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Functional Diversity of Neotropical Aquatic Hyphomycetes: Insights Into Environmental Drivers

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Palavras-chave: fungos aquáticos | regra de Bergmann | ecologia funcional | decompositores microbianos | riachos neotropicais

ABSTRACT

Aquatic hyphomycetes species traits are critical for organic matter processing in low-order streams. This study evaluated the functional diversity of hyphomycetes associated with *Nectandra angustifolia* leaves in tropical and subtropical streams, presenting data on sporulation rates, species abundance, and decomposition rates. We examined Functional Richness (FRic), Divergence (FDiv), Dispersion (FDis), and Evenness (FEve) in aquatic hyphomycete assemblages, relating these to environmental variables such as temperature, pH, dissolved oxygen, and electrical conductivity. In tropical streams, poor leaf quality promoted wood saprotroph and foliar endophyte dominance. Moreover, our findings indicated increased functional diversity (FRic and FDis) in subtropical streams compared to tropical streams, reflecting larger conidiophores, diverse conidia shapes, and the prevalence of litter saprotrophs. We also linked colder waters to an increase in trait diversification. Additionally, environmental fluctuations, such as cooler temperature, more dissolved oxygen, and neutral pH, increased FRic, which reflects greater dissimilarity among co-occurring taxa. Our results underscore the significant role of water properties in shaping aquatic hyphomycete assemblage functional diversity.

RESUMO

As características funcionais das espécies de hifomicetos aquáticos são fundamentais para o processamento da matéria orgânica em riachos de pequena ordem. Este estudo avaliou a diversidade funcional de hifomicetos associados a folhas de *Nectandra angustifolia* em riachos tropicais e subtropicais, apresentando dados sobre taxas de esporulação, abundância de espécies e taxas de decomposição. Foram analisadas as métricas de Riqueza (FRic), Divergência (FDiv), Dispersão (FDis) e Uniformidade (FEve) Funcional das assembleias de hifomicetos aquáticos, relacionando-as a variáveis ambientais como temperatura, pH, oxigênio dissolvido e condutividade elétrica. Nos riachos tropicais, a baixa qualidade foliar favoreceu a dominância de sapróbios de madeira e endófitos foliares. Além disso, os resultados indicaram maior diversidade funcional (FRic e FDis) em riachos subtropicais em comparação aos tropicais, refletindo a presença de conidióforos maiores, diversidade nas formas de conídios e predominância de sapróbios de serapilheira. Também observamos que águas mais frias estão associadas ao aumento da diversificação de traços funcionais. Adicionalmente, flutuações ambientais, como temperaturas mais baixas, maiores concentrações de oxigênio dissolvido e pH neutro, aumentaram o FRic, refletindo maior dissimilaridade entre os táxons co-ocorrentes. Nossos resultados ressaltam o papel significativo das propriedades da água na configuração da diversidade funcional das assembleias de hifomicetos aquáticos.

1 | Introduction

Understanding the diverse functions performed by aquatic organisms is vital for unraveling the complex interactions and ecological processes that drive ecosystem homeostasis (Biggs et al. 2020; Laureto et al. 2015). However, certain groups, such as bacteria, protozoa, and fungi, like aquatic hyphomycetes, remain relatively understudied in terms of their functional diversity in aquatic environments (Arias-Real et al. 2023). Aquatic hyphomycetes play an essential role in decomposition and nutrient cycling in freshwater ecosystems (Barreto et al. 2023; Duarte et al. 2016; Quintão et al. 2013). As these fungi decompose allochthonous detritus, like leaf litter, they play a crucial role in biogeochemical processes (Cid et al. 2019; de Souza Rezende et al. 2019). Additionally, understanding the importance of functional diversity is essential for these often overlooked organisms, as they make major contributions to ecosystem metabolism (Arias-Real et al. 2023), particularly in forest streams (Graça et al. 2016; de Souza Rezende et al. 2021).

Aquatic hyphomycetes exhibit functional traits, such as morphology (e.g., conidia and conidiophore size) and nutritional strategies (e.g., saprobic vs. endophytic lifestyles), which vary according to their ecological roles (Gulis 2001; Põlme et al. 2020). This diversity in functional traits enables them to decompose complex organic detritus like leaves and dead wood, thereby facilitating nutrient cycling and enhancing resource availability for other aquatic organisms (Alvim et al. 2015; Barreto et al. 2023; Sales et al. 2015). In this way, aquatic hyphomycetes contribute to nutrient cycling through the leaf decomposition process (Graça et al. 2016; Quintão et al. 2013), enhancing the overall availability of resources for other aquatic organisms (Cid et al. 2019; de Souza Rezende et al. 2019).

Functional diversity, the variety of roles played within fungal assemblages, enhances the coverage of these distinct ecological functions (Gulis et al. 2020; Põlme et al. 2020). For aquatic hyphomycetes, this diversity is crucial for maintaining the structural stability of stream ecosystems, particularly given the temporal and spatial heterogeneity characteristic of aquatic environments (Arias-Real et al. 2023; Graça et al. 2016). However, the extent to which these functions occur may vary depending on temporal (de Souza Rezende et al. 2019; Sales et al. 2015) and spatial scales (Barreto et al. 2023; Nuven et al. 2022) associated with the specific environmental characteristics of each aquatic ecosystem (Sena et al. 2023; Tonin et al. 2017).

Environmental characteristics, such as temperature, can influence the distribution and activity of aquatic hyphomycetes in freshwaters (Barlocher et al. 2013; Martins et al. 2017; Pérez et al. 2018). In tropical streams, where water temperatures are warmer, a lower diversity of these fungi is expected (Duarte et al. 2016; Graça et al. 2016), due to their origin in colder environments (Belliveau and Bärlocher 2005). However, their metabolic activity is anticipated to be greater in tropical streams with warmer waters (Barreto et al. 2023; Graça et al. 2016). In contrast, in subtropical streams, where temperatures are cooler and environmental characteristics have a broader range of fluctuations, aquatic hyphomycetes may exhibit greater functional diversity in response to temporal heterogeneity (Barreto et al. 2023; Graça et al. 2016). Moreover, favorable local habitat characteristics (Rezende et al. 2014), such as high dissolved oxygen (Medeiros et al. 2009), neutral pH (Rosset and Bärlocher 1985), and low electrical conductivity (Pérez et al. 2018; Sales et al. 2015), enhance spatial heterogeneity (Barreto et al. 2023; Jabiol et al. 2013).

