Received: 24 October 2023 | Revised: 10 May 2024 | Accepted: 11 June 2024

DOI: 10.1111/fwb.14305

ORIGINAL ARTICLE

Freshwater Biology WILEY

Habitat complexity versus habitat heterogeneity: Invertebrates prefer macrophyte stands with intermediate biomass and high functional diversity

Matheus Henrique Ferreira Aleixo[1] | **Luana Caroliny Possamai**[1] | **Karis Soares Pereira de Castro**[1] | **Kátia Yasuko Yofukuji**[2] | **Ana Lúcia Paz Cardozo**[3] | **Rosemara Fugi**[1,4]

[1]Programa de Pós-Graduação Em Ecologia de Ambientes Aquáticos Continentais, Centro de Ciências Biológicas, Universidade Estadual de Maringá (UEM), Maringá, Brazil

[2]Centro de Investigação de Montanha (CIMO), Instituto Politécnico de Bragança, Bragança, Portugal

[3]Grupo de Gestão, Ecologia e Tecnologia Marinha (GTMar), Departamento de Engenharia de Pesca e Ciências Biológicas, Universidade do Estado de Santa Catarina (UDESC), Laguna, Brazil

[4]Núcleo de Pesquisas Em Limnologia, Ictiologia e Aquicultura (NUPÉLIA), Universidade Estadual de Maringá (UEM), Maringá, Brazil

Correspondence
Matheus Henrique Ferreira Aleixo, Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, Centro de Ciências Biológicas, Universidade Estadual de Maringá, Maringá, Brazil.
Email: matheusferreiraaleixo@gmail.com

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 141720/2020-4; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 88881.846239/2023-01, 88887.967152/2024-00 and 8887.968266/2024-00

Abstract

1. Aquatic macrophytes serve as shelter and a direct source of food for invertebrates, in addition to indirectly providing items such as algae, detritus, and microorganisms. Thus, aquatic macrophytes act as habitat structuring elements, requiring a distinction between habitat complexity (physical formations such as fractal dimensions, density and biomass) and habitat heterogeneity (diversity of these structures). Here we explore the effects of habitat complexity and habitat heterogeneity on the invertebrate community.
2. We collected macrophytes and invertebrates from 28 sampling sites along a 13.7-km stretch of the Baía River in Brazil, and examined specific groups (insects, microcrustaceans, and other invertebrates). Environmental variables in the sites were also measured. We aimed to explore the effects of habitat complexity (measured by macrophyte biomass) and habitat heterogeneity (evaluated through macrophyte functional diversity) on the richness and abundance of invertebrates.
3. We found that overall invertebrate richness was positively influenced solely by habitat heterogeneity. For invertebrate abundance, intermediate habitat complexity had more invertebrates, while habitat heterogeneity had a positive impact. Environmental variables influenced only the abundance. For specific groups, insect richness was positively influenced by habitat heterogeneity, while insect abundance decreased with high complexity and increased with high heterogeneity. Microcrustacean abundance was positively influenced by habitat complexity. Richness and abundance of other invertebrates was positively influenced by habitat heterogeneity.
4. Invertebrates prefer macrophyte stands with intermediate complexity and high heterogeneity. Abundance is linked to structural complexity and heterogeneity, while species richness is more strongly associated with heterogeneity. Furthermore, the impact of these factors varies among invertebrate groups.
5. These findings emphasise the importance of integrating a broad range of metrics, such as macrophyte biomass and functional diversity, to gain a thorough

understanding of invertebrate community dynamics in future studies. Additionally, our study demonstrates that preserving macrophyte stands with high heterogeneity significantly enhances the diversity of associated invertebrate species.

KEYWORDS

aquatic ecology, community attributes, habitat structuring, invertebrate–plant relationship, upper Paraná River

1 | INTRODUCTION

Aquatic macrophytes constitute essential components of aquatic and transitional ecosystems (Thomaz & Cunha, 2010), particularly within freshwater environments such as reservoirs, rivers, and floodplains where they colonise across extensive areas (Dias et al., 2017; Dibble & Pelicice, 2010; Yofukuji et al., 2021). Aquatic plants exhibit various structures and life forms (Kovalenko et al., 2012; Thomaz, 2023). In aquatic habitats, macrophyte stands host a high abundance and diversity of invertebrates by providing them shelter or feeding grounds (Thomaz, 2023; Warfe & Barmuta, 2006). Moreover, macrophytes serve as substrates for the development of attached periphytic algae (Osório et al., 2019; Warfe & Barmuta, 2006), bacteria, protozoa (Kurbatova & Yershov, 2020), and detritus (Kurbatova & Yershov, 2020; Warfe et al., 2008), which offer a variety of food resources for invertebrates, including herbivores and detritivores. Consequently, the richness and diversity of invertebrates are strongly influenced by the complexity and heterogeneity of macrophytes (Thomaz, 2023; Yofukuji et al., 2021).

When considering aquatic macrophytes as habitat structuring elements, it is important to distinguish between structural complexity and habitat heterogeneity. Structural complexity can be related to physical formations, encompassing factors such as fractal dimensions, density, and biomass (Tokeshi & Arakaki, 2012). Habitat heterogeneity refers to the diversity of these structures within a given environment (Loke & Chisholm, 2022; Tokeshi & Arakaki, 2012). While the complexity can be measured by abundance/density of plants, habitat heterogeneity is associated with the variety of habitat forms available (August, 1983; Loke & Chisholm, 2022; Tokeshi & Arakaki, 2012). Therefore, macrophyte stands can exhibit high complexity but low heterogeneity, for example, in the case of stands with high biomass of a single macrophyte species, e.g. monospecific stands, resulting in minimal variation in the present structures.

Different metrics can be used to determine the structural complexity and heterogeneity of invertebrate habitats. Most studies assess differences in invertebrate communities in areas with and without macrophytes (Santos et al., 2020; Zingel et al., 2019) or among different species and macrophyte architectures (Meerhoff et al., 2007). Other studies have demonstrated that macrophyte biomass strongly increases both richness and abundance of invertebrates (Aleixo et al., 2022; Choi et al., 2014), and some studies have shown the same influence by macrophyte diversity, a metric that assesses habitat heterogeneity (e.g., McAbendroth et al., 2005; Yofukuji et al., 2021).

Diversity becomes important because invertebrate communities associated with macrophytes exhibit different life forms with distinct requirements (McAbendroth et al., 2005) and can perceive and use their habitat in unique ways (Stahr & Kaemingk, 2017). Therefore, while aquatic macrophytes provide refuge from predators for various invertebrates, they can also function as biological traps (Aleixo et al., 2022), as other fishes seeking refuge in these habitats may feed on these invertebrates (e.g., Aleixo et al., 2022; Cunha et al., 2019; Yofukuji et al., 2021). Studies that use macrophyte diversity as a predictor of habitat heterogeneity generally employ only a taxonomic approach. However, using the functional approach as a measure of habitat heterogeneity for invertebrates can provide new and complementary information. Functional traits, which serve as precursors to functional diversity, are defined as any phenological, physiological, or morphological characteristics that can be quantified (Díaz et al., 1998; Fu et al., 2015; Pérez-Harguindeguy et al., 2016). Each species exhibits a range of measurable characteristics, and, in the context of aquatic macrophytes, life forms, morphology, reproductive traits, and productivity are frequently employed as key functional traits (Lansac-Tôha et al., 2022; Vecchia et al., 2020).

In floodplains, environmental variables can play a crucial role in associated invertebrate communities (Branco et al., 2002; Castilho-Noll et al., 2023; Diniz et al., 2021; Sousa et al., 2017), as well as physical structure, given by macrophyte density (Pierre & Kovalenko, 2014). Thus, the increase in habitat heterogeneity is also a product of the presence and disposition of macrophytes in floodplain areas (Kovalenko et al., 2012; Pierre & Kovalenko, 2014), which constitute more structured, complex, and productive environments (Chambers et al., 2008). In these environments, macrophytes include a diverse group of plants, which have particularities in terms of their complexity and heterogeneity (Kovalenko et al., 2012).

In the Upper Paraná River floodplain, a substantial diversity of aquatic macrophyte stands exists, characterised by varying life forms, morphologies, and reproductive strategies (Lopes et al., 2015; Yofukuji et al., 2021). These macrophyte communities serve as habitats for both aquatic and terrestrial invertebrates, exhibiting differences in their abundance and species richness within each stand (Aleixo et al., 2022; Choi et al., 2014; Yofukuji et al., 2021). Hence, the primary aim of this study was to assess the influence of habitat complexity (assessed herein through macrophyte biomass) and habitat heterogeneity (assessed herein through macrophyte functional diversity) on the richness and abundance of invertebrates.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in the Upper Paraná River floodplain, which is part of the Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná, an environmental protection area located in the last undammed stretch of the river in Brazilian territory. Sampling was conducted on the Baía River (22° 43′23″ S, 53°17′25″ W; Figure 1), a tributary that varies in flow velocity depending on the hydrological cycle and generally maintains a moderate flow (0.11–0.50 m/s) with an average depth of 3.2 m (Lopes et al., 2015). The sampled region features an extensive riverine area, encompassing nearly the entire perimeter of aquatic macrophyte populations, and hosts a rich and diverse collection of macrophyte species with varying morphologies (Lopes et al., 2015; Yofukuji et al., 2021).

