Merritt and Cummins 2009; Trivinho-Strixino 2011) and classified the functional traits (feeding habits and reproduction) according to specific literature (Tachet et al. 2002; Cummins et al. 2005; Conceição et al. 2020). For the body size functional trait, we adapted a millimetre blade to measure the length of all individuals of each taxon in millimetres and calculated the averages for each taxon. For the traits, stage of development, and body shape, we assigned the categories based on visualisation of the sampled individuals (Table 3).

Data analysis. We determined the richness, the total abundance of taxa, the frequency of occurrence of each taxon and the density of invertebrates (individuals g/DW) for each macrophyte degree of complexity, and the frequency of functional traits. We evaluated the composition and structure of the

Table 3. Categorization of the functional traits of aquatic invertebrates used to characterize the sampling.

Tabla 3. Categorización de los rasgos funcionales de los invertebrados acuáticos utilizados para caracterizar el muestreo.

Functional trait	Trait category	Category code
	Collector-scavenger	FFG1
	Collector-filter	FFG2
Feeding habit	Shredder	FFG3
	Scraper	FFG4
	Predator	FFG5
	0.5 - 1.5mm	BS1
Body size	1.51 - 3.0mm	BS2
	3.1 - 5mm	BS3
	Isolated eggs, cemented or fixed	R1
Reproduction	Free egg mass	R2
	Egg mass, cemented or fixed	R3
	Larvae	EA1
Stage of life	Pupa	EA2
	Adult	EA3
	Cylindrical	BF1
Body shape	Flat	BF2
	Shell only	BF3

invertebrate fauna at the different degrees of complexity through (Shannon-Wiener index), Simpson dominance and equitability in each macrophyte for each collection. To test for differences in the invertebrate total abundance, richness, density, and diversity indices between the degrees of complexity for each season, we used one-way analysis of variance (ANOVA), following its assumptions of homoscedasticity and normality of data. We used Tukey's post hoc test for multiple comparisons to determine differences between the degrees of complexity.

To verify whether environmental variables influence the functional traits of aquatic invertebrates, we used the multivariate analysis of RLQ ordination. This analysis performs the ordering of three matrices simultaneously, where R=environmental variables of each site; L=abundance of taxa per site, and Q=functional traits of the taxa (Dolédec et al. 1996; Dray et al. 2014). In addition, we applied the Monte Carlo randtest to verify significance (P<0.05). We performed the Forth Corner analysis, model 6, to evaluate the relationships between environmental variables and functional traits, using Pearson's correlation. The analyses were performed using the ade4 package with the rlq and fouthcorner functions and the vegan package for the adonis function (Oksanen et al. 2017), developed in the R software (R Core Team 2024).

Results

The stream was more oxygenated in the spring and with a slightly alkaline pH in the autumn (Table 4). The average water temperature ranged between 17.2 and 19.9 °C, and the conductivity, between 188 and 90 μS/cm in the autumn and spring seasons, respectively (Table 4). The highest concentrations of chlorophyll-*a* (μg/L) were observed in the fall (10.5±4.98 μg/L) (Table 4). The stream was richer in total nitrogen in the spring (1.5±0.27 mg/L) and total phosphorus in the fall (0.08±0.007 mg/L) (Table 4). The stream was characterized as a mesotrophic environment, and the greatest depth (0.7±0.47 m) and average width (8.1±1.88 m) were observed in the spring, as well as the fastest average flow (3.2±1.29 m/s) (Table 4). Between the two seasons, we counted 2878 aquatic invertebrates distributed in 29 taxa, with 1650 individuals in autumn —distributed in 27 taxa— and 1228 organisms in spring —distributed in 14 taxa—. Almost all the taxonomic metrics showed differences between the three analysed macrophyte degrees of complexity in both sampled seasons (P<0.05) (Table 5).

The exception in autumn was in the evenness values, which only differed for C3 (P<0.05), with higher values for this parameter, as well as higher Shannon diversity values. In this same season, C2 showed the highest invertebrate richness, while C1 had the highest total abundance, density and dominance (Table 5). In spring, the exception was for density values: only C1 differed from the other macrophyte degrees of complexity (P<0.05), with higher values for this parameter (Table 5).