Increased spatial and temporal heterogeneity in the lotic habitat (e.g., rivers and streams) may promote greater diversity and colonization by aquatic hyphomycetes (Barreto et al. 2023; Jabiol et al. 2013), potentially leading to faster leaf decomposition rates, and consequently, enhancing ecosystem processes such as organic matter cycling (Sales et al. 2015). The changes in environmental characteristics between subtropical and tropical ecosystems could impact the functional diversity of aquatic hyphomycetes in freshwaters (Barreto et al. 2023; Jabiol et al. 2013). This may reflect a broader biogeographic pattern consistent with Bergmann's rule, which posits that organisms from cooler environments tend to exhibit larger body sizes or, in a functional context, larger structures as an adaptation to cooler temperatures (Dickey et al. 2021; for more see also Kingsolver and Huey 2008). Consequently, alterations in aquatic hyphomycete assemblages may affect nutrient availability in Neotropical streams (Biasi et al. 2020; Breda et al. 2021; Graça et al. 2016).

Knowledge about the functional diversity of aquatic hyphomycetes is crucial for grasping the intricate dynamics of Neotropical streams (Barreto et al. 2023; Graça et al. 2016), specifically regarding leaf decomposition processes (Rezende et al. 2014; Sales et al. 2015). Herein we assessed the functional diversity and species traits of aquatic hyphomycete assemblages associated with decaying leaves of *Nectandra angustifolia* (Spreng.) Mez. (Lauraceae) in streams of subtropical and tropical zones in Brazil. Also, our aim is to assess whether the functional diversity of aquatic hyphomycete assemblages in tropical and subtropical streams can be explained by a combination of environmental drivers, such as temperature, dissolved oxygen, and water conductivity. We also evaluate sporulation rates, species richness, and the decomposition of

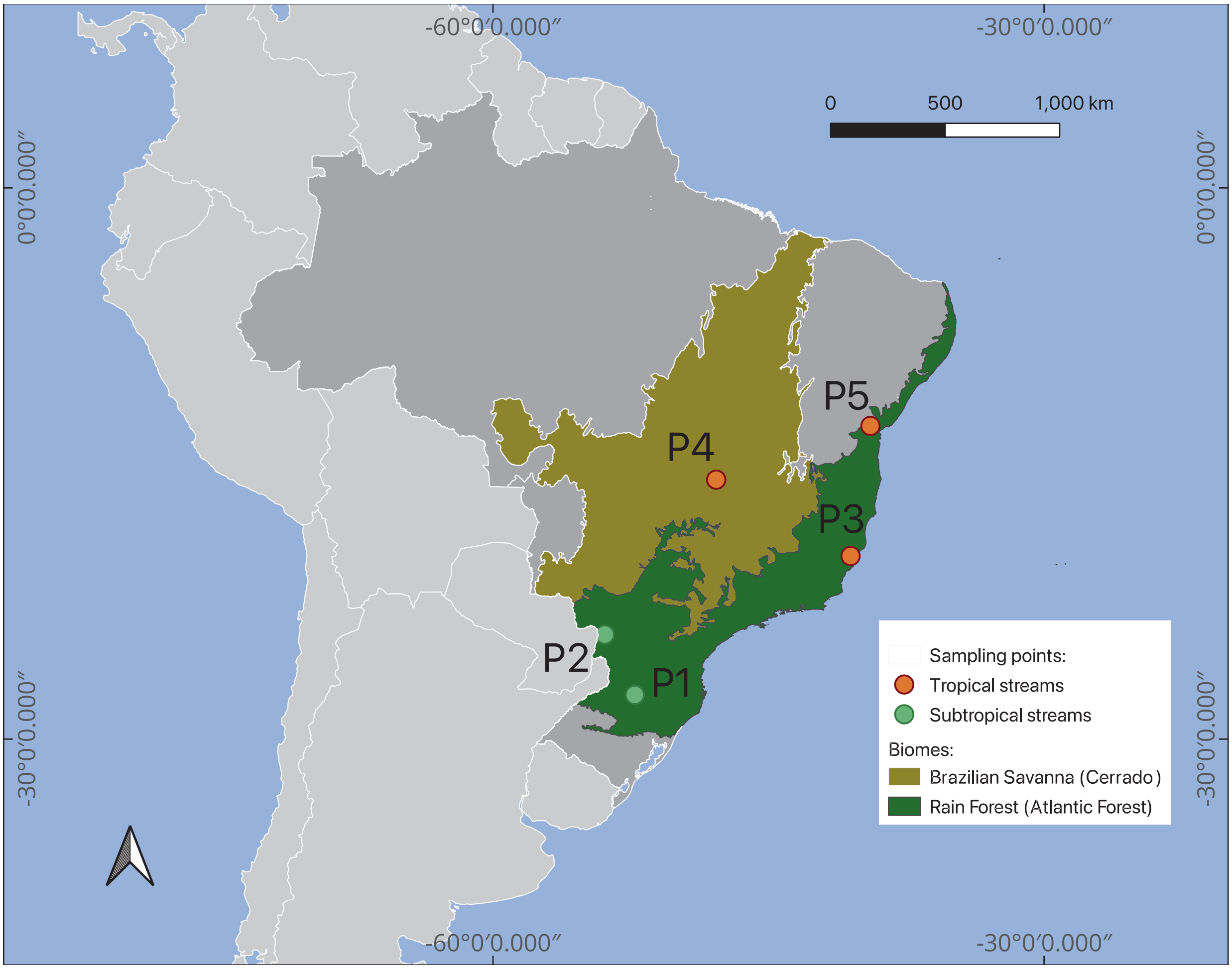

FIGURE 1 | Geographical location of the study sites in the Atlantic Forest (in dark green) and Cerrado (Brazilian savannah, in olive). Green dots indicate subtropical streams and orange dots indicate tropical streams.

N. angustifolia leaves across these distinct regions to better understand the environmental drivers behind fungal community distribution.

We structure our approach around three key premises that logically build towards our hypothesis: (i) Firstly, at a regional scale, the distinct environmental characteristics of subtropical and tropical ecosystems lead to differences in water properties and, consequently, the functional diversity of aquatic hyphomycetes. Variations in climate (colder systems), hydrology (turbulent stretches), and organic matter inputs (nutrient-rich systems) can result in more diverse fungal assemblages and functions between these regions (Barreto et al. 2023; Graça et al. 2016); (ii) Secondly, at a local scale, water properties significantly influence ecological processes (e.g., litter decomposition) and the traits of aquatic hyphomycetes. Factors such as temperature, pH, and nutrient availability can alter litter decomposition rates and impact fungal community composition (Gulis 2001; Medeiros et al. 2015; Põlme et al. 2020; Rezende et al. 2025); (iii) Thirdly, following Bergmann's rule, organisms in cooler environments tend to have larger body sizes. This size variation, as an adaptation to the regional and local conditions mentioned above, can support a greater diversity of organismal forms and, consequently, enhance functional diversity within communities (Dickey et al. 2021; Kingsolver and Huey 2008). We hypothesized that streams at higher latitudes will exhibit greater functional diversity of aquatic hyphomycete assemblages.

