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The cooler the better: Increased aquatic hyphomycete diversity in subtropical streams along a neotropical latitudinal gradient

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ABSTRACT

Aquatic hyphomycetes are microbial decomposers in freshwater environments that, together with detritivores, play an essential role in the functioning of low-order streams. Here, we evaluated aquatic hyphomycetes communities associated with decomposing leaves of *Nectandra megapotamica*, a common Neotropical riparian tree, along a subtropical-tropical latitudinal gradient. Two forest streams located in subtropical regions and 3 in tropical regions were selected. We identified 29 species of aquatic hyphomycetes, 22 (75.8%) in subtropical streams and 15 (51.7%) in tropical streams. We also found a higher fungal biomass in subtropical streams. However, the amounts of leaf mass loss did not differ between regions, but the values were higher in summer than in winter. High temperature, pH and electrical conductivity values, as well as low dissolved oxygen levels, negatively affected spore production. These results suggest that the subtropical-tropical gradient is an important predictor of aquatic hyphomycete diversity; however, the observed species had different sensitivities to local environmental factors.

1. Introduction

Microorganisms play an essential role in ecosystem function through the decomposition of organic matter (Findlay, 2010). Aquatic hyphomycetes are the dominant microbial decomposers of allochthonous organic matter in low-order streams (Duarte et al., 2016). These fungi have a worldwide distribution (Barros and Seena 2022) and are ecologically important because they have an enzymatic capability to decompose plant structural polymers, such as cellulose, hemicellulose, and lignin (Krauss et al., 2011). Aquatic hyphomycetes constitute a polyphyletic group whose representatives can be easily found in well-aerated and nonpolluted stream reaches (Medeiros et al., 2009; Graça et al., 2016).

Several studies have shown the relative sensitivity of aquatic hyphomycetes to high temperatures in terms of physiology and community composition (Krauss et al., 2011; Gonçalves et al., 2013; Bärlocher and Boddy, 2016), although species differ in their temperature requirements for growth and reproduction (Rajashekhar and Kaveriappa, 2000; Pérez et al., 2021). Other environmental factors, such as pH, electrical conductivity, and water nutrient contents, can also influence the diversity and structure of aquatic hyphomycetes communities (Breda et al., 2021). According to Medeiros et al. (2009), low dissolved oxygen negatively affects aquatic hyphomycetes richness, biomass, reproduction, and, consequently, leaf decomposition rates. Aquatic hyphomycete species have different tolerance thresholds with respect to pH variations (Rosset and Bärlocher, 1985) but prefer neutral to slightly acidic waters. Under these conditions, there is increased diversity and competition among species (Krauss et al., 2011). In acidic

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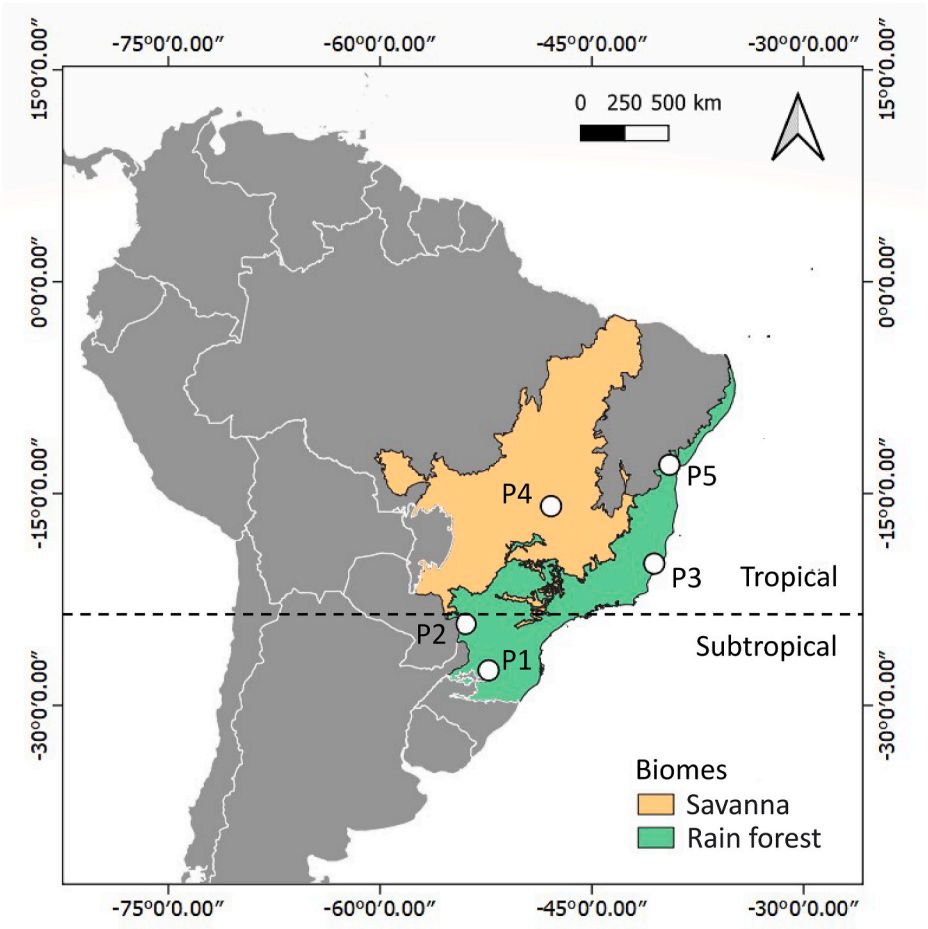

Fig. 1. Geographic location of the study sites in Atlantic Forest and Cerrado Savanna along the subtropical-tropical gradient.

waters, i.e., pH $\leq$ 5.5, reductions in microbiota associated with decomposing leaves normally occur, including several species of aquatic hyphomycetes (Baudoin et al., 2008). The electrical conductivity can also influence the richness and reproduction of aquatic hyphomycetes (Breda et al., 2021); low conductivity values decrease spore production, which affects species dispersal (Sales et al., 2015).