For that same season, C3 had the highest richness and abundance, but it showed greater dominance and lower Shannon diversity and evenness (Table 5). In autumn, *Orthocladius* (61.39%), Cicadellidae (55.61%) and *Zavrelimyia* (39.29%) had the highest frequencies for C1, C2, and C3, respectively. In spring, the taxa with the highest frequencies were *Rienthia* (60.99%) for C1 and *Chironomus* (46.38% for C2 and 90.76% for C3) (Table 6).

Table 4. Values of environmental variables in Cabeças Stream. SD: standard deviation. Min: minimum. Max: maximum.

Tabla 4. Valores de las variables ambientales en el Arroyo Cabeças. SD: desviación estándar. Min: mínimo. Max: máximo.

Environmental variables	Autumn		Spring	
	Mean±SD	Min-Max	Mean±SD	Min-Max
Electric conductivity (μS/cm)	188±1.22	187-191	90±0.88	93-95
Dissolved oxygen (mg/L)	6.9±0.83	5.9-8.6	13.4±1.41	12.1-18.0
pH	7.8±0.82	7.0-9.5	7±0.68	6.4-8.5
Temperature (°C)	17.2±0.36	16.7-17.8	19.9±0.06	19.8-20.0
Chlorophyll-*a* (μg/L)	10.5±4.98	2.53-18.6	5.0±3.73	1.5-11.1
Total phosphorus (mg/L)	0.08±0.007	0.08-0.1	0.05±0.01	0.03-0.08
Total nitrogen (mg/L)	0.7±0.10	0.6-0.9	1.5±0.27	1.1-1.8
Width (m)	7.4±2.03	4.2-12.6	8.1±1.88	5.5-11.5
Depth (m)	0.4±0.23	0.2-1.0	0.7±0.47	0.2-1.7
Flow (m/s)	4.7±1.68	2.7-9.1	3.2±1.29	2.0-5.5

Table 5. Values of richness, total abundance, density of individuals and diversity indices of the invertebrates associated with macrophytes with different structural complexity degree. Different letters indicate statistical difference (P<0.05). Density: density of individuals. C1: low complexity (*Stuckenia pectinata*). C2: medium complexity (*Ludwigia hexapetala*). C3: high complexity (*Eichhornia azurea*).

Tabla 5. Valores de riqueza, abundancia total, densidad de individuos e índices de diversidad de los invertebrados asociados a macrófitas con diferente grado de complejidad estructural. Letras diferentes indican diferencias estadísticas (P<0.05). Densidad: densidad de individuos. C1: baja complejidad (*Stuckenia pectinata*). C2: complejidad media (*Ludwigia hexapetala*). C3: alta complejidad (*Eichhornia azurea*).

		Richness	Total abundance	Density (g/DW)	Dominance	Shannon	Equitability
Autumn	C1	13a	764a	3.0a	0.404a	1.426a	0.555a
	C2	22b	606b	1.2b	0.339b	1.702b	0.550a
	C3	18c	280c	0.4c	0.224c	1.927c	0.666b
Spring	C1	6a	282a	4.9a	0.477a	0.926a	0.517a
	C2	5a	203b	1.9b	0.380b	1.072b	0.665b
	C3	9b	743c	2.1b	0.835c	0.416c	0.189c

Table 6. Abundance and frequency of occurrence of colonizing invertebrates of the three structural complexities of aquatic macrophytes for each collection season. Ab: abundance (number of individuals). Frec: frequency (%). C1: low complexity (*Stuckenia pectinata*). C2: medium complexity (*Ludwigia hexapetala*). C3: high complexity (*Eichhornia azurea*).

Tabla 6. Abundancia y frecuencia de ocurrencia de invertebrados colonizadores de las tres complejidades estructurales de macrófitas acuáticas para cada temporada de recolección. Ab: abundancia (número de individuos). Frec: frecuencia (%). C1: baja complejidad (*Stuckenia pectinata*). C2: complejidad media (*Ludwigia hexapetala*). C3: alta complejidad (*Eichhornia azurea*).