2 | Material and Methods

2.1 | Study Sites

We conducted coordinated experiments in five forest streams located in subtropical and tropical regions in Brazil (Figure 1). Two streams were chosen in subtropical regions, and three in tropical regions (see Barreto et al. 2023 for more information). The Dourado Stream (P1; 27°36′07″S–52°16′12″W), situated at an elevation of 783 m a.s.l., is a second-order stream with a mixture of subtropical forests that include riparian species distributed in tropical-subtropical regions of upper Uruguay and mixed rainforests in the Atlantic Forest of Rio Grande do Sul, southern Brazil (Barreto et al. 2023). The Quati Stream (P2; 24°18′57.13″S–53°54′38.55″W), situated at an elevation of 341 m a.s.l., is a first-order stream surrounded by natural riparian vegetation consisting of a tropical seasonal semideciduous forest of the Atlantic Forest domain that is located in the Conservation Unit of São Camilo State Park, Paraná, southern Brazil (Rezende et al. 2019). The Banana Stream (P3; 20°02′22.44″S–40°31′50.89″W), situated at an elevation of

519 m a.s.l., is a second-order stream with well-preserved riparian vegetation in a fragment of the Atlantic Forest in Espírito Santo, southeastern Brazil (Casotti et al. 2015). The Cabeça de Veado (P4; 15°53′11.74″S–47°50′33.27′′W), situated at an elevation of 1172 m a.s.l., is a second-order stream located in a preserved area of the Cerrado (Brazilian savannah) within the Federal District, central-west Brazil (Rezende et al. 2014). The Cai Camarão stream (P5; 12°57′35.8″S–39°26′55.9″W), situated at an elevation of 327 m a.s.l., is a second-order stream located in a region that is mostly covered by the Atlantic Forest in Serra da Jiboia, a mountainous massif in the southern region of Bahia, northeastern Brazil (Barreto et al. 2023).

2.2 | Experimental Design

We used leaves of *N. angustifolia*, a tree species that occurs in different biomes of Brazil, including the Amazonia, Cerrado, and Atlantic Forest (for more see also; Sena et al. 2023). Its choice is based on their availability and ecological relevance as leaf litter in these ecosystems. We collected leaves using litter traps fixed 1.5 m above the ground on both stream banks at the P1 study site. The traps were regularly checked, and the leaves were air dried in the laboratory to constant weight and stored in the dark until the start of the experiments. We mixed and divided the collected leaves into six portions; five portions were used in the experiments developed at each study site, and the sixth portion was used for the determination of initial leaf chemistry (time 0 leaves). This standardization was important because leaf chemistry can affect microbial colonization and, consequently, leaf decomposition (Graça et al. 2016).

We conducted coordinated experiments at all study sites between June and August 2013 (winter in the Southern Hemisphere) and from January to March 2014 (summer). At each site, we incubated 30 fine mesh (0.5 mm) litter bags containing 3.0 ± 0.1 g of leaves tied to submerged cobbles and roots at similar depths and flow. Fine mesh litter bags were used to exclude invertebrates. The litter bags (five replicates) were sampled from each site after 15, 30, and 60 days of incubation in each season (dry and rainy). The bags (five locations × two seasonal periods × three temporal periods × five replicates = 150 sampled units) were individually placed in plastic bags and transported in an ice chest to the laboratory. All samples were processed on the same sampling day to characterize the aquatic hyphomycete assemblages (such as sporulation rates and taxonomic composition). We also measured water properties, that is, temperature, dissolved oxygen, pH, and electrical conductivity, on each sampling occasion with a handheld multiparameter probe (model U-52G, Horiba Ltd., Kyoto, Japan).

In the laboratory, the leaves were removed from the litter bags and washed with distilled water. From each sample, five leaves were randomly selected, and three sets of five leaf discs were cut (12 mm in diameter). These sets of leaf discs were used to determine the taxonomic composition of aquatic hyphomycetes associated with leaves, sporulation rates, and ash-free dry mass (AFDM) of leaf discs. The remaining leaves were oven-dried (60°C, 72 h), weighed (0.01 mg), ignited (550°C, 4 h), and reweighed for AFDM estimation (see Barreto et al. 2023 for more information). Further additional information is given in Barreto et al. (2023).

2.3 | Sporulation Rates

For the determination of sporulation rates and taxonomic composition of aquatic hyphomycete assemblages associated with incubated leaves, one set of leaf discs from each sample was placed in 200 mL Erlenmeyer flasks containing 30 mL of distilled water (Table SM1). The Erlenmeyer flasks were placed on an orbital shaker (90 rpm) for 48 h at 20°C (room temperature). Subsequently, the spore suspensions were fixed in 4% formalin, filtered through Millipore membrane filters with a pore size of 5 μm (Millipore SMWP, Millipore Corporation, Bedford, USA), and the filters were stained using a solution of cotton blue (0.05%) in 60% lactic acid. Samples were examined under an optical microscope (400×; Olympus B×43) for spore quantification and identification. For the identification of aquatic hyphomycetes, the count of 100 fields was standardized and the conversion was made to the total number of fields in the filter. The sporulation rates were determined as the number of spores produced per mg of leaf AFDM per day (Bärlocher et al. 2020). Sporulation rates and species composition were determined following established protocols (Bärlocher et al. 2020).

2.4 | Taxonomic and Functional Identification

Spore morphologies were used to identify the taxonomic composition of aquatic hyphomycetes in each sample according to taxonomic keys (Duarte et al. 2016; Fiuza et al. 2014, 2019; Gulis et al. 2020). The chosen functional attributes provide a concise representation of production and dispersal structures (conidiophore size, conidia size and shape), the fungal resource exploitation capacity (primary lifestyle and preferential decay substrate; Gulis 2001; Põlme et al. 2020), and its endurance in the environment (drought tolerance; Põlme et al. 2020). For more, see also Tables 1 and 2.

For the functional structure approaches, several indices were used (quantitative and qualitative). These included functional richness (FRic), which measures the range of combinations of assemblage attributes; functional divergence (FDiv), which considers the abundance of species distributed in functional space; functional dispersion (FDis), which estimates species dispersion in functional space; and functional evenness (FEve), which assesses the regularity of species abundances distributed in functional space. All of these indexes were calculated using the "*dbFD*" function (Villéger et al. 2008) from the "*FD*" package in the R environment, as described by Laliberte and Legendre (2010). Additionally, we calculated the Community-Weighted Means (CWM) to compare differences in the most important traits between systems (Ricotta and Moretti 2011). Sampling with fewer than three taxonomic occurrences does not generate index values, which may cause the sample size to vary among the tested treatments.

2.5 | Data Analysis

We conducted a Principal Coordinates Analysis (PCoA) to identify variation in the composition of aquatic hyphomycete assemblages based on their functional traits. We used mixed variables (quantitative and qualitative) standardized by the

TABLE 1 | Traits of aquatic hyphomycetes species considered in this study grouped into three broad categories: (i) recruitment and life history, (ii) resource and habitat use, and (iii) body size.