Tropical zones have the highest biodiversity on the planet, and this is at least in part related to the greater homogeneity of climatic conditions, mainly temperature (Willig and Presley, 2018; Seena et al., 2019). Moreover, an increasing latitudinal diversity gradient toward the tropics has been described for several but not all taxonomic groups (Willig and Presley, 2018). According to Seena et al. (2019), temperature is the key factor that determines the occurrences and composition of fungal communities associated with leaf decomposition. Temperature is therefore an essential environmental factor in determining the diversity and distribution of aquatic hyphomycetes (Chauvet and Suberkropp, 1998; Gonçalves et al., 2013). The importance of temperature is due to its role as a modulator of biological processes; therefore, thermal variations can result in the replacement of fungal species, possibly related to species-specific thermal physiological limits (Gonçalves et al., 2013).

Both the abundance and diversity of aquatic hyphomycetes are relatively low in tropical and subtropical regions. Stream physical conditions, nutrient availability, substrate types, seasonality, and even competition with other decomposer species provide possible explanations for this pattern (Graça et al., 2016). On the other hand, the remarkable taxonomic similarity of aquatic hyphomycete communities found in geographically distant locations in temperate zones probably resulted from the variety of ecological niches occupied by different species in those streams (Shearer et al., 2007; Duarte et al., 2016, 2017). However, to what extent the latitudinal pattern identified by Shearer et al. (2007) was biased by the significant differences in sampling efforts across regions is still unknown, which have been much more intense in temperate streams than elsewhere. Studies encompassing broad geographical areas across latitudinal gradients have largely been restricted to literature reviews, such as Duarte et al. (2016). Recently, the first broad-scale coordinated surveys using standardized methods were conducted by Seena et al. (2019) and demonstrated the great influence of water temperature on the diversity and distribution of litter-associated fungi in streams.

We conducted a coordinated field experiment to evaluate the aquatic hyphomycete communities in forest streams located along a subtropical-tropical gradient in Brazil. Our aims were (i) to determine the taxonomic compositions of aquatic hyphomycetes associated with the decomposing leaves of a common riparian tree species along this gradient and (ii) to identify the thresholds in water properties that determine the abundance and occurrence of different aquatic hyphomycetes species. We hypothesized that: (i) aquatic hyphomycete communities are more diverse in subtropical streams due to the lower water temperatures, regardless of seasonality, i.e., both in summer and winter seasons; (ii) aquatic hyphomycete species respond differently to the local environmental factors found along latitudinal gradients.

2. Material and methods

2.1. Study sites

Coordinated experiments were developed in five low-order forest streams located along a subtropical-tropical gradient in Brazil (Fig. 1).

We chose two streams in subtropical regions and three in tropical regions. Descriptions and the geographic coordinates of each stream studied are presented below.

P1 – Dourado (27° 36′ 07" S – 52° 16′ 12"W) is a second-order subtropical stream located in the Atlantic Forest of Rio Grande do Sul (southern Brazil). The vegetation consists of a mixture of subtropical forests composed of species that are distributed in the tropical-subtropical regions of upper Uruguay and mixed rainforests (Oliveira-Filho et al., 2015).

P2: Quati (24° 18′ 57.13" S – 53° 54' 38.55" W) is a first-order subtropical stream located in the conservation unit of São Camilo State Park (total area of 385.34 ha) in the western part of Paraná state (southern Brazil). The natural vegetation consists of a tropical seasonal semideciduous forest of the Atlantic Forest domain (Rezende et al., 2019).

P3 – Banana (20° 02′ 22,44'' S – 40° 31′ 50,89'' W) is a second-order tropical stream located at an altitude of 519 m a.s.l. within a fragment of the Atlantic Forest in Espírito Santo (SE Brazil). The riparian vegetation is well preserved, and there are no signs of erosion on the stream banks (Casotti et al., 2015).

P4: Cabeça de Veado (15° 53′ 11.74″ S – 47° 50′ 33.27″ W) is a second-order tropical stream located in the Botanical Garden of Brasília, which is an important preservation area within the Federal District (central-west Brazil) composed of substantial areas representing many of the Cerrado physiognomies (Gomes et al., 2016).

P5 – Cai Camarão (12° 57′ 35.8" S – 39° 26′ 55.9" W) is a second-order tropical stream located in Serra da Jibóia, a mountainous massif located in the southern region of Bahia (NE Brazil), which is mostly covered by the Atlantic Forest (Blengini et al., 2015).