2.2 | Sampling

Sampling was conducted in August 2018, during the dry season, and included invertebrates and macrophytes. We sampled 28 multispecific macrophyte stands along a 13.7-km stretch of the Baía River (Figure 1). The selection of stands was based on three criteria: (1) a minimum distance of at least 350 m from the nearest sampled stand to prevent spatial dependency; (2) a suitable depth (≥0.5 m) for sampling; and (3) observable differences in macrophyte complexity (amount of plant matter) and heterogeneity (number of macrophyte species). The assessment of complexity and heterogeneity was conducted visually in the field, and findings were subsequently confirmed in the laboratory.

Macrophyte collection in each stand involved removing all plant material within a 0.5 m × 0.5 m square, starting from the water surface to a depth of 0.5 m to standardise the collected volume, resulting in a total of 28 sample units (stands). The plants were transferred to a plastic container, washed to remove the invertebrates, and then filtered using a hand net with a 160 μm mesh size (for more details, see Campos et al., 2017). The retained invertebrates were preserved in 70% alcohol buffered with sodium tetraborate for later identification and quantification (Campos et al., 2017). After collecting the invertebrates, the macrophytes were identified to determine the complexity and heterogeneity in each stand.

To characterise the environmental conditions in each macrophyte stand, we measured temperature (°C), pH, electrical conductivity (μS/cm), turbidity (NTU), and dissolved oxygen (mg/L; YSI digital meters) in the water subsurface. To assess the impact of abiotic factors on invertebrates throughout a full day, physicochemical measurements were taken at four different time points: (1) 24 hr before; (2) 16 hr before; (3) 8 hr before; and (4) at the moment when macrophytes and invertebrates were sampled (Aleixo et al., 2022; Yofukuji et al., 2021). The data were aggregated to calculate a mean value for each sampled site (Table S1).

2.3 | Habitat complexity and heterogeneity

For each sample, the sum of the biomass of all macrophyte species was employed as a measure of habitat complexity. Consequently, the macrophytes were identified, and all samples were rinsed and subsequently dried for 7 days in an oven at 60°C to achieve a constant dry weight (DW). Macrophyte biomass was expressed as $gDW/0.125\,m^3$,

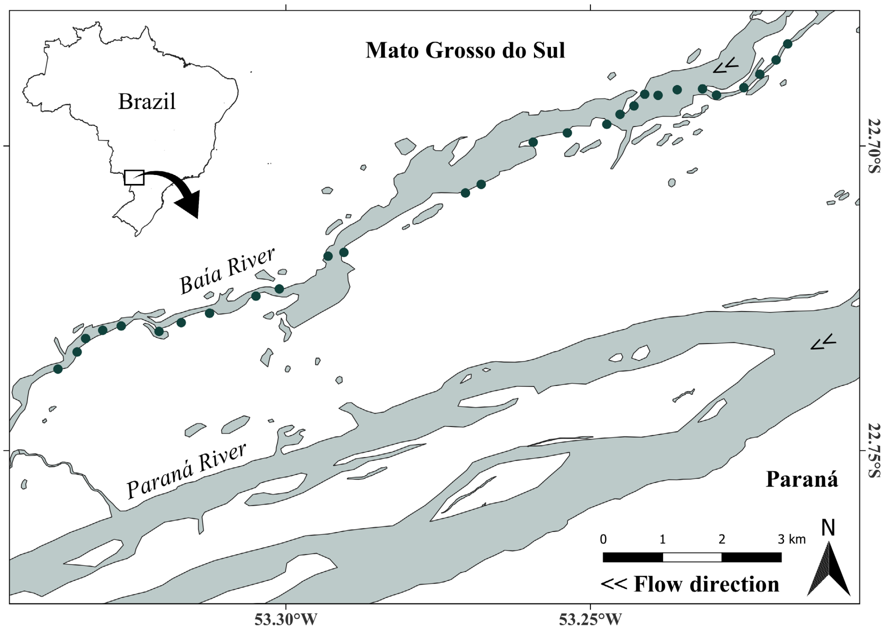


FIGURE 1 Map of the sampling area in the Upper Paraná River floodplain. Points indicate the sampling stations in the Baía River. EPSG: 4618.

TABLE 1 Functional traits used for the classification of morphological and reproductive characteristics of the macrophyte species.

Trait	Type	Category	Trait importance
Life mode	Categorical	Emergent Epiphyte Free floating Rooted floating	Habitat use
Body size	Continuous	Average length (m)	Influence on dispersal ability, secondary productivity, and energy transfer
Leaf type	Categorical	Broadleaved Cylindrical Triangular	Structural complexity
Dispersion	Categorical	Hydrochory Zoochory and hydrochory Autochory and hydrochory	Dispersal ability and invertebrate association
Propagule type	Categorical	Epiphytic Fragment/ Epiphytic Seed/Fragment Seed/ Epiphytic Seed/Rhizome Seed/Stolon Spore/ Epiphytic Spore/Fragment Stolon Stolon/Seedling	Dispersal ability, establishment success, and growth
Seasonality	Categorical	Annual Perennial Semi-perennial	Persistence and resource sharing

given that depth values allow for the estimation of the volume of the water column in which the plants were collected.

For the habitat heterogeneity, we calculated the functional diversity of macrophytes. The functional traits of the collected macrophyte species were characterised following the methodology of Lansac-Tôha et al. (2022), with the addition of the leaf type trait. Categorical and continuous traits (Table 1) related to morphological characteristics (characterised by life mode, body size, and leaf type), as well as reproductive characteristics (evaluated by dispersal mode, propagule unit, and seasonality), were used. All functional data were obtained from the literature (further details in Table S2).

A distance matrix was calculated using the functional traits of species and the Gower distance metric through the *gowdis* function (FD package; Laliberté et al., 2014), which is suitable for mixed data (a matrix with both numerical and categorical data) (Gower, 1966). A cluster analysis was then performed on the distance matrix using the *hclust* function (STATS package; R Core Team, 2023). Subsequently, a tree of functional traits was constructed using the *dendextend* package (Galili, 2015; Figure 2). Subsequently, functional α diversity was calculated using the taxonomic dissimilarity matrix and the results of the cluster analysis through the *alpha* function (BAT package; Cardoso et al., 2015).

2.4 | Richness and abundance of invertebrates

The total invertebrate abundance was quantified as the cumulative count of invertebrates sampled within each study site, employing a stereoscopic microscope for identification. Invertebrates were taxonomically identified using reference keys (Elmoor-Loureiro, 1997; McCafferty, 1983) and expert guidance. The richness of invertebrates was determined by the sum of different taxa identified within each macrophyte stand, as described by Yofukuji et al. (2021). This approach acknowledges that different taxonomic resolutions offer a practical compromise between analytical details and overall biodiversity patterns. By focusing on higher taxonomic categories, the analysis becomes more streamlined while retaining essential information necessary to comprehend broader ecological trends (Oliveira et al., 2020). Thus, the use of higher taxonomic categories is sufficient to capture and represent biodiversity patterns, as demonstrated in studies by Oliveira et al. (2020) and Vilmi et al. (2016). Similarly, the separation between larvae and adults adds another layer of precision to biodiversity assessments, recognising the ecological nuances of these developmental stages (Hershey et al., 2010; Lancaster & Downes, 2018). This separation could be especially valuable in habitats with complex structures,