	Autumn season						Spring season					
	C1		C2		C3		C1		C2		C3	
	Ab	Freq	Ab	Freq	Ab	Freq	Ab	Freq	Ab	Freq	Ab	Freq
Arachnida	0	0.00	1	0.17	2	0.71	0	0.00	0	0.00	0	0.00
Hydracarina	28	3.66	16	2.64	0	0.00	0	0.00	4	1.93	4	0.54
Annelida												
Hirudinea	50	6.54	15	2.48	9	3.21	0	0.00	1	0.48	10	1.34
Gastropoda												
Ancylidae	0	0.00	13	2.15	2	0.71	0	0.00	0	0.00	1	0.13
Hydrobiidae	6	0.79	4	0.66	1	0.36	0	0.00	0	0.00	2	0.27
Planorbidae	1	0.13	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Coleoptera												
Curculionidae	0	0.00	0	0.00	1	0.36	0	0.00	0	0.00	0	0.00
Hydrophilidae	5	0.65	1	0.17	6	2.14	0	0.00	0	0.00	0	0.00
Elmidae	0	0.00	0	0.00	1	0.36	0	0.00	0	0.00	0	0.00
Diptera												
Culicidae	0	0.00	1	0.17	0	0.00	0	0.00	0	0.00	1	0.13
Simuliidae	17	2.23	1	0.17	0	0.00	6	2.13	29	14.01	0	0.00
Ceratopogonidae	0	0.00	0	0.00	0	0.00	1	0.35	0	0.00	0	0.00
Chironomidae	29	3.80	15	2.48	4	1.43	9	3.19	2	0.97	30	4.02
Chironomus	35	4.58	16	2.64	18	6.43	91	32.27	96	46.38	678	90.76
Rienthia	102	13.35	32	5.28	0	0.00	172	60.99	75	36.23	0	0.00
Orthocladius	469	61.39	85	14.03	60	21.43	3	1.06	0	0.00	0	0.00
Tanytarsus	0	0.00	11	1.82	8	2.86	0	0.00	0	0.00	0	0.00
Cladopelma	0	0.00	3	0.50	4	1.43	0	0.00	0	0.00	0	0.00
Zavrelimyia	0	0.00	35	5.78	110	39.29	0	0.00	0	0.00	0	0.00
Trichoptera												
Hydroptilidae	14	1.83	14	2.31	4	1.43	0	0.00	0	0.00	0	0.00
Hemiptera												
Cicadellidae	5	0.65	337	55.61	34	12.14	0	0.00	0	0.00	0	0.00
Ephemeroptera												
Caenidae	3	0.39	2	0.33	0	0.00	0	0.00	0	0.00	1	0.13
Amphipoda												
Hyalellidae	0	0.00	1	0.17	0	0.00	0	0.00	0	0.00	19	2.54
Hymenoptera												

Table 6. Continuation.
Tabla 6. Continuación.

Ichneumonoidae	0	0.00	1	0.17	0	0.00	0	0.00	0	0.00	0	0.00
Diapriidae	0	0.00	1	0.17	1	0.36	0	0.00	0	0.00	0	0.00
Colembolla												
Isotomidae	0	0.00	0	0.00	14	5.00	0	0.00	0	0.00	0	0.00
Odonata												
Gomphidae	0	0.00	0	0.00	1	0.36	0	0.00	0	0.00	0	0.00
Nematoda	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.13
Total	764	100	606	100	280	100	282	100	207	100	747	100

Regarding the functional traits for autumn, the invertebrate functional feeding groups varied according to the macrophyte degree of complexity of the aquatic macrophytes. For C1, there was a higher frequency of collector-scavengers, while for C2 and C3 there was a higher frequency of predators (Figure 2A1). On the other hand, in spring we found a higher frequency of collector-scavengers for the three degrees of complexity (Figure 2A2). For the size trait in autumn, C1 and C3 had a higher frequency of intermediate sizes (1.51-3.0 mm), while there was a predominance of smaller sizes (0.5-1.5 mm) for C2 (Figure. 2B1). In spring, there was a pattern of larger sizes (3.1-5.0 mm) for each degree of complexity (Figure 2B2).

Reproduction in autumn varied between the three degrees of complexity: we noted the dominance of free egg mass for C1, isolated egg cemented for C2, and cemented or fixed egg mass for C3 (Figure 2C1). In spring, cemented or fixed egg mass dominated for each degree of complexity (Figure 2C2). For life stage trait in autumn, there was a higher frequency of larvae for C1 and C3, while for C2, there was a predominance of adults (Figure 2D1). For spring, the stage did not vary between the degrees of complexity, with a predominance of larvae (Figure 2D2). For the body shape functional trait, the cylindrical shape predominated in autumn and spring for each degree of complexity (Figure 2E).