2.2. Experimental design

We used *Nectandra megapotamica* leaves in the coordinated experiments. This tree species occurs in different Brazilian phytogeographic domains, including the Amazon, Cerrado Savannah, and Atlantic Forest (Flora e Funga do Brasil, 2020). Senescent leaves of this species were collected using litter traps fixed 1.5 m high in both stream banks of one of the study sites (P1). The litter traps were checked regularly, and captured leaves were air dried at the laboratory and stored in the dark until the start of the experiments. The collected leaves were well mixed and divided into 6 portions; 5 portions were used in the experiments developed at each study site, and the last portion was used for determinations of the initial leaf chemistries (time 0 leaves). We adopted these procedures to standardize the leaf chemical and physical characteristics in our study because leaf chemistry can influence microbial colonization and, consequently, leaf decomposition (Graça et al., 2016). The initial chemistry determinations of *N. megapotamica* leaves included total phosphorous, total phenolics, tannins, cellulose and lignin based on the protocols described in Bärlocher et al. (2020).

We conducted coordinated experiments during the periods from June to August 2013 (winter in the Southern Hemisphere) and from January to March 2014 (summer) at all study sites. A total of 12 fine mesh (0.5 mm) litter bags (15 × 20 cm), containing 3.0 ± 0.1 g of leaves each, were incubated on the streambed of each study site and were tied to submerged cobbles and roots at similar depths. Fine mesh bags were utilized to exclude as many invertebrates as possible. Four litter bags (replicates) were sampled from each site after 15, 30, and 60 d of incubation. The litter bags were placed in plastic bags and transported in an ice box to the laboratory. All samples were processed on the day of sampling to characterize the aquatic hyphomycete communities (e.g., ergosterol contents, sporulation rates, and taxonomic compositions) and leaf mass loss amounts. On each sampling occasion, water physical and chemical properties (e.g., temperatures, dissolved oxygen levels, pH values, and electrical conductivities) were determined *in situ* with a handheld multiparameter meter.

In the laboratory, leaves were removed from the litter bags and washed with distilled water. Three sets of five leaf discs were cut (using a 12 mm cork borer) from five leaves randomly chosen from each sample. These sets of leaf discs were used to (i) determine the ergosterol contents (an estimate of fungal biomass); (ii) the taxonomic compositions of aquatic hyphomycetes associated with decomposing leaves, as well as the sporulation rates; and (iii) sample ash-free dry mass (AFDM) amounts. Leaf mass losses were determined from the remaining leaves of each sample. This material was oven-dried (60 °C), weighed (0.01 mg), ignited (500 °C, 4 h), and reweighed. The remaining leaf dry mass, corrected with the weight of the sets of leaf discs removed, was then expressed as a percentage of the initial AFDM (Bärlocher et al., 2020).

2.3. Ergosterol content

Ergosterol contents were determined according to Gessner (2020). The first set of leaf discs was stored in 10 mL of methanol/KOH at −20 °C until extraction. Lipid extraction and saponification were performed at 80 °C for 30 min. The extract was then purified by solid-phase extraction (Sep-Pak Vac-RC-500 mg, Waters, USA) and quantified by high-performance liquid chromatography (HPLC, Dionex Ultimate 3000) by measuring the absorbances at 282 nm at 35 °C. The results were expressed as μg ergosterol. g leaf $AFDM^{-1}$.

2.4. Sporulation rates

To determine the sporulation rates and taxonomic compositions of the aquatic hyphomycete communities associated with incubated leaves, a second set of discs from each sample was placed in 200 mL Erlenmeyer flasks containing 30 mL of distilled water. The Erlenmeyer flasks were agitated on an orbital shaker (90 rpm) for 48 h at 20 °C (room temperature). The spore suspensions were then fixed in formalin (4%) and filtered (Millipore, pore size 5 mm, Billerica, MA, USA), and the filters were stained with cotton blue (0.05%) in 60% lactic acid. The filters were observed under an optical microscope (400 × magnification, Olympus B×43) to estimate the number of spores and species richness. The sporulation rates were expressed as the number of spores. mg leaf $AFDM^{-1}$. day^{-1} (Bärlocher, 2020).

2.5. Taxonomic identification

Spore morphologies were used to identify the taxonomic composition of aquatic hyphomycetes in each sample according to specific taxonomic keys (e.g., Fiuza et al., 2015, 2017; Gulis et al., 2020).

2.6. Data analysis

We used generalized linear mixed-effects models ("glmer" function in "lme4" package in R) to evaluate the effects of study sites, seasonality (summer and winter experiments), and interactions between these two factors (explanatory variables) on the biomass and taxonomic richness of aquatic hyphomycetes (response variables) by Gaussian (link = identity) and Poisson (link = log) distributions (Bates et al., 2015). The incubation periods (e.g., 15, 30, and 60 days) were included in the models as a random factor (time) to remove temporal pseudoreplication (see Crawley, 2007). The p values were obtained by likelihood ratio tests (Chi-square distribution) of the full model against a partial model without the explanatory variables (Crawley, 2007). Contrast analysis was used to determine the differences among study sites and seasons (Crawley, 2007). In this orthogonal analysis, sites were ordered in ascending order and tested pairwise (with the closest values). The study sites that had no differences were sequentially added to the model, and tests were performed with the following values in a simplified stepwise model (see Crawley, 2007).

A redundancy analysis (RDA) was used to evaluate the differences in aquatic hyphomycete communities along the latitudinal gradient (standardized) and to identify the potential environmental requirements

Table 1
Water properties (mean ± SD, n = 4) of the study sites determined during the coordinated experiments developed during the winter and summer.