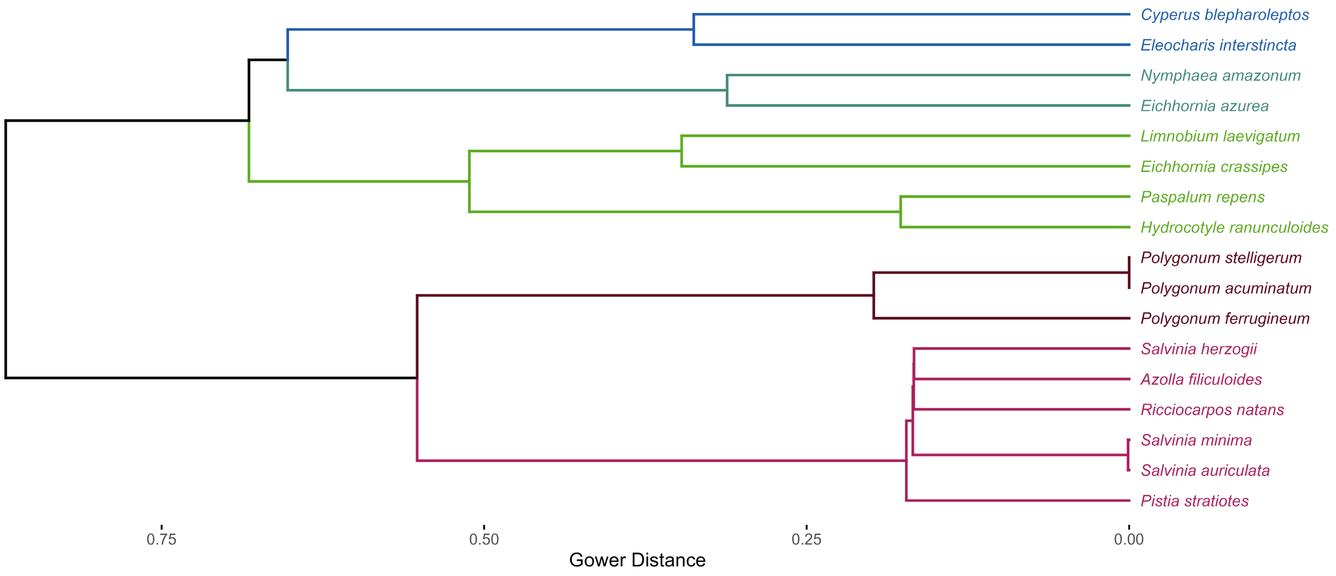
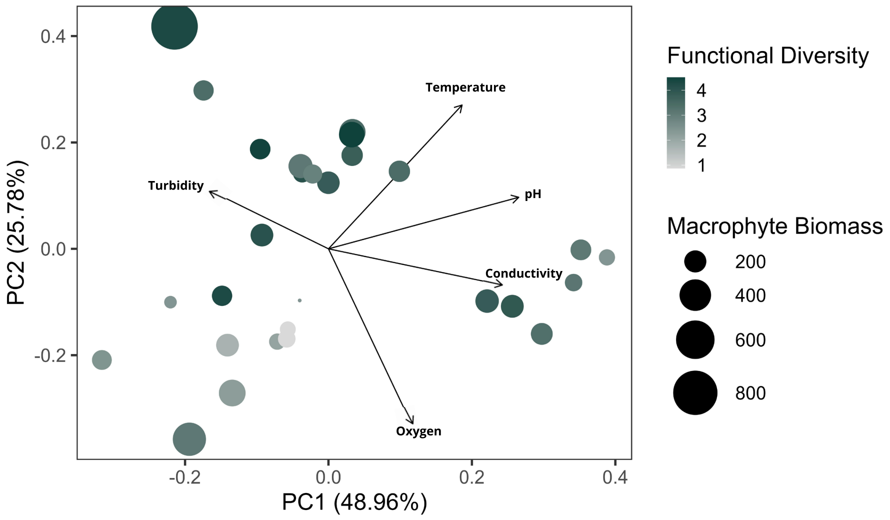


FIGURE 2 Cluster dendrogram based on functional traits using average linkage clustering of 17 macrophyte species based on the Gower's distance matrix calculated on their functional traits.

FIGURE 3 First two axes of the principal component analysis (PCA) ordination diagram summarising the abiotic variables of 28 macrophyte stands.



such as those associated with macrophytes, where distinct environmental niches cater to the unique needs of larvae and adults (Lancaster & Downes, 2018).

2.5 | Statistical analyses

Statistical analyses were performed using the R software (R Core Team, 2023), with the *ggplot2* package used for creating graphs (Wickham, 2016). All assumptions were verified, and *p*-values <0.05 were considered statistically significant.

The matrix of abiotic data, including temperature, pH, conductivity, turbidity, and dissolved oxygen, was summarised using principal component analysis (PCA) with the *PCA* function from the *FactoMineR* package (Lê et al., 2008). The axes with eigenvalues >1 (Kaiser–Guttman criterion; Jackson, 1993) were retained to interpret the ordination of abiotic variables.

We employed generalised mixed models to investigate the impact of habitat complexity and heterogeneity on invertebrate richness and abundance. For both invertebrate richness and abundance, we used macrophyte biomass (representing habitat complexity), macrophyte functional diversity (indicating habitat heterogeneity), and the first and second axes of PCA (capturing abiotic data) as predictors.

We constructed models to address the third question regarding the differential influence of habitat complexity and heterogeneity on distinct invertebrate groups. These models incorporated richness and abundance of distinct invertebrate groups (insects, microcrustaceans, and other invertebrates) as response variables. Explanatory variables included habitat complexity, habitat heterogeneity, and the first and second axes of PCA corresponding to abiotic variables.

For all analyses, log transformation ($\log_{10}[x+1]$) was applied to habitat complexity and heterogeneity. This transformation was implemented due to a substantial difference in complexity values, aiming to mitigate the impact of outliers. During our data exploration, nonlinear relationships were identified for invertebrate abundance and abundance of insects in function of habitat complexity (macrophyte biomass). In such cases, a second-order model was used for the habitat complexity. All models were conducted using the *glm.nb* function from the *MASS* package (Venables & Ripley, 2002) employing the negative binomial family, as it is suitable for log-transformed data.

3 | RESULTS

Among the 28 macrophyte stands, we collected 17 macrophyte species with different functional traits (Table S2). Macrophyte biomass, considered as an explanatory variable of habitat complexity in this study, ranged from 45.77 to 883.29 gDW/0.125 m^3. The functional diversity of macrophytes, used as an explanatory variable of heterogeneity in the study, ranged from 0.88 to 4.51.

Water temperature among the macrophyte stands ranged from 18.3°C to 19.9°C, pH from 6.21 to 7.51, conductivity from 0.017 to 0.060 µS/cm, turbidity from 6.75 to 80.35 NTU, and dissolved oxygen from 4.07 to 9.43 mg/L (details in Table S1). The first and the second axis of the PCA was used to assess the influence of abiotic data on the invertebrate community (eigenvalue PC1 = 2.45, eigenvalue PC2 = 1.29). The first PCA axis was negatively correlated with turbidity and positively correlated with pH, conductivity and temperature (Table S3; Figure 3). The second axis was negatively correlated with dissolved oxygen and positively correlated with temperature (Table S3; Figure 3).

In total, 32,531 invertebrates belonging to 40 different taxa were collected (Table 2 and Table S3). The richness of invertebrates per macrophyte stand varied from 13 to 32, and the abundance ranged from 315 to 3,806 individuals. Among the collected invertebrates, insects had a total richness of 24 (13 larvae, 2 pupae, 1 nymph and 8 adults) and an abundance of 13,169 individuals, microcrustaceans had a richness of 7 and an abundance of 12,532, and other invertebrates had a richness of 9 and an abundance of 6,830.

The overall invertebrate richness was solely influenced by habitat heterogeneity, assessed through the functional diversity of macrophytes, revealing a significant positive relationship (Figure 4 and Table 3). Concerning invertebrate abundance, habitat complexity exhibited a quadratic influence, suggesting that in locations with high macrophyte biomass, there is a reduction in invertebrate abundance. Conversely, habitat heterogeneity exerted a positive influence on abundance. The first principal component of the PCA (PC1) positively influenced invertebrate abundance, suggesting that an increase in pH, conductivity, and temperature, coupled with a decrease in turbidity, is linked to an increase in invertebrate abundance. In contrast, the second principal component of the PCA (PC2) negatively influenced invertebrate abundance, indicating that an increase in dissolved oxygen is associated with an increment in invertebrate abundance.

Insect richness was positively influenced solely by habitat heterogeneity (Figure 5 and Table 4). Conversely, for insect abundance,

TABLE 2 Abundance and frequency (%) of invertebrates across the 28 macrophyte stands along the Baía River in the Upper Paraná River floodplain, Brazil.

Taxon	Abundance	Frequency (%)
Insects		
Chironomidae (L)	6662	100
Ceratopogonidae (L)	3794	92.9
Trichoptera (L)	967	85.7
Coleoptera (A)	317	92.9
Culicidae (L)	316	64.3
Odonata (N)	303	71.4
Ephemeroptera (L)	215	75.0
Diptera (P)	101	85.8
Coleoptera (L)	86	57.1
Plecoptera (L)	82	42.9
Hemiptera (A)	72	53.6
Isoptera (A)	46	28.6
Thysanoptera (A)	45	35.7
Lepidoptera (L)	40	35.7
Sarcophagidae (L)	37	14.3
Chaoboridae (L)	33	17.9
Hymenoptera (A)	22	39.3
Diptera (A)	9	28.6
Simulidae (L)	6	14.3
Orthoptera (A)	5	17.9
Sarcophagidae (P)	5	14.3
Muscidae (L)	4	3.6
Homoptera (A)	1	3.6
Odonata (L)	1	3.6
Microcrustaceans		
Ostracoda	4254	100
Cyclopoida	3460	96.4
Harpacticoida	2399	96.4
Chydoridae	2178	89.3
Daphiniidae	180	71.4
Bosminidae	36	10.7
Calanoida	25	14.3
Other invertebrates		
Amphipoda	4786	85.7
Oligochaeta	1121	64.3
Acarina	333	82.1
Collembola	187	85.7
Bivalvia	185	75.0
Gastropoda	94	64.3
Araneae	77	75.0
Hirudinea	46	42.9
Nematoda	1	3.6

Abbreviations: A, adult; L, larvae; N, nymph; P, pupa.

high levels of complexity (i.e., high macrophyte biomass) had a negative impact (Figure 5, Table 4). Habitat heterogeneity had a positive influence on insect abundance (Figure 5 and Table 4). Additionally, insect abundance was negatively influenced by PC1 (Figure 5 and Table 4), indicating that an increase in dissolved oxygen leads to a decrease in insect abundance.

For microcrustaceans, no variable exhibited an influence on richness (Figure 5 and Table 4). However, habitat complexity and PC1 demonstrated a positive linear influence on microcrustacean abundance (Figure 5 and Table 4), indicating that an increase in macrophyte biomass, pH, conductivity, and temperature, coupled with a decrease in turbidity, results in an increase in microcrustacean abundance.