The ordering generated by the RLQ indicated differences between the different degrees of complexity (C1, C2, C3) of the two collections (autumn and spring) according to the environmental variables and functional characteristics (Figure 3). The first axis of the ranking explained 99.32% of the variation in the data, and the second explained 0.61% (randtest Monte Carlo P=0.03). All the functional characteristics evaluated in this study (i.e., eating habits, body size, body shape, type of reproduction and stage of development) showed some kind of correlation with environmental variables (Figure 4). Among the 17 categories assigned, only 4 did not present a significant correlation (Figure 4).

Collector-scavenger organisms were more correlated with C1 in spring sampling, positively associated with stream width, and negatively associated with water flow (Figure 4). On the other hand, the filter collectors were more associated with C2 in the spring and showed a positive correlation with depth and a negative correlation with total water phosphorus (Figure 4). The fragmenter invertebrates were more correlated with C1 in the spring, but this feeding trait did not correlate with any environmental variable (Figure 4). The scraper organisms showed greater associations with C1 and C2 in the fall and were positively correlated with flow and negatively correlated with width (Figure 4). Predators were more related to C3 in the autumn sampling; however, this trait did not correlate with any environmental variable (Figure 4).

Smaller invertebrates were associated with water flow, however, negatively correlated with stream width (Figure 4). Individuals of intermediate size were positively associated with electrical conductivity and negatively correlated with total nitrogen and water temperature (Figure 4). On the other hand, larger organisms were associated with stream width and showed a negative correlation with water flow (Figure 4).

Isolated, cemented or fixed eggs were associated with flow and negatively correlated with stream width (Figure 4). Organisms with a strategy of reproduction of free egg mass were the ones that presented the highest type of correlation (Figure 4). Free egg masses were associated with electrical conductivity, pH, chlorophyll-*a* and total phosphorus of