	Subtropical		Tropical		
	P1	**P2**	**P3**	**P4**	**P5**
Winter					
Temperature (°C)	12.4 ± 2.4	18.7 ± 0.5	19.2 ± 0.7	18.6 ± 1.0	21.4 ± 0.5
Dissolved oxygen (mg L^{-1})	12.9 ± 0.8	8.7 ± 0.3	8.5 ± 0.4	7.7 ± 0.9	10.2 ± 5.7
Electrical conductivity (mS cm^{-1})	50 ± 1	42 ± 1.9	27.1 ± 4.9	54 ± 3.3	52.9 ± 15.0
pH	6.6 ± 0.6	6.5 ± 0.4	7.4 ± 0.1	6.6 ± 0.7	4.1 ± 0.2
Summer					
Temperature (°C)	19.4 ± 1.3	19.6 ± 0.6	21.8 ± 0.1	21.0 ± 0.2	24.1 ± 0.3
Dissolved oxygen (mg L^{-1})	10.7 ± 0.5	8.0 ± 0.2	8.3 ± 0.3	7.0 ± 0.4	6.37 ± 1.0
Electrical conductivity (mS cm^{-1})	70 ± 1	37.8 ± 1.1	28.2 ± 0.9	58 ± 3.6	43.8 ± 7.8
pH	7.2 ± 0.5	6.7 ± 0.7	7.3 ± 0.1	5.8 ± 0.8	6.5 ± 0.2

of the communities found (Hellinger transformed; "rda" function from "vegan" package in R) (Legendre and Legendre, 1998). In the RDA, only species with at least three occurrences were considered. The statistical significance of the correlations among the environmental factors and biotic variables extracted from the RDA was determined by a Monte Carlo test based on 5000 permutations ($p < 0.05$; "envfit" function in R). Permutational multivariate analysis of variance (PERMANOVA) was also used to test for composition differences among the study sites and seasons (Oksanen et al., 2014). We used pairwise comparisons corrected by Bonferroni as a post hoc test.

The thresholds of water properties (e.g., temperature, dissolved oxygen, electrical conductivity, and pH) for aquatic hyphomycetes species were analyzed using the Threshold Indicator Taxa Analysis ("titan" function from the "TITAN2" package in R) in four individual models (Baker and King, 2010). Threshold indicator taxon analysis is based on indicator species analysis (Dufrêne and Legendre, 1997) and change point analysis (King and Richardson, 2003). Based on the occurrence frequencies and relative abundances of aquatic hyphomycete species, this analysis evaluates the changes in species distributions along environmental gradients (King et al., 2011). Therefore, threshold indicator taxon analysis highlights the change points based on alterations in the means and variances of the response variable, with z- (negative responders, or decliners) and z+ (positive responders, or increases) of the species associated with the lowest and highest values of the analyzed environmental gradient, respectively (Baker and King, 2010). These species distribution changes from threshold indicator taxon analysis were detected in space or over time and were associated with individual species with different environmental and temporal scores (King et al., 2011). In the threshold indicator taxon analysis, only those species with at least three occurrences were considered. Additionally, for the threshold indicator taxon analysis, the significance was set to $p \leq 0.05$ (IndVal), and purities and reliabilities $\geq$0.70 were considered (Baker and King, 2010). The relationships between the taxonomic compositions of aquatic hyphomycetes and environmental gradient were assessed by ranking the relative abundances of species and comparing this rank with the temperature, dissolved oxygen, electrical conductivity, and pH scores (individually).

3. Results

3.1. Leaf decomposition and microbial colonization

The initial chemistry of *Nectandra megapotamica* leaves was (mean ± SD, n = 4) 0.20 ± 0.04% for total phosphorous, 5.30 ± 0.45% for total phenolics, 0.04 ± 0.01% for tannins, 27.7 ± 3.9% for cellulose, and 39.4 ± 3.7% for lignin. The chemical and physical characteristics of the study sites are represented in Table 1.

At the end of the experiments, the mean leaf mass loss across all

Table 2
Results of the generalized linear mixed-effects models fitted for leaf litter mass loss (a), ergosterol content (b), taxonomic richness (c), and sporulation rates (d), with the analysis of contrasts between study sites (tropical and subtropical), seasons (winter and summer) and their interactions.

	Df	AIC	BIC	logLik	deviance	Chisq Chi	Df	Pr(>Chisq)	Analysis of contrasts
A. Mass Loss %									
null	4	697.1	707.5	−344.5	689.1				
Zone	6	699.9	715.6	−343.9	687.9	1.18	2	0.555	
null	6	699.9	715.6	−343.9	687.9				
Seasonality	7	565.4	583.7	−275.7	551.4	136.46	1	<0.001	Winter < Summer
null	3	700.9	708.8	−347.5	694.9				
Interaction	6	699.9	715.6	−343.9	687.9	7.06	3	0.070	
B. Ergosterol μg.g AFDM									
null	4	1490.8	1501.3	−741.41	1482.8				
Zone	7	1430.9	1449.2	−708.43	1416.9	65.96	3	<0.001	Tropical < Subtropical
null	7	1430.9	1449.2	−708.43	1416.9				
Seasonality	7	1430.9	1449.2	−708.43	1416.9	0.00	0	1.000	
null	3	1503.4	1511.2	−748.68	1497.4				
Interaction	7	1430.9	1449.2	−708.43	1416.9	80.50	4	<0.001	
C. Number of species									
null	3	348.8	356.7	−171.4	342.8				
Zone	5	342.1	355.1	−166.0	332.1	10.74	2	0.004	Tropical < Subtropical
null	5	342.1	355.1	−166.0	332.1				
Seasonality	6	335.3	351.0	−161.6	323.3	8.79	1	0.003	Winter < Summer
null	2	401.6	406.9	−198.8	397.6				
Interaction	5	342.1	355.1	−166.0	332.1	65.56	3	<0.001	
D. Mean conidia mg.AFDM.day									
null	4	792.9	803.4	−392.5	784.9				
Zone	6	796.1	811.8	−392.0	784.1	0.83	2	0.659	
null	6	796.1	811.8	−392.0	784.1				
Seasonality	7	794.8	813.2	−390.4	780.8	3.24	1	0.072	
null	3	801.5	809.4	−397.8	795.5				
Interaction	6	796.1	811.8	−392.0	784.1	11.44	3	0.010	