In contrast, for other invertebrates, habitat heterogeneity had a significantly positive impact on both the richness and abundance of the group (Figure 5 and Table 4) Furthermore, PC1 (i.e., pH, conductivity, and temperature) demonstrated a positive linear influence on the abundance of other invertebrates (Figure 5 and Table 4).

4 | DISCUSSION

4.1 | The influence of habitat complexity and heterogeneity on invertebrate community

Invertebrate richness was not influenced by habitat complexity, indicating that invertebrate richness may be more associated with heterogeneity than just physical complexity (Yofukuji et al., 2021). Invertebrate abundance was higher in stands with intermediate habitat complexity and declined in stands with higher biomass. These results were expected, as an increase in habitat complexity benefits several invertebrates by providing a larger physical structure that can be used as a refuge from predators (Meerhoff et al., 2007; Thomaz, 2023; Thomaz & Cunha, 2010), as well as by increasing various food resources such as periphytic algae, detritus, bacteria, and protozoa (Kurbatova & Yershov, 2020; Osório et al., 2019; Warfe et al., 2008; Warfe & Barmuta, 2006). Thus, these invertebrates use macrophytes as both a feeding site and a refuge for predators

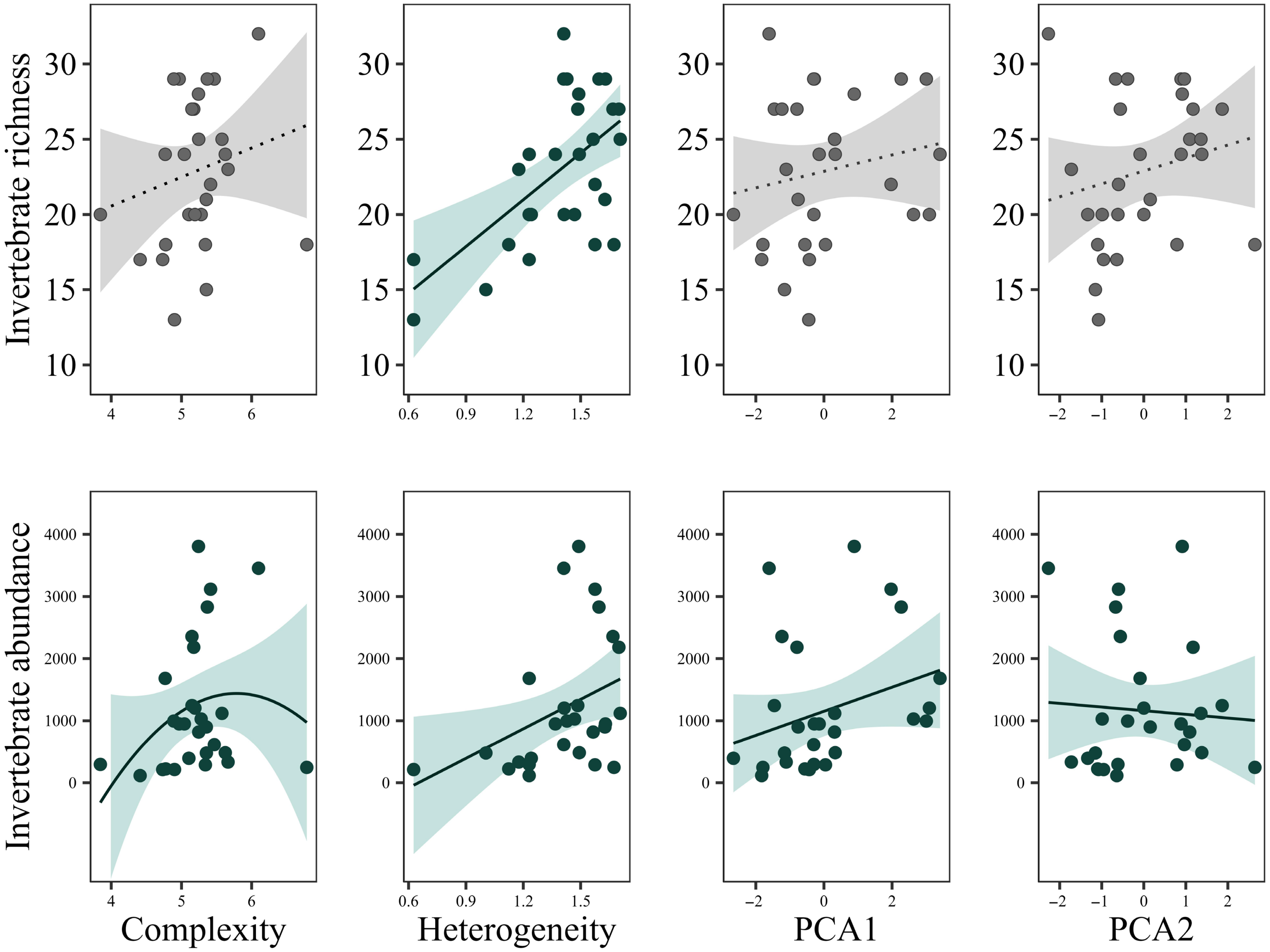


FIGURE 4 Invertebrate richness and abundance as a function of habitat complexity, habitat heterogeneity, and abiotic variables summarised in a principal component analysis (PC1 = negatively correlated with turbidity and positively correlated with pH, conductivity, and temperature. PC2 = negatively correlated with dissolved oxygen and positively correlated with temperature). Coloured graphs with filled lines represent the significance of the data in the model and grey graphs with dotted lines non-significance.

TABLE 3 Results of mixed effects regression models of invertebrate richness and abundance as a function of habitat complexity (assessed through macrophyte biomass), habitat heterogeneity (assessed through functional diversity) and abiotic characteristics (summarised with the first two axes of a principal component [PC] analysis).

Richness					**Abundance**				
	Estimate	***SE***	***z*-Value**	***p*-Value**		**Estimate**	***SE***	***z*-Value**	***p*-Value**
Intercept	2.383	0.45	5.33	**<0.001**	Intercept	3.706	0.758	4.89	**<0.001**
Complexity	−0.012	0.09	−0.14	0.889	Complexity[a]	0.590	0.691	0.85	0.393
Heterogeneity	0.578	0.20	2.88	**0.004**	Complexity[b]	−1.342	0.641	−2.09	**0.036**
PC1	0.011	0.03	0.43	0.666	Heterogeneity	2.252	0.541	4.16	**<0.001**
PC2	−0.032	0.04	−0.80	0.424	PC1	0.155	0.077	2.00	**0.045**
					PC2	−0.244	0.120	−2.03	**0.043**

Note: *p*-values <0.05 are in bold. PC1 = negatively correlated with turbidity and positively correlated with pH, conductivity and temperature. PC2 = negatively correlated with dissolved oxygen and positively correlated with temperature. Superscript numbers represent a quadratic relationship of the variable.

[a] On the ascending phase.

[b] On the descending phase of the quadratic curve.

in these stands (Santos et al., 2020; Thomaz, 2023; Thomaz & Cunha, 2010). In the case of higher complexity, there is a potential for hypoxia, as areas with excessive biomass may lead to oxygen consumption by plants through cellular respiration exceeding production, impacting sensitive invertebrates (Bunch et al., 2010; Caraco & Cole, 2002). Additionally, for some larger animals, such as certain terrestrial invertebrates, access may be impaired by physical barriers (Cunha et al., 2019; Thomaz & Cunha, 2010). Our results demonstrated a clear trend, as the stand with the highest complexity also exhibited reduced dissolved oxygen levels and elevated turbidity.

Our study revealed a positive relationship between the habitat heterogeneity and the richness and abundance of invertebrates. This can be explained by the functional traits of macrophytes in present study. In terms of morphological traits, free-floating macrophytes, such as *Azolla filiculoides* Lam. and *Eichhornia crassipes* (Mart.) Solms, create an aerial surface that can facilitate the colonisation of allochthonous invertebrates, such as Coleoptera, Orthoptera, Thysanoptera, Hymenoptera, and Collembola. Species with a large complex submerged area, such as rooted-floating plants (e.g. *Eichhornia azurea* [Swartz] Kunth and *Paspalum repens* P. J. Bergius) and emergent macrophytes (e.g. *Eleocharis interstincta* [Vahl] Roem. & Schult. and *Polygonum* species), offer refuge and food for various aquatic invertebrates, including microcrustaceans, amphipods, and insect larvae. Consequently, stands with greater heterogeneity provide diverse structures that can be colonised by different groups of invertebrates.

Moreover, the variation in the life form of each type of macrophyte substantially influences the richness and abundance of periphytic algae (Osório et al., 2019; Warfe & Barmuta, 2006), which serves as food for many invertebrates. Therefore, habitat heterogeneity influences the invertebrate community. Additionally, Hansen et al. (2011) observed that some invertebrates exhibit colonisation preferences for specific plants, indicating that stands with a greater heterogeneity can support various invertebrate taxa.

4.2 | Responses of invertebrate groups to habitat complexity and heterogeneity

For insects, we observed greater abundance in stands of intermediate macrophyte biomass (i.e., habitat complexity). Conversely, habitat heterogeneity exhibited a positive linear influence, leading to higher values of richness and abundance of insects in more diverse stands. Our study encompassed a variety of terrestrial, aquatic, and semi-aquatic insects, which may differ in size, life stage, and resource use patterns (Lancaster & Downes, 2018).