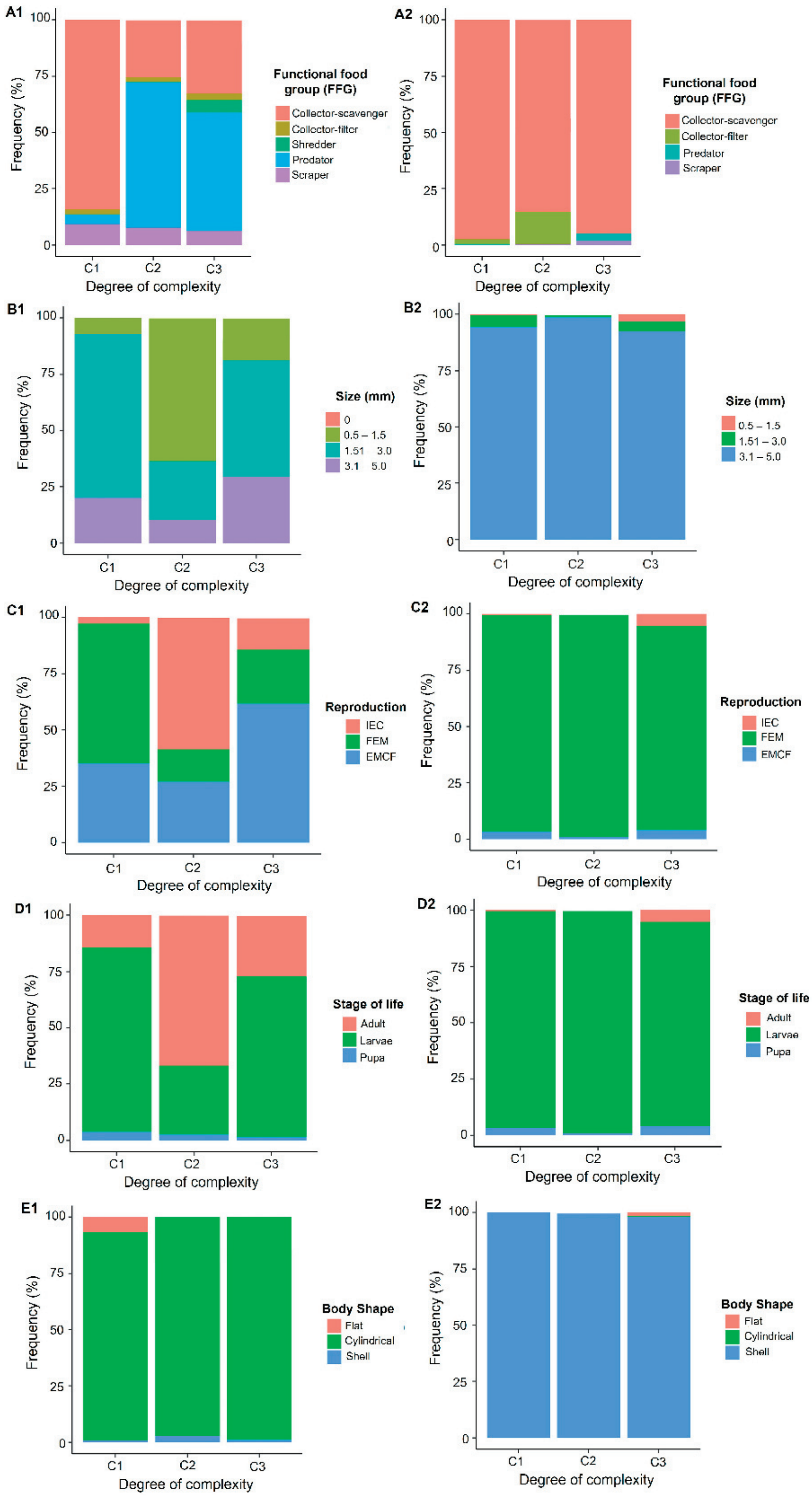

Figure 2. Frequency (%) of functional traits for each aquatic macrophyte complexity. A) Functional feeding habit. B) Body size (mm). C) Reproduction (IEC: cemented isolated eggs; FEM: free egg mass; EMCF: egg mass, cemented or fixed). D) Stage of life. E) Body shape. 1: autumn season. 2: spring season. C1, C2, C3: degree of complexity.

Figura 2. Frecuencia (%) de características funcionales para cada complejidad de macrófitas acuáticas. A) Hábito alimentario funcional. B) Tamaño del cuerpo (mm). C) Reproducción (IEC: huevos cementados aislados; FEM: masa de huevos libres; EMCF: masa de huevos cementados o fijos). D) Etapa de la vida. E) Forma del cuerpo. 1: Otoño. 2: Primavera. C1, C2, C3: grado de complejidad.

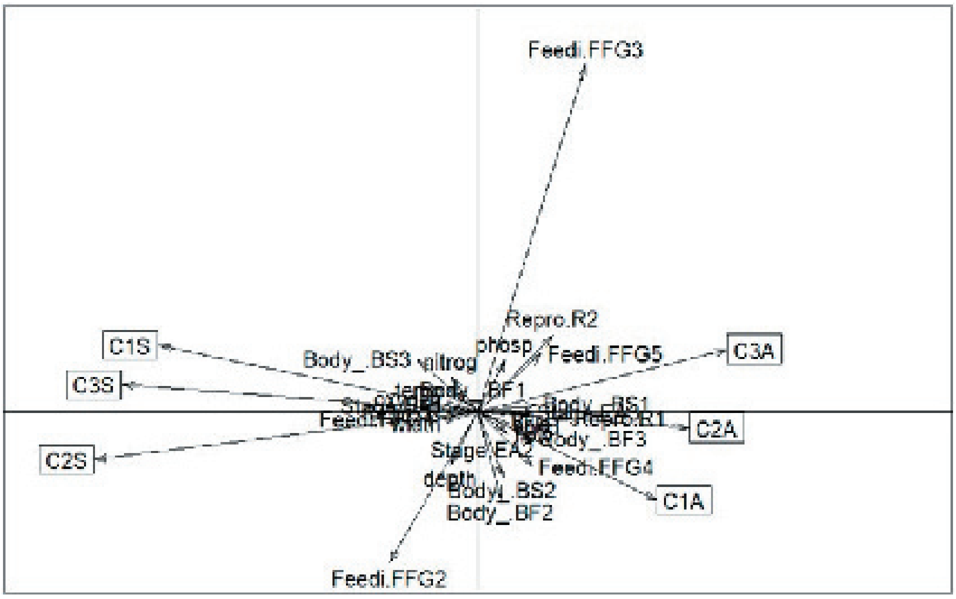

Figure 3. RLQ analysis of aquatic invertebrate composition, functional traits and environmental variables for the levels of complexity of aquatic macrophytes. Axis 1=99.32%. Axis 2=0.61%.