Functional component	Functional attribute	Functional or ecological importance
Quantitative	Conidiophore size (μm)	Provide a suitable structure for the production and dispersal of conidia (Duarte et al. 2016; Fiuza et al. 2014, 2019; Gulis et al. 2020)
	Conidia size (μm)	Determines fungal dispersal ability within streambed sediments, colonization of substrates, and selective interactions with detritivores and decomposers (Duarte et al. 2016; Fiuza et al. 2014, 2019; Gulis et al. 2020)
Qualitative	Conidia shape (tetraradiate, filiform, sigmoid, spiked, elliptic, cross, geniculated, subclaved, basiverticulate or subulate)	Determines fungal dispersal ability within streambed sediments, which allows them to survive during the dry phase and become physiologically active in the wet phase (Duarte et al. 2016; Fiuza et al. 2014, 2019; Gulis et al. 2020)
	Primary lifestyle (litter saprotroph, unspecified saprotroph, foliar endophyte or wood saprotroph)	Determines the enzymatic capacity of aquatic hyphomycetes to decompose plant organic detritus (Duarte et al. 2016; Fiuza et al. 2014, 2019; Gulis et al. 2020)
	Preferential decay substrate (leaf, fruit and seed, wood or unspecified)	Determines the enzymatic capacity of aquatic hyphomycetes to decompose organic detritus of plant origin (Gulis 2001; Põlme et al. 2020)
	Drought tolerance (resistant, tolerant or vulnerable)	Determines fungal dispersal ability within streambed sediments, which allows them to survive during the dry phase and become physiologically active in the wet phase. (Põlme et al. 2020)

Gower index and the "*pcoa*" function of the "*ape*" package (Legendre and Gallagher 2001). Among the functional traits (Tables 1 and 2), conidia size and conidiophore size were quantitative, whereas the others were qualitative (primary lifestyle, fruitbody type, decay substrate, nutritional strategy, and drought tolerance). The functional trait variables were filtered by the variance inflation index using the "*vif*" function of the "*car*" package (Fox and Monette 1992). This index helped us exclude highly correlated variables through a gradual procedure to address multicollinearity problems. We incorporated environmental variables as explanatory factors in the analysis and plotted the contribution of each variable to each axis to better explain community patterns. The most ecologically relevant functional trait identified by the PCoA (trait size, represented by the conidial-to-conidiophore width ratio) was tested using Generalized Linear Models (GLMs, by Gaussian family with canonical link = identity; test = "F") analysis against the main climatic driver across the latitudinal gradient (temperature). We only included in the analysis samples with more than three species (Dormann et al. 2013; Legendre and Legendre 1998).

We employed Generalized Linear Mixed-Effects Models (GLMMERs; "*glmer*" function in "*lme4*" package) to assess the environmental variables at each study site (explanatory variables) on all functional diversity indices (FRic, FDiv, FDis, and FEve; response variables) (Crawley 2007). A random effect GLMMER analysis considering the sampling unit at the sampling point nested in time and seasonal period was performed to account for the sampling unit variation and the specific features (local and temporal) of the landscape. Furthermore, all functional diversity indices were individually tested using Generalized Linear Models (GLMs) against stream water temperature, dissolved oxygen, electrical conductivity, and pH (explanatory variables). All models were evaluated for under and overdispersion using the "*hnp*" package and function (Moral et al. 2017). The Gaussian family (canonical link = identity; test = "F") was determined to be the error distribution with the best fit for all models. In addition, we performed pairwise post hoc tests with the "*lsmeans*" function and package (Lenth 2016) to evaluate differences among categorical variables. We utilized the "*ggstatsplot*" function and package for data visualization (Patil 2021). We conducted all analyses using R statistical software, version 4.1.3 (R Core Team 2023).

3 | Results

3.1 | Aquatic Hyphomycete Assemblage by Traits

The analysis of the aquatic hyphomycete assemblages by functional traits (Table 2) revealed two distinct groups, with conidia and conidiophore size emerging as the primary factors separating them (Figure 2). In the PCoA analysis (Figure 2), axis 1 accounted for 18% of the variance (eigenvalue = 2.2),

TABLE 2 | Traits of aquatic hyphomycete species associated with leaves of *Nectandra angustifolia* in subtropical and tropical streams.

	Conidiophore (µm)	Conidia (µm)	Shape	Lifestyle	Decay substrate	Drought tolerance
Alatospora acuminata	37.5	2.2	Tetraradiate	Litter saprotroph	Leaf fruit seed	Tolerant
Anguillospora filiformis	95.0	3.0	Filiform	Litter saprotroph	Leaf fruit seed	Tolerant
Anguillospora furtiva	225.0	6.0	Sigmoid	Litter saprotroph	Leaf fruit seed	Tolerant
Anguillospora longissima	200.0	5.5	Sigmoid	Litter saprotroph	Leaf fruit seed	Tolerant
Anguilospora crassa	150.0	11.0	Sigmoid	Litter saprotroph	Leaf fruit seed	Tolerant
Campylospora chaetocladia	40.0	2.3	Filiform	Litter saprotroph	Leaf fruit seed	Tolerant
Campylospora sp.	19.0	1.5	Tetraradiate	Litter saprotroph	Leaf fruit seed	Tolerant
Camposporium pellucidum	92.5	2.3	Filiform	Wood saprotroph	Wood	Tolerant
Clavariopsis aquatica	42.5	11.0	Spiked	Wood saprotroph	Wood	Resistant
Clavatospora tentacula	52.5	2.0	Tetraradiate	Wood saprotroph	Wood	Vulnerable
Colispora curvata	31.5	8.8	Tetraradiate	Litter saprotroph	Leaf fruit seed	Tolerant
Condylospora gigantea	81.0	4.0	Elliptic	Litter saprotroph	Leaf fruit seed	Tolerant
Crucispora ponapensis	45.0	2.5	Cross	Litter saprotroph	Leaf fruit seed	Tolerant
Culicidospora aquatica	60.0	15.0	Spiked	Litter saprotroph	Leaf fruit seed	Tolerant
Diplocladiella scalaroides	35.0	3.0	Geniculated	Unspecified saprotroph	Unspecified	Resistant
Flagellospora curvula	105.0	1.9	Filiform	Litter saprotroph	Leaf fruit seed	Resistant
Gyoerffyella gemellipara	45.0	8.5	Sigmoid	Litter saprotroph	Leaf fruit seed	Tolerant
Heliscus submersus	37.5	3.5	Subclaved	Unspecified saprotroph	Unspecified	Vulnerable
Lemoniera filiformis	105.0	25.0	Basiverticulate	Litter saprotroph	Leaf fruit seed	Tolerant
Lemoniera pseudofoscula	31.5	4.5	Obclaved	Litter saprotroph	Leaf fruit seed	Tolerant
Lunulospora curvula	115.0	3.8	Sigmoid	Litter saprotroph	Leaf fruit seed	Vulnerable
Mycofalcela calcarata	150.0	9.5	Filiform	Litter saprotroph	Leaf fruit seed	Tolerant