Macrophyte biomass has a direct impact on the insect's community by increasing refuges and food resources, thereby enhancing habitat complexity. However, it also results in inaccessibility for larger animals in cases of extreme complexity (Kurbatova & Yershov, 2020; Osório et al., 2019; Warfe et al., 2008; Warfe & Barmuta, 2006), which explains a greater abundance of insects in intermediate habitat complexities. Regarding the interplay between insects and habitat heterogeneity, these organisms leverage aquatic macrophytes for various purposes, encompassing direct or indirect oviposition, protection, and feeding (Lancaster & Downes, 2018). Consequently, the differences in heterogeneity among macrophyte stands can influence the community structure in various ways: (1) several terrestrial and aquatic insects lay their eggs on specific macrophyte species, which can harbour insect larvae differently based on the structures of the plants (Webster & Cardé, 2017); (2) about 20% of aquatic insects feed exclusively on aquatic macrophytes, and the palatability of these plants can influence their feeding patterns (Lancaster & Downes, 2018; Newman, 1991); (3) insects that indirectly use macrophytes as a feeding site are of influenced by the structure of the plants. Those with more floating structures tend to offer better conditions for terrestrial insects (Fontanarrosa et al., 2013; Gallardo et al., 2017), while macrophytes with more submerged structures provide better conditions for aquatic insects (Behrend et al., 2013; Silva & Henry, 2018); and (4) due to the metamorphosis process, some insects are considered slower

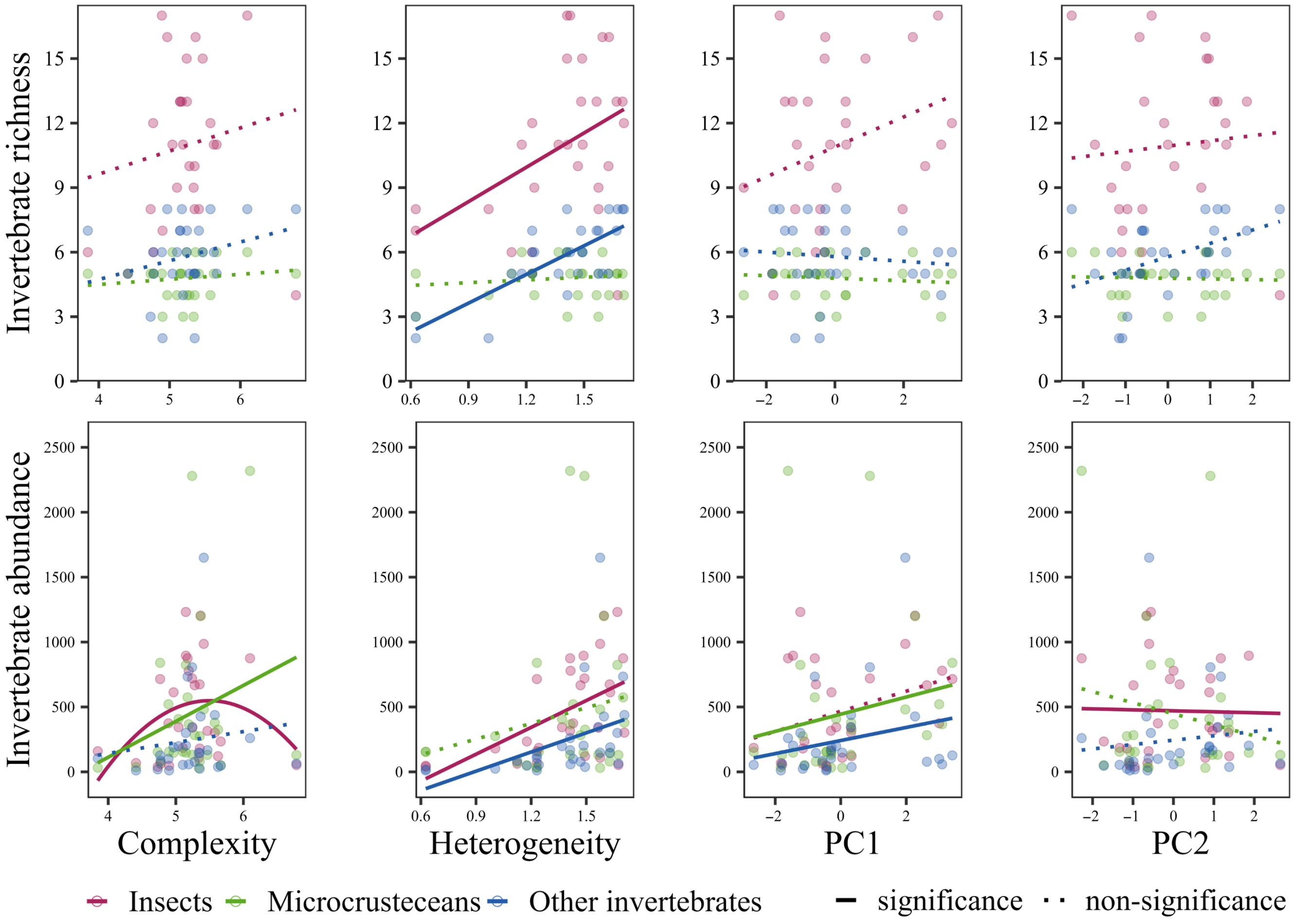


FIGURE 5 Richness and abundance of insects, microcrustaceans and other invertebrates, collected in 28 macrophyte stands, as a function of habitat complexity, habitat heterogeneity, and abiotic variables summarised in a principal component analysis (PC1 = negatively correlated with turbidity and positively correlated with pH, conductivity, and temperature. PC2 = negatively correlated with dissolved oxygen and positively correlated with temperature). Filled lines represent the significance of the data in the model and dotted lines non-significance.

colonisers (Lancaster & Downes, 2018), and as a result, the seasonality of macrophytes influences the colonisation of these insects (Hargeby, 1990).

Microcrustacean richness remained unaffected by either habitat complexity or heterogeneity. However, habitat complexity positively influenced the abundance of microcrustaceans. The importance of macrophytes in microcrustacean community has been extensively documented in the literature (e.g., Santos et al., 2020; Strzałek & Koperski, 2019; Warfe & Barmuta, 2006). In contrast to insects, microcrustaceans are much smaller invertebrates (Castilho-Noll et al., 2023; Horne et al., 2002), allowing microcrustaceans to seek refuge in various microhabitats. Consequently, extreme biomass may not provide a physical barrier for these invertebrates. Additionally, some species of microcrustaceans do not swim and are typically found in macrophytes stands (Higuti et al., 2017; Santos et al., 2020; Strzałek & Koperski, 2019; Warfe & Barmuta, 2006), primarily in macrophytes characterised by a complex root system (Matsuda et al., 2015).

Our study showed no influence of habitat complexity on other invertebrates but showed a linear positive influence of the heterogeneity on the richness and abundance of other invertebrates. Thus, not only for insects but also for other invertebrates, such as Oligochaeta and Aranae, unique characteristics of each plant such as architecture, way of life, and associated microorganisms and detritus, can influence the abundance and composition of invertebrate species present in each stand (Behrend et al., 2013; Raizer & Amaral, 2001). This variation in colonisation may explain why the habitat heterogeneity influenced the abundance of other invertebrates in our study.

4.3 | Influence of environmental variables on invertebrates associated with macrophytes

Our study showed that the availability of dissolved oxygen in water and temperature are crucial factors influencing the abundance of invertebrates, especially insects. Water temperature is closely linked to levels of dissolved oxygen, and an increase in temperature can compromise the water's capacity to retain oxygen (Lopez et al., 2019). Numerous studies emphasise the significance of daily thermal patterns in the lives of aquatic insects. This fluctuation in water temperature is a predominant abiotic factor, particularly impacting aquatic eggs and larvae (Lopez et al., 2019; Mondal

TABLE 4 Results of mixed effects regression models of invertebrate richness and abundance, divided by groups, as a function of habitat complexity (assessed through macrophyte biomass), habitat heterogeneity (assessed through functional diversity) and abiotic characteristics (summarised with the first two axes of a principal component [PC] analysis).