Figura 3. Análisis RLQ de la composición de invertebrados acuáticos, rasgos funcionales y variables ambientales para los niveles de complejidad de macrófitas acuáticas. Eje 1=99.32%. Eje 2=0.61%.

the water, and negatively correlated with dissolved oxygen, stream width and depth (Figure 4). The cemented or fixed egg mass correlated positively with the width and negatively with the water flow (Figure 4).

Organisms in larval stages were associated with stream width and negatively correlated with stream flow (Figure 4). The pupal stage did not correlate with any environmental variable, and the adult stage was only negatively

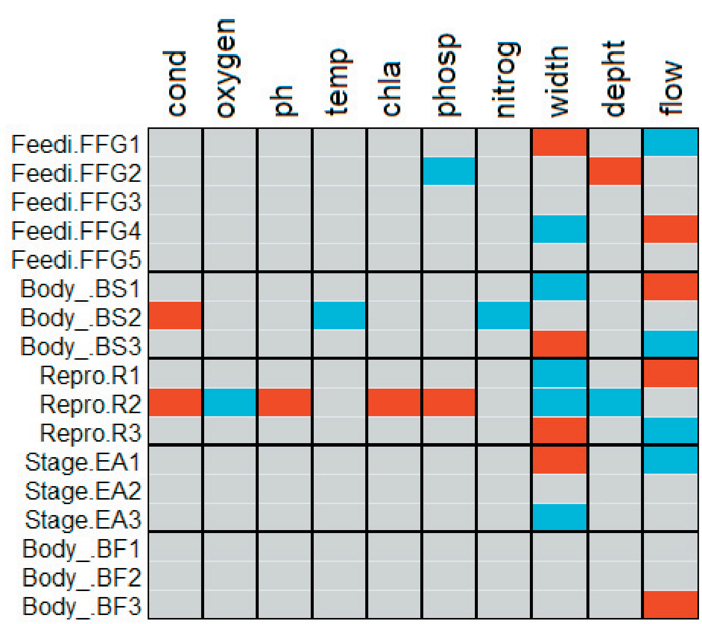

Figure 4. Fourth Corner: Pearson's correlation between functional traits and environmental variables. Red: positive correlation. Blue: Negative correlation. Gray: No significant correlation. Cond: Electrical conductivity. Oxygen: Dissolved oxygen. Temp: Temperature. Chla: Chlorophyll-*a*. Phosp: Total phosphorus. Nitrog: Total Nitrogen. See abbreviations of the functional traits in Table 3.

Figura 4. Cuarta esquina: correlación de Pearson entre los rasgos funcionales y las variables ambientales. Rojo: correlación positiva. Azul: Correlación negativa. Gris: correlación no significativa. Cond: Conductividad eléctrica. Oxygen: Oxígeno disuelto. Temp: Temperatura. Chla=Clorofila-*a*. Phosp: Fósforo total. Nitrog: Nitrógeno total. Ver abreviaturas de los rasgos funcionales en la Tabla 3.

correlated with stream width (Figure 4). Cylindrical and flat body shapes were not correlated with any type of environmental variable, and shells were positively associated with stream flow (Figure 4).

Discussion

Our results indicate that the degrees of complexity of the aquatic macrophytes *Stuckenia pectinata*, *Ludwigia hexapetala* and *Eichhornia azurea*, and the environmental variables of the streams in autumn and spring are important components in the structuring of invertebrate assemblages, in addition to acting as filters for functional traits of these organisms. It was possible to observe that although certain taxa are associated with specific complexities, the disturbances caused by large volumes of precipitation seem to cause considerable effects on the faunal composition. The spring collection was marked by high accumulations of rain, which reflected in the values of width, depth and flow of the stream.

Thus, we found that in the spring collection, a more simplified structure of traits occurred, predominantly selecting the traits: collector-scavenger; larger body size, cylindrical body, larval stage and mass reproduction of cemented or fixed eggs. On the other hand, for autumn, a greater variability of functional traits was observed, with several functional feeding groups and a greater presence of adult organisms.