(Continues)

	Conidiophore (µm)	Conidia (µm)	Shape	Lifestyle	Decay substrate	Drought tolerance
Subulispora procurvata	45.0	14.0	Subulate	Unspecified saprotroph	Unspecified	Tolerant
Triscelophorus sp.	70.5	4.0	Tetraradiate	Foliar endophyte	Leaf	Tolerant
Tripospermum myrti	105.0	6.0	Tetraradiate	Litter saprotroph	Leaf fruit seed	Resistant
Tricladium curvisporum	36.5	2.3	Curved	Litter saprotroph	Leaf fruit seed	Tolerant
Triscelophorus acuminatus	54.5	2.5	Obclaved	Foliar endophyte	Leaf	Tolerant
Triscelophorus monosporus	52.5	3.8	Tetraradiate	Foliar endophyte	Leaf	Tolerant
Ypsilina graminea	33.0	2.3	Elliptic	Litter saprotroph	Leaf fruit seed	Resistant

whereas axis 2 accounted for 13% of the variance (eigenvalue = 1.8). The Broken-Stick model allocated 20% to axis 1 and 14% to axis 2, indicating that axis 2 was not significant for interpretation.

The first group included most taxa sampled from subtropical streams, characterized by larger conidiophores, more diverse conidia shapes, and dominance of litter saprotrophs trophic groups with high drought tolerance (Figure 2). *Anguillospora crassa*, *A. filiformis*, *A. furtiva*, *A. longissima*, *Culicidospora aquatica*, *Gyoerffyella gemellipara*, *Lemonniera filiformis*, *Lunulospora curvula*, *Mycofalcella calcarata*, and *Tripospermum myrti* are located positively along axis 2, while *Alatospora acuminata*, *Campylospora chaetocladia*, *Campylospora* sp., *Colispora curvata*, *Condylospora gigantea*, *Crucispora ponapensis*, *Flagellospora curvula*, *Lemonniera pseudofloscula*, *Tricladium curvisporu*, and *Ypsilina graminea* are located negatively along axis 2 (Figure 2).

The second group represented taxa from tropical streams, generally characterized by smaller conidiophores, less conidial shape diversity, and dominance of wood saprotrophs and foliar endophytes. The drought tolerance in this group was the main trait defining this subdivision. *Camposporium pellucidum*, *Clavariopsis aquatica*, *Heliscus submersus*, *Diplocladiella scalaroides*, and *Subulispora procurvata* are located positively along axis 2, while *Clavatospora tentacula*, *Triscelophorus acuminatus, T. monosporus*, and *Triscelophorus* sp. are located negatively along axis 2 (Figure 2).

The most ecologically relevant functional trait identified by the PCoA was trait size (by CWM), represented by the conidial-to-conidiophore width ratio. This variable was tested through Generalized Linear Models (GLMs) analysis against the key climatic driver across the latitudinal gradient, which was stream water temperature (Figure 3). The relationship between stream temperature and the conidiophore-to-conidium size ratio in aquatic hyphomycete assemblages was significantly negative ($R^2 = 0.05$; $F_{(1,146)} = 7.1$; $p = 0.008$), indicating that taxa occurring in warmer streams tended to exhibit proportionally smaller sizes.

3.2 | Functional Diversity

Our Generalized Linear Mixed-Effects Models (GLMMERs) analysis revealed significantly greater functional richness (FRic) and functional dispersion (FDis) in subtropical streams than in tropical streams (Table 3). Mean FRic in subtropical streams was 0.74, compared to 0.31 in tropical streams, and FDis was 0.45 in subtropical streams compared to 0.27 in tropical streams (Figure 4). No significant differences in functional evenness (FEve) or functional divergence (FDiv) were found between the two regions (Table 3; GLMMERs), with both regions having nearly identical FDiv (0.71 and 0.70) and FEve values of 0.65 and 0.54 for tropical and subtropical streams, respectively (Figure 4).

Temperature (Figure S1; Table S2a) was negatively related to FRic ($F_{(1,56)} = 18.7$, $p < 0.001$; Figure 5), but positively related to FEve (GLMs; $F_{(1,56)} = 8.3$, $p = 0.005$; Figure 5). Dissolved oxygen (Figure S2; Table S2b) was also positively related to FRic (GLMs; $F_{(1,56)} = 16.9$, $p < 0.001$; Figure 5), but negatively related to FEve (GLMs; $F_{(1,56)} = 7.8$, $p = 0.007$; Figure 5). Lastly, electrical conductivity (Figure S3; Table S2c) was negatively related to FDis (GLMs; $F_{(1,146)} = 13.7$, $p < 0.001$; Figure 5), and pH (Figure S4; Table S2d) was positively related to FRic (GLMs; $F_{(1,56)} = 5.1$, $p = 0.028$; Figure 5).

4 | Discussion

4.1 | Aquatic Hyphomycete Assemblages

The larger size of organisms in subtropical (Tseng and Soleimani Pari 2019) and colder regions (Evans et al. 2020), excepting the poles, is a common biogeographic pattern following Bergmann's