Richness of insects					**Abundance of insects**				
	Estimate	***SE***	***z*-Value**	***p*-Value**		**Estimate**	***SE***	***z*-Value**	***p*-Value**
Intercept	1.366	0.66	2.08	**0.038**	Intercept	1.627	0.72	2.25	**0.024**
Complexity	0.030	0.13	0.23	0.816	Complexity[a]	−0.667	0.65	−1.02	0.308
Heterogeneity	0.613	0.29	2.09	**0.037**	Complexity[b]	−1.708	0.61	−2.81	**0.005**
PC1	0.050	0.04	1.39	0.166	Heterogeneity	3.073	0.52	5.96	**<0.001**
PC2	−0.054	0.59	−0.93	0.353	PC1	0.100	0.07	1.38	0.168
					PC2	−0.270	0.11	−2.37	**0.018**
Richness of microcrustaceans					**Abundance of microcrustaceans**				
	Estimate	***SE***	***z*-Value**	***p*-Value**		**Estimate**	***SE***	***z*-Value**	***p*-Value**
Intercept	1.214	0.09	1.28	0.201	Intercept	−0.681	1.85	−0.37	0.714
Complexity	0.029	0.19	0.15	0.879	Complexity	0.972	0.37	2.63	**0.009**
Heterogeneity	0.146	0.41	0.36	0.721	Heterogeneity	1.077	0.78	1.37	0.170
PC1	−0.014	0.06	−0.25	0.800	PC1	0.290	0.11	2.67	**0.008**
PC2	−0.029	0.09	−0.33	0.743	PC2	−0.249	0.17	−1.44	0.151
Richness of other invertebrates					**Abundance of other invertebrates**				
	Estimate	***SE***	***z*-Value**	***p*-Value**		**Estimate**	***SE***	***z*-Value**	***p*-Value**
Intercept	0.705	0.90	0.78	0.434	Intercept	0.594	1.58	0.38	0.708
Complexity	−0.071	0.17	−0.42	0.675	Complexity	−0.111	0.31	−0.35	0.723
Heterogeneity	1.006	0.42	2.38	**0.017**	Heterogeneity	3.668	0.69	5.34	**<0.001**
PC1	−0.041	0.05	−0.79	0.432	PC1	0.185	0.09	2.01	**0.045**
PC2	−0.007	0.08	−0.08	0.935	PC2	−0.116	0.14	−0.79	0.4297

Note: *p*-values <0.05 are in bold. PC1 = negatively correlated with turbidity and positively correlated with pH, conductivity and temperature. PC2 = negatively correlated with dissolved oxygen and positively correlated with temperature. Superscript numbers represent a quadratic relationship of the variable.

[a] On the ascending phase.

[b] On the descending phase of the quadratic curve.

et al., 2017). Water temperature significantly influences the larval development and growth of certain insects, such as Ephemeroptera and Odonata, which exhibit increases at higher temperatures (Mendonça et al., 2018; Ross-Gillespie et al., 2018). Similarly, the availability of oxygen directly affects the metabolism of aquatic insects. Adequate oxygen levels are essential for sustaining vital activities such as feeding, reproduction, and movement (Lopez et al., 2019). In a laboratory bioassay, Mondal et al. (2017) suggest that the rate of insect prey consumption is positively correlated with an increase in temperature. These findings underscore the complex interplay between temperature, oxygen, and aquatic insects, highlighting the critical importance of these factors in the ecology of these organisms in aquatic environments.

The abundance of microcrustaceans and other invertebrates exhibited a negative correlation with turbidity and a positive correlation with pH, conductivity, and temperature. Abiotic factors, such as pH, temperature, and turbidity, play pivotal roles in shaping the communities of diverse microcrustaceans, rendering them valuable bioindicators of environmental quality (Branco et al., 2002; Castilho-Noll et al., 2023; Diniz et al., 2021; Sousa et al., 2017). Due to the short life cycle of microcrustaceans (ranging from 16 to 28 days), in less than a month their entire population can be impacted by changing environmental variables (Castilho-Noll et al., 2023; Melão & Rocha, 2004; Moreira et al., 2016). Furthermore, the longevity of the populations is highly linked to environmental conditions, such as temperature (Melão & Rocha, 2004). Environmental variables such as pH, conductivity, and turbidity can alter the richness and abundance of microcrustaceans in distinct ways, depending on the species (Castilho-Noll et al., 2023).

4.4 | The importance of combining habitat complexity with habitat heterogeneity metrics

Aquatic macrophytes play a valuable role in structuring various communities (Hansen et al., 2011; Kovalenko et al., 2012; Thomaz & Cunha, 2010; Yofukuji et al., 2021). Although quantifying habitat complexity remains a challenge, the most used components for characterisation include plant density and the diversity of physical structures (Thomaz, 2023; Tokeshi & Arakaki, 2012). In our study, we observed that a combination of different metrics can elucidate the patterns of communities in distinct macrophyte stands. Studies using macrophyte biomass as a metric can capture physical characteristics that serve as barriers, protection, and feeding sites for aquatic invertebrates (Aleixo et al., 2022; Butakka et al., 2016; McAbendroth et al., 2005), but this metric alone may be insufficient for understanding the specificities of each invertebrate group.

The use of macrophyte functional diversity as a metric for habitat heterogeneity, when combined with macrophyte biomass, provides a more comprehensive understanding of the richness and abundance of invertebrate groups. Functional traits related to morphological characteristics, such as life mode, can influence the colonisation of various invertebrates depending on whether they have more floating or submerged parts (Campos et al., 2021; Choi et al., 2014; Fontanarrosa et al., 2013; Gallardo et al., 2017). Additionally, functional traits related to reproductive characteristics, including seasonality and dispersion of each macrophyte species, impact invertebrate composition. Plants with seasonality may limit the establishment of dense invertebrate populations, particularly for slower colonisers, whereas perennial plants do not impose such limitations (Hargeby, 1990).

4.5 | The importance of aquatic macrophytes for the conservation of associated invertebrates

Species invasion represent a significant factor contributing to global-scale biodiversity decline (Simberloff, 2009), often resulting in substantial impacts on ecosystem services, ecological dynamics, and economic burdens (Havel et al., 2005; Simberloff, 2009). In the case of aquatic macrophytes, the introduction of species can lead to the death of native species, resulting in an excessive biomass of the invasive species (Schultz & Dibble, 2012; Vecchia et al., 2020). This introduction can be detrimental to invertebrates due to increased habitat complexity, hypoxia, allelopathic chemicals, facilitation of other exotic species, and reduced food quality (Schultz & Dibble, 2012).

Our study highlights the importance of greater diversity in morphological and reproductive traits among macrophytes within an ecosystem to enhance the overall richness and abundance of invertebrates. Thus, our results underscore the critical need to preserve the diversity of plants with different functional traits, which may be impacted by the introduction of other species.

5 | CONCLUSION

In general, invertebrates prefer macrophyte stands with intermediate complexity and high heterogeneity. Invertebrate abundance is linked to structural complexity (evaluated through biomass) and heterogeneity (provided by plant functional diversity). Invertebrate richness shows a stronger connection to heterogeneity. The impact of habitat complexity and heterogeneity on invertebrate groups varies; insects respond to both metrics, microcrustaceans primarily to complexity, and other invertebrates solely to heterogeneity. These findings highlight the importance of using a combination of metrics, such as biomass and functional diversity to comprehensively assess invertebrate community dynamics. Additionally, they demonstrate that conserving more heterogeneous macrophyte stands ensures a greater diversity of associated invertebrate species.

AUTHOR CONTRIBUTIONS

Conceptualisation: M.H.F.A. and R.F. Developing methods: M.H.F.A. and R.F. Conducting the research: M.H.F.A., L.C.P., K.S.P.d.C., K.Y.Y., A.L.P.C., and R.F. Data analysis: M.H.F.A. Data interpretation: M.H.F.A., L.C.P., K.S.P.d.C., K.Y.Y., A.L.P.C., and R.F. Preparation of figures and tables: M.H.F.A., L.C.P., and R.F. Writing: M.H.F.A., L.C.P., K.S.P.d.C., K.Y.Y., A.L.P.C., and R.F.

ACKNOWLEDGEMENTS

The authors would like to express their gratitude to S.M. Thomaz, M.S. Dainez-Filho, and T. Deruza-Garcia for their assistance in data collection. Furthermore, we would like to thank F.M. Lansac-Tôha and J. Rosa for their valuable input, reading, and suggestions on the initial version of the manuscript. Our appreciation also goes to the Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais (PEA-UEM), the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for their financial support and infrastructure provided for the execution of this study.

FUNDING INFORMATION

Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant no: 141720/2020-4); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; grant nos: 88881.846239/2023-01, 88887.967152/2024-00, 8887.968266/2024-00).

CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

ETHICS STATEMENT

The survey was approved by the Animal Use Ethics Committee of the State University of Maringá (CEUA/UEM) under protocol number 5980040618.

ORCID

Matheus Henrique Ferreira Aleixo https://orcid.org/0000-0001-5329-0548
Luana Caroliny Possamai https://orcid.org/0009-0007-4097-1425
Karis Soares Pereira de Castro https://orcid.org/0009-0009-6335-6497

Kátia Yasuko Yofukuji https://orcid.org/0000-0002-0889-7524
Ana Lúcia Paz Cardozo https://orcid.org/0000-0002-6543-7946
Rosemara Fugi https://orcid.org/0000-0002-7230-0817

REFERENCES

Aleixo, M. H. F., Quirino, B. A., Yofukuji, K. Y., Cardozo, A. L. P., & Fugi, R. (2022). Macrophyte biomass mediates trophic relationships between congeneric fishes and invertebrate communities. *Limnologica*, *93*, 125957. https://doi.org/10.1016/j.limno.2022.125957

August, P. V. (1983). The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology*, *64*, 1495–1507. https://doi.org/10.2307/1937504

Behrend, R. D. L., Teixeira, M. C., Fernandes, S. E. P., Camargo, J. C., Rosin, G. C., & Takeda, A. M. (2013). Effects of a native and a non-native macrophyte species of Hydrocharitaceae on Chironomidae and Oligochaeta assemblages structure. *Acta Scientiarum – Biological Sciences*, *35*, 351–358. https://doi.org/10.4025/actascibiolsci.v35i3.10855