The dominance of these traits in spring can be explained largely by the high abundance of Chironomidae individuals. Chironomidae withstand a wide range of variations in environmental conditions, which reflects the great adaptive capacity of these organisms (Strixino 2023). However, it was possible to observe a preference of some genera for the complexities of the macrophytes evaluated, where *Rienthia* was more associated with the lowest degree of complexity, while *Chironomus*, with the highest degree of complexity in this season. In other studies, it was found that the different architectures provided by aquatic macrophytes influence the availability of food resources (Quirino et al. 2021), as well as affect the substrate and protection conditions of the species associated with these plants (Santana et al. 2021). Another study also indicates that the surface area provided per unit of weight per plant is also a limiting factor (Diarra et al. 2018), contributing to a specific richness and abundance, which was found in our study.

The order Diptera was also the most frequent in the fall, where the diversity indices elucidated that C1 presented the lowest evenness —and consequently, a greater dominance— mainly related to the high occurrence of the genus *Orthocladius* (61.39%), and in C3, due to *Zavrelimyia* (39.29%). The same pattern of dipteran dominance has been reported for lotic systems (Milesi et al. 2009; Serra et al. 2019) and lentic systems (Albertoni et al. 2007; Nascimento-Filho et al. 2021; Santana et al. 2021). Within this family, the morphological (Durdevic et al. 2023), physiological and behavioral characteristics of the larvae are quite variable (Merritt and Cummins 2009), which allows the establishment of communities in aquatic ecosystems with different nutrient conditions, currents and availability of food resources. For this reason, the larval stage of Chironomidae was used in ecological studies to indicate the quality of aquatic systems (Kleine and Trivinho-Strixino 2005), as this family has genera that are sensitive and tolerant to environmental changes (Saito et al. 2015).

The second most frequent order in our study was Hemiptera. Organisms of this order have a wide variety of lifestyles, feeding habits and body shapes (Triplehorn and Johnson 2011), which underly their adaptations and ecological niches (Merritt and Cummins 2009); they can be classified as aquatic, semi-aquatic or terrestrial. In autumn, we found a predominance of Hemiptera associated with C2. The complexity provided by the amphibious biological form of *L. hexapetala* offers opportunities for colonization mainly by terrestrial insects (Santana et al. 2021), which we confirmed based on the frequency (55.61%) of adults of the Cicadellidae family.

Studies involving functional traits mainly consider eating habits (Cummins et al. 2005; Albertoni et al. 2018; Gomes et al. 2018). Feeding habits are associated with resource availability, and any change can directly influence the associated invertebrate assemblage (Conceição et al. 2020). We found the occurrence of the five functional feeding groups, and the diversity of these groups evidences the trophic niches existing in the ecosystem (Ehlert et al. 2021). In the fall, a higher frequency of collectors was observed in the macrophyte of lower complexity, which indicates that this plant may be rich in fine particulate organic matter

(Madomguia et al. 2016). On the other hand, predators —mostly associated with a higher degree of complexity— may be associated with this type of vegetation in search of food resources, since the roots of floating plants have the potential to shelter prey (Brito et al. 2021). Prey, in turn, seek the same structures as protection against predators. However, for predators, environmental variables do not appear to have any positive or negative effect on this trait. In spring, the dominance of collector-scavenger was observed in the three degrees of complexity, which was represented as a result of the high predominance of the genera of Chironomidae. In this season, the accumulated precipitation (mm) was the main responsible for the structuring of aquatic invertebrate assemblages.

The smaller body size was often associated with macrophytes of intermediate complexity in the fall. This relationship can be explained by the dominance of the family Cicadellidae —which is of aerial insects—, since *L. hexapetala* develops at the interface between the aquatic and terrestrial environment, and the stream flow is related to this size category. On the other hand, the intermediate-sized organisms were found mainly in the lowest and highest degree of complexity for this collection —and most were Diptera larvae— and the electrical conductivity of the stream generates effects on this trait. In the spring, due to the dominance of Diptera mentioned above, the largest size category was more frequent, and the width of the stream was the only environmental variable positively correlated to the trait. Another study that evaluated the effects of aquatic macrophyte architectures on the invertebrate community indicated that the greater the complexity of the plant, the greater the size of the invertebrates (McAbendroth et al. 2005). However, in our study for autumn, the greatest complexity was related to intermediate sizes, and in spring, the high accumulated rainfall may have had effects on the structuring of the fauna.