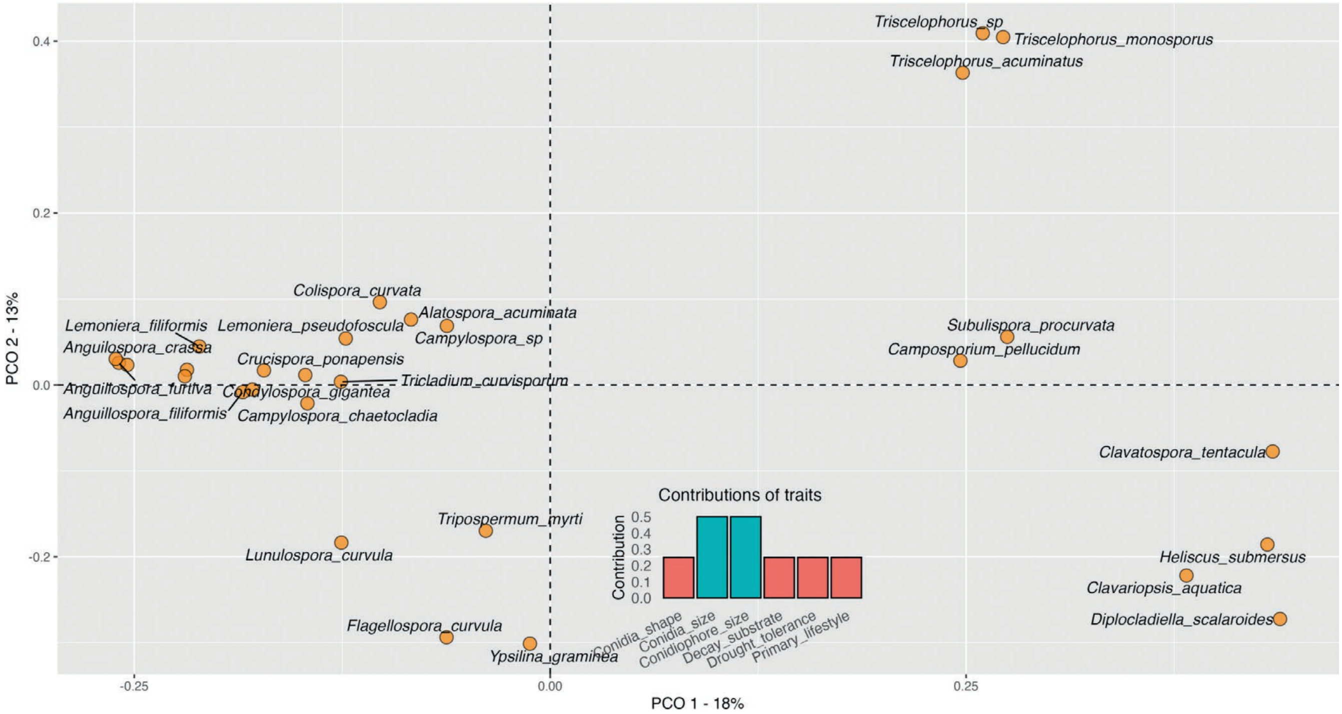

FIGURE 2 | Principal coordinate analysis of aquatic hyphomycete species associated with leaves of *Nectandra angustifolia* in subtropical and tropical streams by functional traits.

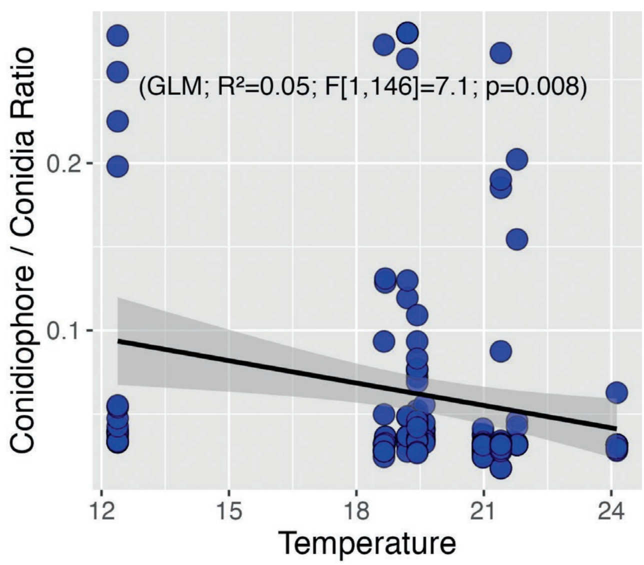

FIGURE 3 | Relationship between water temperature (°C) and the conidiophore-to-conidium size ratio (from communityweighted means values; µm/µm) in aquatic hyphomycete assemblages. The solid line indicates the linear regression trend (±95% confidence interval shaded in gray).

rule (Dickey et al. 2021; for more see also Kingsolver and Huey 2008). It serves as a strategy for energy conservation in response to environmental characteristics (Evans et al. 2020; Kingsolver and Huey 2008). Aquatic hyphomycete fungi have evolutionarily originated from colder aquatic ecosystems (Belliveau and Bärlocher 2005), which could explain the greater diversity of conidial forms, likely reflecting greater taxonomic diversity (Barreto et al. 2023; Duarte et al. 2016). This evolutionary origin in colder water areas may also contribute to a significant aspect of diversification in subtropical streams (Barreto et al. 2023), and possibly to the enhanced desiccation tolerance (drought and frost protection).

The evolutionary origin of these organisms is in colder regions, which may have also provided plentiful opportunities for speciation (Belliveau and Bärlocher 2005; Naranjo-Ortiz and Gabaldón 2019), explaining the high functional and taxonomic diversity and the convergence of traits (Duarte et al. 2016), as observed in subtropical stream assemblages. In this context, subtropical streams embedded in forested landscapes, particularly those located in ecotonal or transitional zones, may support a greater variety of environmental conditions at broader spatial scales (Oliveira-Filho et al. 2015). This environmental heterogeneity likely promotes the coexistence of functionally diverse fungal taxa (Barreto et al. 2023), which could explain the elevated levels of functional richness and dispersion detected in the subtropical systems in our study. Rather than classifying them strictly as biodiversity "hotspots" in the traditional conservation sense, we interpret these subtropical streams as functionally rich assemblages shaped by both evolutionary legacy and environmental filtering.

On the other hand, in the tropical streams, organisms exhibited smaller conidiophores, reduced diversity in conidia shape, and a dominance of wood saprotrophs and foliar endophytes as trophic groups. The smaller size of conidiophores may be associated with the lower quality of leaf litter in tropical streams (Arias-Real et al. 2018; Ormeño et al. 2006; de Souza Rezende et al. 2021). Some study sites in the tropical region are located in the Cerrado, a savannah-like ecosystem in Brazil, or nearby Caatinga, a Brazilian ecoregion of dry forests, which

TABLE 3 | Simplified one-way generalized linear mixed-effects models (GLMMER; random factor = sampling unit nested at the site nested in time and seasonal period) and contrast analysis from comparisons of functional richness (FRic), functional divergence (FDiv), functional dispersion (FDis), and functional evenness (FEve) of aquatic hyphomycete assemblages between subtropical and tropical streams.

	npar	AIC	BIC	logLik	Deviance	χ^2	df	Pr(>χ^2)	Contrast analysis
FRic									
Null model	3	71.4	77.1	−32.7	65.4				
System	4	62.8	71.0	−27.4	54.8	10.679	1	**0.010**	Tropical < Subtropical
FDiv									
Null model	3	−29.2	−23.1	35.2	−35.2				
System	4	−27.5	−19.2	35.5	−35.5	0.215	1	0.642	
FDis									
Null model	3	69.1	78.1	−31.5	63.1				
System	4	64.6	76.6	−28.3	56.6	6.474	1	**0.010**	Tropical < Subtropical
FEve									
Null model	3	15.7	21.8	1.7	−4.8				
System	4	15.4	23.7	1.9	−3.7	2.241	1	0.134	

Note: Values in bold correspond to significant differences.