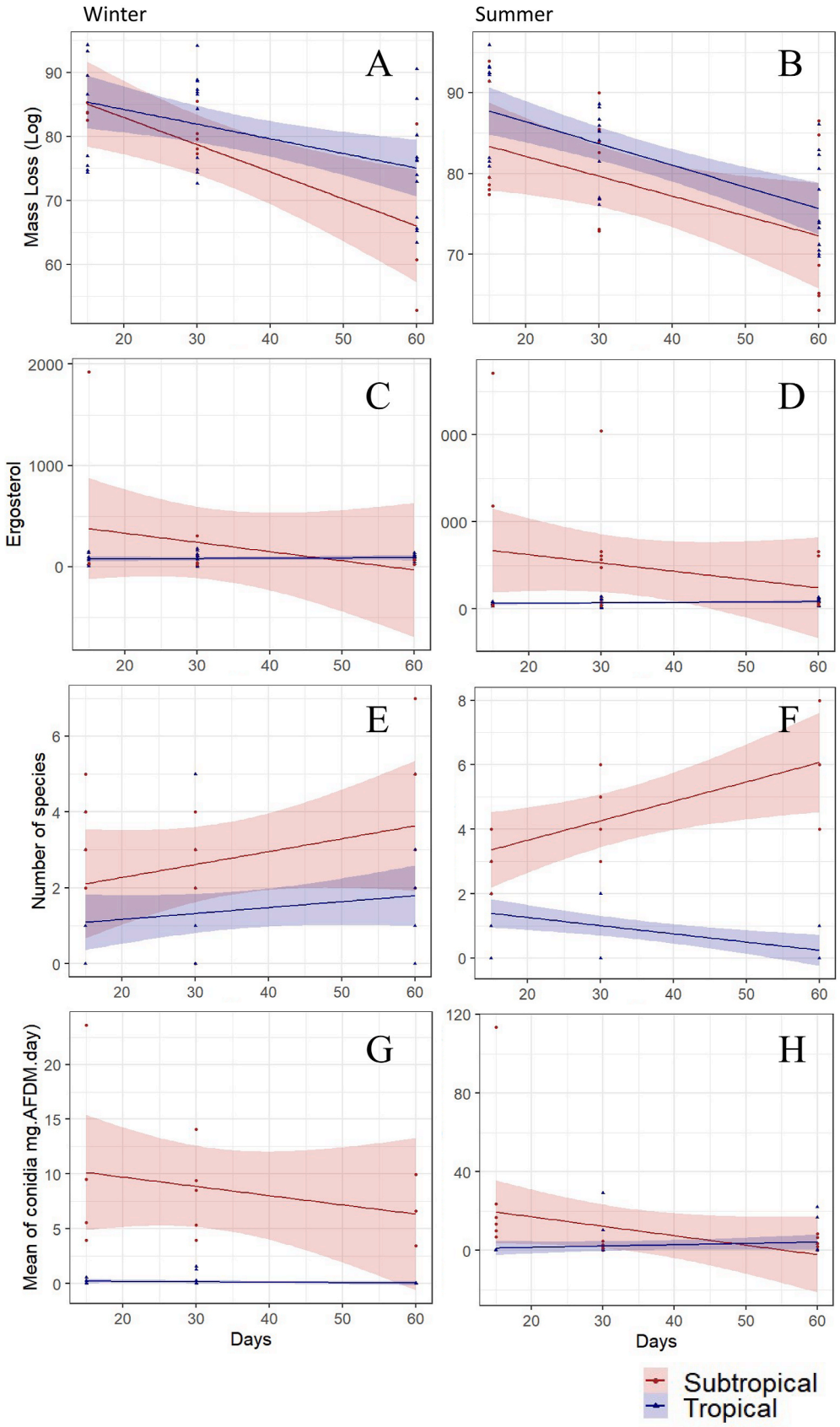

Fig. 2. (A, B) Leaf mass remaining (%), (C, D) ergosterol contents (μg.g^{-1} leaf AFDM), (E, F) taxonomic richness (# species), and (G, H) sporulation rates (conidia.mg AFDM^{-1}) of aquatic hyphomycetes found associated with leaves incubated for 15, 30 and 60 d in (A, C, E, G) winter and (B, D, F, H) summer coordinated experiments.

Table 3
Occurrence of the 29 species of aquatic hyphomycetes found in the five study sites along the subtropical-tropical gradient.