Autumn reproduction varied among the three complexities of aquatic macrophytes. The predominance of free egg mass in low complexity can be explained by the greater availability of water and moisture to maintain the conditions necessary for egg development, considering that *S. pectinata* is a submerged macrophyte. And the environmental variables electrical conductivity, pH, chlorophyll-*a* and total phosphorus of the water are important filters of this trait. The higher occurrence of isolated eggs in the intermediate complexity for the same season is associated with the fact that this plant is amphibious, where some plant structures may be more susceptible to desiccation due to exposure to the sun, and others are more related to water, favoring the laying of eggs in specific locations to provide a greater possibility of success in the development of the organism. Finally, the predominance of cemented or fixed egg mass in greater complexity in autumn is also associated with the search for structures with greater moisture availability and adequate luminosity for the eggs, since *E. azurea* is a macrophyte with floating leaves. However, in spring, we found that all degrees of complexity showed the same pattern based on the dominance of Chironomidae, which seek to lay their eggs through cemented or fixed masses in places with specific humidity, temperature and luminosity suitable for their development, usually associated to branches, leaves and other substrates (Strixino 2023).

In the fall, the organisms associated with the lowest and highest degree of complexity were mostly of larval stages, while the intermediate complexity of adults. Our findings were like those found by Santana et al. (2021), where they found a predominance of adults in *Ludwigia* sp. In the spring, the larval stage was dominant in three degrees of complexity. The functional trait body shape was similar for the three degrees of complexity, regardless of the collection period; this indicates that body shape does not act as a filter between the degrees of complexity of macrophytes, and the cylindrical and flat body did not present a correlation with any environmental variable. According to Lamouroux et al. (2004), some traits are more related to habitat (e.g., breeding patterns and life stage) because individuals may develop specific preferences at different stages of their life cycle.

Based on functional traits (i.e., feeding habits, body size, reproduction, life stage and body shape) and taxonomic data, we observed that the different degrees of complexity of aquatic macrophytes and environmental variables influenced the composition of aquatic invertebrate assemblages. The hypothesis that aquatic macrophytes with the highest degree of complexity (C3) in the autumn season present higher values of richness, abundance and diversity of functional traits than in the spring season, and that the functional traits will have some kind of correlation with environmental variables was partially accepted. The highest richness in the autumn was observed in the macrophyte of intermediate degree of complexity (C2), and the highest abundance was associated with the lowest degree of complexity (C1). However, a greater number of functional trait categories were found in the highest degree of complexity (C3). All functional traits evaluated in this study showed some type of correlation (positive/negative) with environmental variables, with few categories that were not correlated.

These findings highlight the importance of the different degrees of macrophyte complexity in lotic systems, and that each biological type of macrophyte plays a different role for aquatic invertebrate assemblages, supporting a distinct diversity. In this way, the same plant has the potential to act as a substrate, protection for larvae and a food resource (Brito et al. 2021; Santana et al. 2021), which can act as a filter, selecting specific functional characteristics within an aquatic system. However, environmental variables seem to play a primary role in composition, and body shape categories seem to be the least sensitive to these variations.

Conclusions

The different degrees of complexity of aquatic macrophytes influenced the metrics and functional traits of aquatic invertebrate assemblages. However, environmental characteristics primarily affect these communities. The high precipitation accumulations may have affected the faunal composition, reflecting the dominance of some Diptera groups that are highly adapted to these environmental variations. Our study indicates that organisms of the order Diptera —especially Chironomidae— are mostly dominant in the different degrees of complexity in both seasons, except for the intermediate complexity in autumn, which was predominated by Hemiptera of the family Cicadellidae. The variables that showed the most positive correlations with functional traits were stream width and flow.

Among the functional traits evaluated, the body shape categories were the least positively or negatively correlated with the environmental variables, with the type of reproduction being the variable most correlated with the environment. Thus, environmental characteristics seem to be an important tool to explain the predominance of some taxa and their functional traits. For future studies, we suggest evaluating the effects of other plant components for the definition of complexities, such as plant biomass combined with other morphological metrics (e.g., leaf area, root length, leaf shape).

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