Branco, C. W. C., Rocha, M. I. A., Pinto, G. F. S., Gômara, G. A., & Filippo, R. (2002). Limnological features of Funil reservoir (RJ, Brazil) and indicator properties of rotifers and cladocerans of the zooplankton community. *Lakes & Reservoirs: Research and Management*, *7*, 87–92. https://doi.org/10.1046/j.1440-169X.2002.00177.x

Bunch, A. J., Allen, M. S., & Gwinn, D. C. (2010). Spatial and temporal hypoxia dynamics in dense emergent macrophytes in a Florida lake. *Wetlands*, *30*, 429–435. https://doi.org/10.1007/s13157-010-0051-9

Butakka, C. M. M., Ragonha, F. H., Train, S., Pinha, G. D., & Takeda, A. M. (2016). Chironomidae feeding habits in different habitats from a Neotropical floodplain: Exploring patterns in aquatic food webs. *Brazilian Journal of Biology*, *76*, 117–125. https://doi.org/10.1590/1519-6984.14614

Campos, R., Conceição, E. O., Pinto, M. B. O., Bertoncin, A. P., Dos, S., Higuti, J., & Martens, K. (2017). Evaluation of quantitative sampling methods in pleuston: An example from ostracod communities. *Limnologica*, *63*, 36–41. https://doi.org/10.1016/j.limno.2017.01.002

Campos, R., Rosa, J., Ferreira, V. G., Conceição, E. O., Martens, K., & Higuti, J. (2021). Macrophyte life forms influence the effects of environmental and spatial factors on the beta-diversity of associated ostracod communities (Crustacea). *Aquatic Sciences*, *83*, 27. https://doi.org/10.1007/s00027-021-00777-9

Caraco, N. F., & Cole, J. J. (2002). Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecological Applications*, *12*, 1496–1509. https://doi.org/10.1890/1051-0761(2002)012[1496:CIOANA]2.0.CO;2

Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT – biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, *6*, 232–236. https://doi.org/10.1111/2041-210X.12310

Castilho-Noll, M. S. M., Perbiche-Neves, G., Santos, N. G., Schwind, L. T. F., Lansac-Tôha, F. M., Silva, A. C. S., Meira, B. R., Joko, C. Y., Morais-Júnior, C. S., Silva, E. E., Eskinazi-Sant, E. M., & Simões, R. R. (2023). A review of 121 years of studies on the freshwater zooplankton of Brazil. *Limnologica*, *100*, 1–10. https://doi.org/10.1016/j.limno.2023.126057

Chambers, P. A., Lacoul, P., Murphy, K. J., & Thomaz, S. M. (2008). Global diversity of aquatic macrophytes in freshwater. *Hydrobiologia*, *595*, 9–26. https://doi.org/10.1007/s10750-007-9154-6

Choi, J., Jeong, K. S., Kim, S. K., La, G. H., Chang, K. H., & Joo, G. J. (2014). Role of macrophytes as microhabitats for zooplankton community in lentic freshwater ecosystems of South Korea. *Ecological Informatics*, *24*, 177–185. https://doi.org/10.1016/j.ecoinf.2014.09.002

Cunha, E. R., Winemiller, K. O., Silva, J. C. B., Lopes, T. M., Gomes, L. C., Thomaz, S. M., & Agostinho, A. A. (2019). α and β diversity of fishes in relation to a gradient of habitat structural complexity supports the role of environmental filtering in community assembly. *Aquatic Sciences*, *81*, 38. https://doi.org/10.1007/s00027-019-0634-3

Dias, R. M., Ortega, J. C. G., Gomes, L. C., & Agostinho, A. A. (2017). Trophic relationships in fish assemblages of Neotropical floodplain lakes: Selectivity and feeding overlap mediated by food availability. *Iheringia. Série Zoologia*, *107*, 1–11. https://doi.org/10.1590/1678-4766e2017035

Díaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, *9*, 113–122. https://doi.org/10.2307/3237229

Dibble, E. D., & Pelicice, F. M. (2010). Influence of aquatic plant-specific habitat on an assemblage of small neotropical floodplain fishes. *Ecology of Freshwater Fish*, *19*, 381–389. https://doi.org/10.1111/j.1600-0633.2010.00420.x

Diniz, L. P., Braghin, L. S. M., Pinheiro, T. S. A., Melo, P. A. M. C., Bonecker, C. C., & Melo, J. M. (2021). Environmental filter drives the taxonomic and functional β-diversity of zooplankton in tropical shallow lakes. *Hydrobiologia*, *848*, 1881–1895. https://doi.org/10.1007/s10750-021-04562-5

Elmoor-Loureiro, M. L. A. (1997). *Manual de identificação de cladóceros límnicos do Brasil*. Editora Universo.

Fontanarrosa, M. S., Chaparro, G. N., & O'Farrell, I. (2013). Temporal and spatial patterns of macroinvertebrates associated with small and medium-sized free-floating plants. *Wetlands*, *33*, 47–63. https://doi.org/10.1007/s13157-012-0351-3

Fu, H., Zhong, J., Yuan, G., Guo, C., Lou, Q., Zhang, W., Xu, J., Ni, L., Xie, P., & Cao, T. E. (2015). Predicting changes in macrophyte community structure from functional traits in a freshwater lake: A test of maximum entropy model. *PLoS One*, *10*, e0131630. https://doi.org/10.1371/journal.pone.0131630

Galili, T. (2015). Dendextend: An R package for visualizing, adjusting and comparing trees of hierarchical clustering. *Bioinformatics*, *31*, 3718–3720. https://doi.org/10.1093/bioinformatics/btv428

Gallardo, L. I., Carnevali, R. P., Porcel, E. A., & Poi, A. S. G. (2017). Does the effect of aquatic plant types on invertebrate assemblages change across seasons in a subtropical wetland? *Limnetica*, *36*, 87–98. https://doi.org/10.23818/limn.36.07

Gower, J. C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, *53*, 325–338. https://doi.org/10.2307/2333639

Hansen, J. P., Wikström, S. A., Axemar, H., & Kautsky, L. (2011). Distribution differences and active habitat choices of invertebrates between macrophytes of different morphological complexity. *Aquatic Ecology*, *45*, 11–22. https://doi.org/10.1007/s10452-010-9319-7

Hargeby, A. (1990). Macrophyte associated invertebrates and the effect of habitat permanence. *Oikos*, *57*, 338–346. https://doi.org/10.2307/3565963

Havel, J. E., Lee, C. E., & Vander Zanden, M. J. (2005). Do reservoirs facilitate invasions into landscapes? *Biological Sciences*, *55*, 518–525.

Hershey, A. E., Lamberti, G. A., Chaloner, D. T., & Northington, R. M. (2010). Chapter 17 – Aquatic insect ecology. In J. H. Thorp (Ed.), *Ecology and classification of North American freshwater invertebrates* (pp. 659–694). Academic Press.

Higuti, J., Campos, R., & Martens, K. (2017). Periphytic community structure of Ostracoda (Crustacea) in the river-floodplain system of the upper Paraná River. *Acta Limnologica Brasiliensia*, *29*, e120. https://doi.org/10.1590/S2179-975X12217

Horne, D. J., Cohen, A., & Martens, K. (2002). Taxonomy, morphology and biology of quaternary and living Ostracoda. *Geophysical Monograph Series*, *131*, 36.

Jackson, D. A. (1993). Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. *Ecology*, *74*, 2204–2214. https://doi.org/10.2307/1939574

Kovalenko, K. E., Thomaz, S. M., & Warfe, D. M. (2012). Habitat complexity: Approaches and future directions. *Hydrobiologia*, *685*, 1–17. https://doi.org/10.1007/s10750-011-0974-z

Kurbatova, S. A., & Yershov, I. Y. (2020). The importance of aquatic plants in maintaining zooplankton diversity and abundance: An experimental approach. *Regulatory Mechanisms in Biosystems*, *11*, 531–535. https://doi.org/10.15421/022081

Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. *R Package version 1.0-12.3*, 1–29.

Lancaster, J., & Downes, B. J. (2018). Aquatic versus terrestrial insects: Real or presumed differences in population dynamics? *Insects*, *9*, 157. https://doi.org/10.3390/insects9040157

Lansac-Tôha, F. M., Heino, J., Bini, L. M., Peláez, O., Baumgartner, M. T., Quirino, B. A., & Machado-Velho, L. F. (2022). Cross-taxon congruence of taxonomic and functional beta-diversity facets across spatial and temporal scales. *Frontiers in Environmental Science*, *10*, 1–12. https://doi.org/10.3389/fenvs.2022.903074

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software*, *25*, 1–18. https://doi.org/10.18637/jss.v025.i01

Loke, L. H. L., & Chisholm, R. A. (2022). Measuring habitat complexity and spatial heterogeneity in ecology. *Ecology Letters*, *25*, 2269–2288. https://doi.org/10.1111/ele.14084

Lopes, T. M., Cunha, E. R., Silva, J. C. B., Behrend, R. D., & Gomes, L. C. (2015). Dense macrophytes influence the horizontal distribution of fish in floodplain lakes. *Environmental Biology of Fishes*, *98*, 1741–1755. https://doi.org/10.1007/s10641-015-0394-4

Lopez, V. M., Tonetto, A. F., Leite, R. C., & Guillermo, R. (2019). Effects of abiotic factors and ecogeographic patterns on the ecology, distribution, and behavior of aquatic insects. In K. Del-Claro & R. Guillermo (Eds.), *Aquatic insects*. Springer. https://doi.org/10.1007/978-3-030-16327-3_4

Matsuda, J. T., Lansac-Tôha, F. A., Martens, K., Velho, L. F. M., Mormul, R. P., & Higuti, J. (2015). Association of body size and behavior of freshwater ostracods (Crustacea, Ostracoda) with aquatic macrophytes. *Aquatic Ecology*, *49*, 321–331. https://doi.org/10.1007/s10452-015-9527-2

McAbendroth, L., Ramsay, P. M., Foggo, A., Rundle, S. D., & Bilton, D. T. (2005). Does macrophyte fractal complexity drive invertebrate diversity, biomass and body size distributions? *Oikos*, *111*, 279–290. https://doi.org/10.1111/j.0030-1299.2005.13804.x

McCafferty, W. P. (1983). *Aquatic entomology: The fishermen's and ecologists' illustrated guide to insects and their relative*. Jones and Bartlett Learning Publishers.