Aquatic hyphomycetes species	SUBTROPICAL		TROPICAL		
	P1	P2	P3	P4	P5
Alatospora acuminata	x	x			
Amniculicula longissima	x	x	x	x	x
Anguillospora filiformis	x	x	x	x	x
Anguillospora furtiva		x			
Anguilospora crassa	x	x	x	x	
Aquanectria submersa	x	x		x	
Campylospora chaetocladia	x	x			
Campylospora sp.	x				
Camposporium pellucidum				x	
Clavariopsis aquatica	x				
Clavatospora tentacula	x				
Colispora curvata			x		x
Condylospora gigantea		x			
Curucispora ponapensis		x		x	
Culicidospora aquatica	x				
Diplocladiella scalaroides		x			
Flagellospora curvula				x	x
Gyoerffyella gemellipara		x			
Lemonniera filiformis	x	x			
Lemonniera pseudofoscula	x	x			
Lunulospora curvula	x	x	x	x	x
Mycofalcella calcarata			x		
Subulispora curvata				x	
Triscelophorus acuminatus	x	x	x		
Triscelophorus monosphorus	x	x	x		
Triscelophorus myrti		x			
Triscelophorus monosporus				x	
Tricladium crucisporum				x	
Ypsilina graminea		x			

study sites was 80.3 ± 8.6% (mean ± SD). The mass losses found in P4 (87.2 ± 5.8%), P2 (86.3 ± 3.5%) and P3 (83.8 ± 6.7%) were higher than those in P5 (73.8 ± 5.1%) and P1 (73.6 ± 8.2%) (glmer; Akaike information criterion/AIC = 561; Bayesian information criterion/BIC = 592; $\chi^2_{(12,97)} = 157$; $p < 0.001$; Figure SM1A and B). There were no differences between the mass losses found in subtropical (78.2 ± 9.2%) and tropical regions (81.3 ± 8.1%; Table 2A; Fig. 2A and B). On the other hand, higher values were found in summer (83.4 ± 3.6%) than in winter (75.1 ± 4.3%; Table 2A).

Regarding microbial colonization, the highest ergosterol contents were found in P2 (985.1 ± 811.3 μg g leaf AFDM^{-1}); the ergosterol contents were more than 10 × lower in the other sites and were (in decreasing order) P5 (95.4 ± 39.5 μg g leaf AFDM^{-1}), P4 (94.6 ± 27.2 μg g leaf AFDM^{-1}), P1 (49.5 ± 26.8 μg g leaf AFDM^{-1}) and P3 (42.9 ± 30.8 μg g leaf AFDM^{-1}) (glmer; AIC = 1438; BIC = 1469; $\chi^2_{(12,97)} = 81$; $p < 0.001$; Figure SM1C and d). These contents were also higher in subtropical regions (389.7 ± 660.1 μg g leaf AFDM^{-1}) than in tropical regions (79.6 ± 41.3 μg g leaf AFDM^{-1}; Table 2B; Fig. 2C and D). In addition, no significant differences were found between the experiments conducted in summer (230.5 ± 479.5 μg g leaf AFDM^{-1}) than in winter (117.3 ± 278.6 μg g leaf AFDM^{-1}; Table 2B).

We identified a total of 29 species across all study sites (Table 3). The highest taxonomic richness was found in P2 (18 species), followed by P1 (15 species), P4 (11 species), P3 (8 species), and P5 (5 species). Streams in the subtropical regions had higher richness (4 ± 2.1; range 0–8) than those in tropical regions (1 ± 1.2; range 0–5; Table 2C; Fig. 2E and F). The values observed in summer (2 ± 1.8; range 0–8; Fig. 2F) were higher than those in winter (1 ± 1.2; range 0–8; Table 2C). The most common species of aquatic hyphomycetes were *Anguillospora filiformis, Lunulospora curvula* and *Amniculicola longissima.* P1, P2, and P4 had exclusive species, i.e., species that were found in only one of the study sites (e.g., P1: *Campylospora* sp., *Clavariopsis aquatica, Clavatospora tentacula,* and *Culicidospora aquatica*; P2: *Alatospora acuminata, Curucispora ponapensis,* and *Triscelophorus myrti;* P4: *Camposporium pellucidum*, *Subulispora curvata,* and *Tricladium crucisporum*) (Table 3).

The highest sporulation rates were found in P1 and P2 (241.3 ± 32.1 and 100.1 ± 25.9 spores. mg AFDM^{-1}. day^{-1}, respectively), followed by P5 (45.7 ± 31.6 spores. mg AFDM^{-1}. day^{-1}), P4 (17.5 ± 41.6 spores. mg AFDM^{-1}. day^{-1}) and P3 (15.8 ± 36.7 spores. mg AFDM^{-1}. day^{-1}) (glmer; AIC = 500; BIC = 532; $\chi^2_{(12,97)} = 65.7$; $p < 0.001$; Figure SM1 G and H). On the other hand, no differences in sporulation rates were found between subtropical (291.4 ± 123.1% spores. mg AFDM^{-1}.day^{-1}) and tropical regions (25.2 ± 63.2% spores. mg AFDM^{-1}. day^{-1}; Table 2D; Fig. 2G and H). No significant differences were found between summer (257.8 ± 23.7% spores. mg AFDM^{-1}. day^{-1}) and winter (193.3 ± 35.9% spores. mg AFDM^{-1}.day^{-1}) seasons (Table 2D).