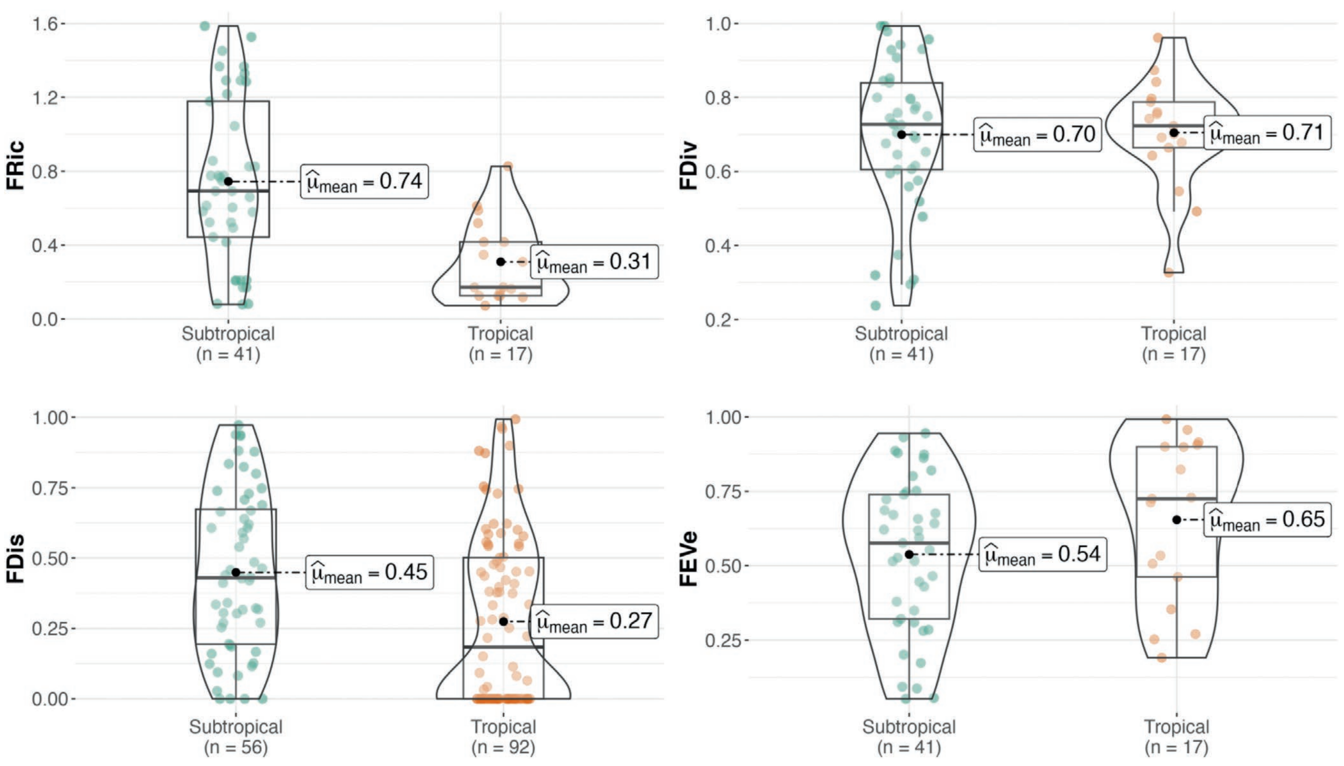

FIGURE 4 | Functional richness (FRic), functional divergence (FDiv), functional dispersion (FDis), and functional evenness (FEve) of aquatic hyphomycete assemblages associated with leaves of *Nectandra angustifolia* incubated in subtropical (green dots) and tropical (orange dots) streams. The boxes represent the quartiles, the black symbols in the horizontal represent the median and the black circles represent the average. The "*n*" is the number of sampling units.

forms a dry corridor between Neotropical humid forests (Tonin et al. 2017). Cerrado tree species are known for their adaptation to dry periods, resulting in more recalcitrant compounds in leaf litter, such as lignin and cellulose, and tougher leaves (Tonin et al. 2021), which reduce leaf palatability and attractiveness to herbivores and decomposers (Rezende et al. 2014; Moretti et al. 2020).

The dominance of recalcitrant compounds in the leaf litter of Cerrado tree species could favor fungal species with smaller

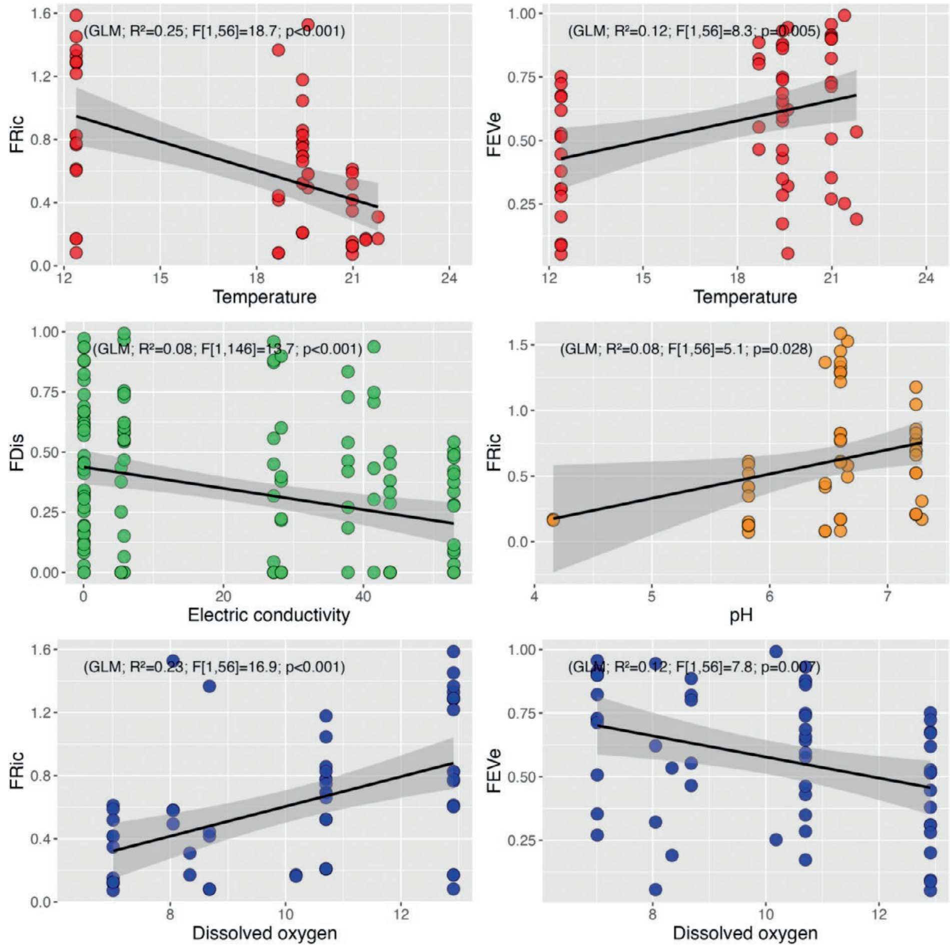

FIGURE 5 | Linear models for the significant effects of environmental variables on functional richness (FRic), functional divergence (FDiv), and functional evenness (FEve) of aquatic hyphomycete assemblages.

reproductive structures due to greater energy expenditure in consuming litter with lower palatability (Arias-Real et al. 2018; Krauss et al. 2011). Thus, harsh environments, with greater variation in water availability and less palatable plant resources, may lead to a more homogeneous habitat with fewer niches (Nuven et al. 2022; Rezende et al. 2014), thereby increasing functional redundancy and explaining the lower diversity in conidia shape (Arias-Real et al. 2023). The dominance of wood saprotrophic fungal species in tropical streams further supports the prevalence of low-quality leaf litter. This environmental filtering may promote the dominance of generalist fungal taxa capable of performing similar ecological roles, resulting in greater functional redundancy.