Meerhoff, M., Iglesias, C., Mello, F. T., Clemente, J. M., Jensen, E., Lauridsen, T. L., & Jeppesen, E. (2007). Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biology*, *52*, 1009–1021. https://doi.org/10.1111/j.1365-2427.2007.01748.x

Melão, M. G. G., & Rocha, O. (2004). Life history, biomass and production of two planktonic cyclopoid copepods in a shallow subtropical reservoir. *Journal of Plankton Research*, *26*, 909–923. https://doi.org/10.1093/plankt/fbh080

Mendonça, F. Z., Bernardy, J. V., Oliveira, C. E. K., Oliveira, P. B. G., & De Marco, P. (2018). Temperature effect on the development of tropical dragonfly eggs. *Neotropical Entomology*, *47*, 484–491. https://doi.org/10.1007/s13744-017-0546-7

Mondal, R. P., Chandra, G., Bandyopadhyay, S., & Ghosh, A. (2017). Effect of temperature and search area on the functional response of *Anisops sardea* (Hemiptera: Notonectidae) against *Anopheles stephensi* in laboratory bioassay. *Acta Tropica*, *166*, 262–267. https://doi.org/10.1016/j.actatropica.2016.11.034

Moreira, R. A., Mansano, A. S., & Rocha, O. (2016). Life cycle traits of *Philodina roseola* Ehrenberg, 1830 (Rotifera, Bdelloidea), a model organism for bioassays. *Anais da Academia Brasileira de Ciências*, *88*(Suppl 1), 579–588. https://doi.org/10.1590/0001-3765201620140729

Newman, R. M. (1991). Herbivory and detritivory on freshwater macrophytes by invertebrates: A review. *Journal of the North American Benthological*, *10*, 89–114. https://doi.org/10.2307/1467571

Oliveira, S. S., Ortega, J. C. G., Ribas, L. G., Dos, S., Lopes, V. G., & Bini, L. M. (2020). Higher taxa are sufficient to represent biodiversity patterns. *Ecological Indicators*, *111*, 105994. https://doi.org/10.1016/j.ecolind.2019.105994

Osório, N. C., Cunha, E. R., Tramonte, R. P., Mormul, R. P., & Rodrigues, L. (2019). Habitat complexity drives the turnover and nestedness patterns in a periphytic algae community. *Limnology*, *20*, 297–307. https://doi.org/10.1007/s10201-019-00578-y

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., & Cornelissen, J. H. C. (2016). *Corrigendum to*: New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *64*, 715–716. https://doi.org/10.1071/BT12225_CO

Pierre, J. I., & Kovalenko, K. E. (2014). Effect of habitat complexity attributes on species richness. *Ecosphere*, *5*, 1–10. https://doi.org/10.1890/ES13-00323.1

R Core Team. (2023). *R: A language and environment for statistical computing*. R Core Team.

Raizer, J., & Amaral, M. E. C. (2001). Does the structural complexity of aquatic macrophytes explain the diversity of associated spider assemblages? *Journal of Arachnology*, *29*, 227–237. https://doi.org/10.1636/0161-8202(2001)029[0227:DTSCOA]2.0.CO;2

Ross-Gillespie, V., Picker, M. D., Dallas, H. F., & Day, J. A. (2018). The role of temperature in egg development of three aquatic insects *Lestagella penicillata* (Ephemeroptera), *Aphanicercella scutata* (Plecoptera), *Chimarra ambulans* (Trichoptera) from South Africa. *Journal of Thermal Biology*, *71*, 158–170. https://doi.org/10.1016/j.jtherbio.2017.11.008

Santos, N. G., Stephan, L. R., Otero, A., Iglesias, C., & Castilho-Noll, M. S. M. (2020). How free-floating macrophytes influence interactions between planktivorous fish and zooplankton in tropical environments? An in-lake mesocosm approach. *Hydrobiologia*, *847*, 1357–1370. https://doi.org/10.1007/s10750-020-04194-1

Schultz, R., & Dibble, E. (2012). Effects of invasive macrophytes on freshwater fish and macroinvertebrate communities: The role of invasive plant traits. *Hydrobiologia*, *684*, 1–14. https://doi.org/10.1007/s10750-011-0978-8

Silva, C. V., & Henry, R. (2018). Chironomidae larvae associated with *Eichhornia azurea* leaf detritus: Decomposition community structure and colonization dynamics. *International Aquatic Research*, *10*, 79–93. https://doi.org/10.1007/s40071-018-0190-9

Simberloff, D. (2009). The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Sousa, F. D. R., Palaoro, A. V., Elmoor-Loureiro, L. M. A., & Kotov, A. A. (2017). Predicting the invasive potential of the cladoceran *Daphnia lumholtzi* Sars, 1885 (Crustacea: Cladocera: Daphniidae) in the Neotropics: Are generalists threatened and relicts protected by their life-history traits? *Journal of Limnology*, *76*, 272–280. https://doi.org/10.4081/jlimnol.2016.1571

Stahr, K. J., & Kaemingk, M. A. (2017). An evaluation of emergent macrophytes and use among groups of aquatic taxa. *Lake and Reservoir Management*, *33*, 314–323. https://doi.org/10.1080/10402381.2017.1339747

Strzałek, M., & Koperski, P. (2019). The effect of dense patches of *Stratiotes aloides* L. on the spatial structure of microcrustacean assemblages in an oxbow lake. *Ecohydrology and Hydrobiology*, *19*, 75–82. https://doi.org/10.1016/j.ecohyd.2018.08.003

Thomaz, S. M. (2023). Ecosystem services provided by freshwater macrophytes. *Hydrobiologia*, *850*, 2757–2777. https://doi.org/10.1007/s10750-021-04739-y

Thomaz, S. M., & Cunha, E. R. (2010). The role of macrophytes in habitat structuring in aquatic ecosystems: Methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. *Acta Limnologica Brasiliensia*, *22*, 218–236. https://doi.org/10.4322/actalb.02202011

Tokeshi, M., & Arakaki, S. (2012). Habitat complexity in aquatic systems: Fractals and beyond. *Hydrobiologia*, *685*, 27–47. https://doi.org/10.1007/s10750-011-0832-z

Vecchia, A. D., Villa, P., & Bolpagni, R. (2020). Functional traits in macrophyte studies: Current trends and future research agenda. *Aquatic Botany*, *167*, 103290. https://doi.org/10.1016/j.aquabot.2020.103290

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.

Vilmi, A., Karjalainen, S. M., Nokela, T., Tolonen, K., & Heino, J. (2016). Unravelling the drivers of aquatic communities using disparate organismal groups and different taxonomic levels. *Ecological Indicators*, *60*, 108–118. https://doi.org/10.1016/j.ecolind.2015.06.023

Warfe, D. M., & Barmuta, L. A. (2006). Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia*, *150*, 141–154. https://doi.org/10.1007/s00442-006-0505-1

Warfe, D. M., Barmuta, L. A., & Wotherspoon, S. (2008). Quantifying habitat structure: Surface convolution and living space for species in complex environments. *Oikos*, *117*, 1764–1773. https://doi.org/10.1111/j.1600-0706.2008.16836.x

Webster, B., & Cardé, R. T. (2017). Use of habitat odour by host-seeking insects. *Biological Reviews*, *92*, 1241–1249. https://doi.org/10.1111/brv.12281

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer.

Yofukuji, K. Y., Cardozo, A. L. P., Quirino, B. A., Aleixo, M. H. F., & Fugi, R. (2021). Macrophyte diversity alters invertebrate community and fish diet. *Hydrobiologia*, *848*, 913–927. https://doi.org/10.1007/s10750-020-04501-w

Zingel, P., Karus, K., Agasild, H., & Nõges, T. (2019). The influence of macrophytes on the feeding of fish larvae in a shallow brackish sea. *Journal of Marine Systems*, *189*, 127–136. https://doi.org/10.1016/j.jmarsys.2018.11.001

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Aleixo, M. H. F., Possamai, L. C., de Castro, K. S. P., Yofukuji, K. Y., Cardozo, A. L. P., & Fugi, R. (2024). Habitat complexity versus habitat heterogeneity: Invertebrates prefer macrophyte stands with intermediate biomass and high functional diversity. *Freshwater Biology*, *00*, 1–14. https://doi.org/10.1111/fwb.14305