3.2. Aquatic hyphomycete communities and environmental requirements

The RDA (total inertia of 0.682) of the abiotic variables and aquatic hyphomycete communities (Fig. 3) exhibited high explanatory power (50%, inertia of 0.341). Axis 1 of the RDA ordination explained 35% (inertia of 0.238) of the total variance, while axis 2 explained 13% (inertia of 0.088). The structures and compositions of communities changed between subtropical and tropical regions (PERMANOVA, $F_{(4,143)} = 26.58$; $p = 0.001$) and between summer and winter (PERMANOVA, $F_{(1,146)} = 4.31$; $p = 0.004$). Water temperatures and tropical streams were positively correlated with axis 1, whereas, the dissolved oxygen contents, electrical conductivity, pH, and subtropical streams were negatively correlated with axis 1.

Only 11 species of aquatic hyphomycetes had the predetermined requirements for TITAN analysis: *A. filiformis, Aquanectria submersa, Colispora curvata, Campylospora chaetocladia, C. pellucidum, C. tentacula, Flagellospora curvula, L. curvula, Triscelophorus monosphorus, Triscelophorus acuminatus*, and *Flagellospora curvula.* Based on the temperature gradient, the community thresholds were 19–24 °C (sum z+) and 12–19 °C (sum z-; Table SM2). According to the significance criteria adopted ($p \leq 0.05$, reliability and purity ≥0.70), seven species (e.g., *A. submersa, C. curvata, C. chaetocladia, C. tentacula, F. curvula, L. curvula,* and *T. acuminatus*) exhibited relationships with temperature. Except for *F. curvula*, the spore production amounts of all other species decreased with increasing temperature (Fig. 4; Table SM2). Again, seven species had relationships with dissolved oxygen (e.g., *A. submersa, C. curvata, C. chaetocladia, C. tentacula, F. curvula, L. curvula,* and *T. monosphorus*). All these species except *F. curvula* increased their spore production with increased dissolved oxygen contents (Fig. 4). Based on the dissolved oxygen gradient, the community thresholds were 10.18–10.70 mg. L^{-1} (sum z+) and 7.01–7.71 mg. L^{-1} (sum z-) (Table SM2). The electrical conductivity was related to six species (e.g., *A. submersa, C. chaetocladia, C. pellucidum, C. tentacula, L. curvula,* and *F. curvula*). The spore production amounts of these species decreased with increasing electrical conductivity, except for *C. pellucidum* and *F. curvula*. Based on the electrical conductivity gradient, the community thresholds were 33.25–70.00 μS cm^{-1} (sum z+) and 5.79 to 27.18 μS cm^{-1} (sum z-). Finally, only four species exhibited relationships with the pH gradient. Spore production of *A. filiformis* and *F. curvula* decreased with increasing pH, while the spore production of *C. chaetocladia* and *C. tentacula* increased with decreasing pH (Fig. 4). The community thresholds, based on the pH gradient, were 6.56–6.66 (sum z+) and 5.82 to 7.29 (sum z-; Table SM2).

4. Discussion

Despite the high diversity of aquatic hyphomycetes at the subtropical sites, the levels of leaf litter decomposition did not differ from those at tropical sites.

Nectandra megapotamica leaves decomposed more rapidly in the summer but this did not differ between tropical and subtropical sites. However, the taxonomic richness of aquatic hyphomycetes was higher in subtropical sites, with no observed differences between summer and