Functional redundancy allows different species to perform similar ecological functions in an ecosystem (Biggs et al. 2020), resulting in more homogeneous microbial-mediated leaf decomposition rates in tropical streams (Biasi et al. 2020; Martínez et al. 2019). In this way, the more prevalent functional redundancy in tropical regions results in reduced diversity but ensures that key ecological processes remain stable despite environmental stressors (Biggs et al. 2020). The low variability in conidial forms found in tropical streams reflects a more homogeneous environment with fewer ecological niches. Thus, although tropical fungal assemblages exhibited lower functional trait diversity, their potential for maintaining key ecological processes remains relatively stable due to trait overlap among taxa (Petchey and Gaston 2002). In this context, functional redundancy may confer greater resilience to environmental disturbances, even in systems with lower trait differentiation.

4.2 | Functional Diversity

Compared to tropical streams, subtropical streams exhibited aquatic hyphomycete assemblages with elevated functional diversity (FRic and FDis). This observation suggests that environmental characteristics, such as more dissolved oxygen, neutral pH, and colder temperatures, may influence FRic, while lower electrical conductivity may be associated with greater FDis (Barreto et al. 2023; Nuven et al. 2022). Among the environmental variables evaluated, temperature and dissolved oxygen emerged as the factors significantly associated with both FRic and FEVe, suggesting that cooler, oxygen-rich environments may promote broader ecological strategies and trait differentiation (Barreto et al. 2023; Sales et al. 2015). Additionally, there is a broader range of climate fluctuations, including temperature and precipitation (Fenoy et al. 2021; Rezende et al. 2019), which collectively shape the functional diversity of aquatic hyphomycetes (Arias-Real et al. 2023). Jabiol et al. (2013) proposed that the latitudinal diversity patterns of these fungi can be attributed to a range of climate fluctuations. On the other hand, due to a narrower range of climate fluctuations (mainly in temperature), tropical streams may exhibit fewer niche spaces than subtropical streams (Barreto et al. 2023; Sales et al. 2015). This is further influenced by the presence of low-quality leaf litter (Tonin et al. 2021) that decreases the diversity of aquatic hyphomycetes.

In addition, species with diverse niches and functional characteristics can possess competitive advantages depending on specific characteristics of the habitat (de Souza Rezende et al. 2019), thus contributing to an increase in functional diversity. The distribution patterns of species characteristics indicate that the structure of local aquatic hyphomycete assemblages is influenced by either habitat similarity limitation by leaf litter characteristics (Arias-Real et al. 2018) and/or environmental filtering, as a result of climate fluctuations (Fenoy et al. 2021). Habitat pressures may impact the coexistence (Oliveira de Menezes and Schmidt 2020), dispersal (Saito et al. 2015), and functional diversity (in our case on FRic and FDis) of aquatic hyphomycetes (Barreto et al. 2023; Fenoy et al. 2021). Thus, these factors favor a greater number of traits in subtropical streams compared with tropical streams (Barreto et al. 2023; Fenoy et al. 2021) and constrain the similarity among species (Arias-Real et al. 2023; Saito et al. 2015). Therefore, the larger number of niches located in streams at higher latitudes may also enable the coexistence of species that adapt and specialize to different environmental characteristics (Barreto et al. 2023).

The stream temperatures were negatively related to FRic, but positively related to FEve. Warmer temperatures may act as a limiting factor for the functional richness of aquatic hyphomycetes (Fenoy et al. 2021), potentially due to thermal stress on fungal metabolism (Gomes et al. 2017; Krauss et al. 2011), but increase functional evenness. It is a commonly observed pattern in taxonomic data that an increase in evenness occurs as a response to a decrease in richness (Hill 1973; Yeboah et al. 2016). In addition, dissolved oxygen and pH were positively related to FRic. Dissolved oxygen usually positively affects the diversity of aquatic hyphomycetes (Breda et al. 2021), although some species can grow under anaerobic conditions (Barreto et al. 2023; Medeiros et al. 2009).

Aquatic hyphomycete species also exhibit different tolerance thresholds in response to pH variation (Breda et al. 2021; Rosset and Bärlocher 1985), yet they generally prefer neutral to slightly acidic waters (Barreto et al. 2023). Lastly, electrical conductivity, which serves as a proxy for nutrient content in tropical water (Leite et al. 2016; Rezende et al. 2014), exhibited a negative association with FDis. The detrimental influence of electrical conductivity on the activities of some aquatic hyphomycete species can be attributed to its negative impact on their reproduction rates (Rezende et al. 2025; Sales et al. 2015). Therefore, the irregularity in the distribution of attributes in the functional space occupied by all species may decrease with extreme nutrient increases (Gomes et al. 2017; Medeiros et al. 2015). Consequently, changes in these physicochemical factors may have cascading effects on ecosystem functioning and aquatic hyphomycete assemblages (Rezende et al. 2019).

5 | Conclusion

Our study demonstrates that specific environmental conditions, particularly cooler temperatures, more dissolved oxygen, neutral pH, and lower electrical conductivity, are associated with greater functional diversity in aquatic hyphomycete assemblages colonizing leaf litter in Neotropical streams. These findings are consistent with ecological patterns predicted by Bergmann's rule, suggesting that colder environments may favor greater morphological and functional trait variation. Subtropical streams hosted fungal assemblages characterized by greater conidial shape diversity and larger reproductive structures, reflecting greater trait dispersion under more variable but moderate environmental conditions. In contrast, tropical streams showed less trait diversity and a predominance of taxa associated with nutrient-poor or chemically recalcitrant substrates. Rather than emphasizing taxonomic composition alone, our findings highlight the importance of functional traits as indicators of fungal community responses to environmental gradients. This trait-based perspective offers valuable insight into how aquatic fungal diversity may respond to future environmental changes across biogeographic regions.

Author Contributions

L.U.H. and A.O.M. conceived the study. L.U.H., A.O.M., J.F.G.J., M.S.M., Y.M., and R.S.R. collected field data. R.S.R. and R.B. managed and analyzed the data. R.S.R. wrote the manuscript with feedback from L.U.H., A.O.M., J.F.G.J., M.S.M., Y.M., and R.B.

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Ethics Statement

The experimental procedures were conducted following ethical guidelines. The authors have no conflicts of interest to disclose.

Consent

All authors have contributed to the manuscript and approved the submitted version.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.fj6q57471.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** btp70112-sup-0001-Supinfo.docx.