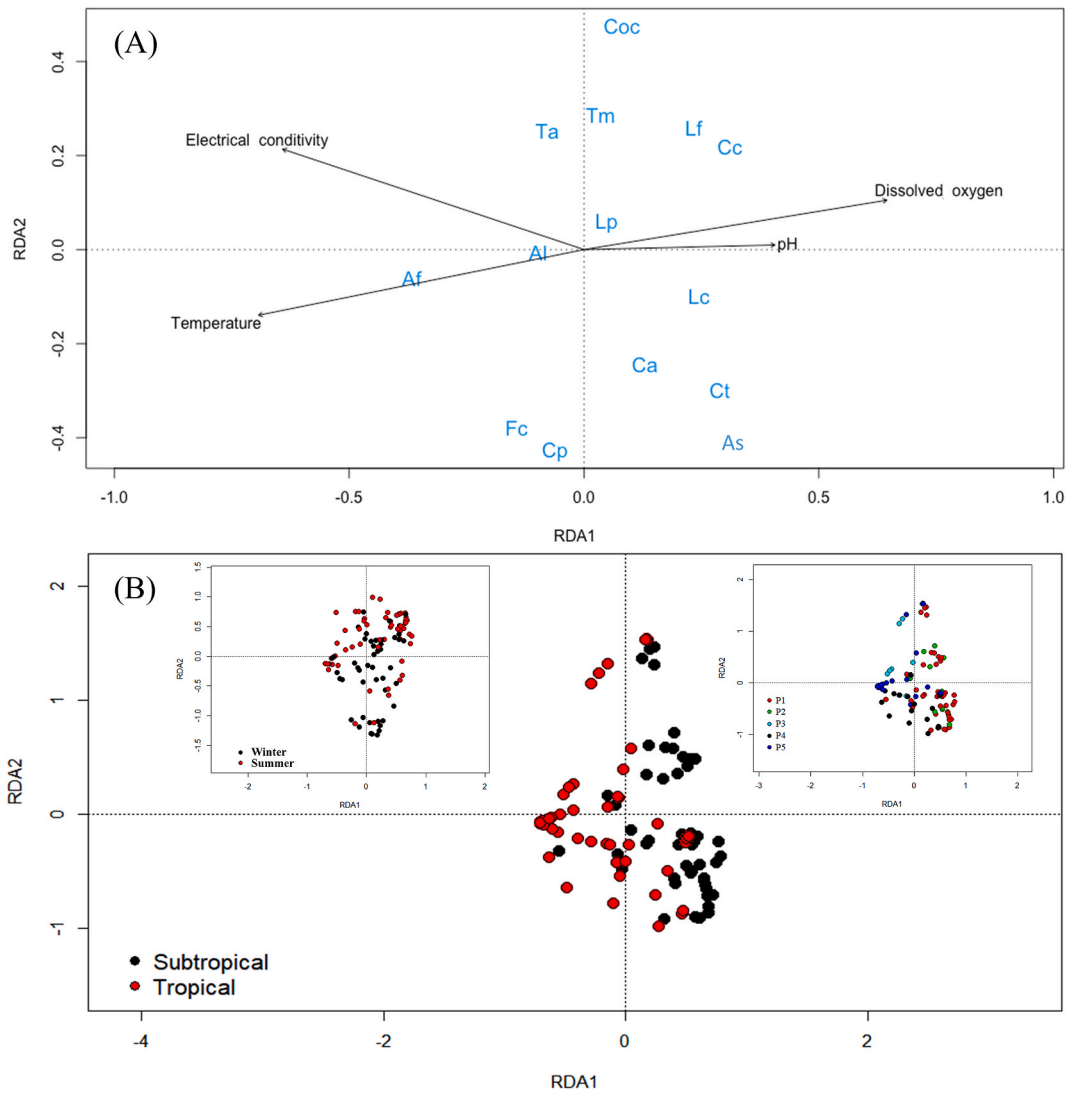

Fig. 3. (A) Redundancy Analysis among water properties and aquatic hyphomycete communities. (B) The subtropical-tropical gradient, as well as the seasons and sites in which the coordinated experiments were developed. Cp = *Campilosporium pellucidum*, As = *Aquanectria submersa*, Fc = *Flagellospora curvula*, Lc = *Lunulospora curvula*, Ct = *Clavatospospora tentacula*, Af = *Anguillospora filiformis*, Ca = *Culicidospora aquatica*, Al = *Anguillospora longissima*, Lp = *Lemoniera pseufloscula*, Lf = *Lemoniera filiformis*, Ta = *Tricelosphorus acuminatus,* Tm = *Tricelosphorus monosporus*, Cc = *Campilospora chaetocladia*, Coc = *Colispora curvula*.

winter. In contrast to the global pattern of increased biodiversity in the tropics, aquatic hyphomycetes are more prevalent in temperate regions (Shearer et al., 2007; Duarte et al., 2016; Graça et al., 2016). According to Jabiol et al. (2013), the latitudinal variations in the diversity of these fungi can be explained by seasonality; because of the slight seasonal variations, tropical regions have reduced niche spaces associated with temperature, resulting in lower aquatic hyphomycete diversity (Shearer et al., 2007). Sites located in the subtropical regions of Brazil have climatic conditions that are similar to those of temperate regions. Therefore, the biomass and taxonomic richness of the aquatic hyphomycete communities observed in the subtropical sites were similar to those found in studies that took place in temperate regions where the decomposition process was faster (Graça et al., 2016). The ergosterol concentrations found (79.6 ± 41.3 μg g leaf AFDM^{-1}) in streams from tropical zones were low compared to those of other tropical (approximately 300 μg g leaf AFDM-1 in Sales et al., 2015 and ~900 μg g leaf AFDM^{-1} in Alvin et al., 2015) and temperate streams (~400 μg g leaf AFDM^{-1} Gonçalves Junior et al., 2006). Alternatively, leaf breakdown rates were similar in tropical and subtropical regions, and these results did not corroborate those reported by Gonçalves Junior et al. (2006), who found that leaf litter decomposition rates were greater in temperate streams than in tropical streams. This could be explained by the sensitivity to organic matter characteristics since plant species with high concentrations of nutrients and concentrations of structural and secondary compounds decompose faster than recalcitrant organic matter (Ferreira et al., 2021).

The results found in the present study diverge from the global pattern of species distributions (Willig and Presley, 2018), as well as temperate aquatic ecosystems, in which increased temperatures favor decomposer microorganisms and decomposition rates. However, reductions in fungal diversity and changes in the structures of their communities with temperature have been observed (Gonçalves et al., 2013). Possible explanations for the low diversity of aquatic hyphomycetes found in the tropical sites of the current study (e.g., P3, P4, and P5) include (i) lower seasonality, which is represented by the low annual temperature variations in tropical zones compared to subtropical regions (Graça et al., 2016) and the nutrient contents in sites P4 (Gomes et al., 2016) and P5 (Medeiros et al., 2015), (ii) competition with other decomposers (Graça et al., 2016), and (iii) other fungal groups, playing greater roles in the decomposition process in tropical regions, such as yeasts (Gonçalves Junior et al., 2006) or even aero aquatic fungi (Fiuza et al., 2019).

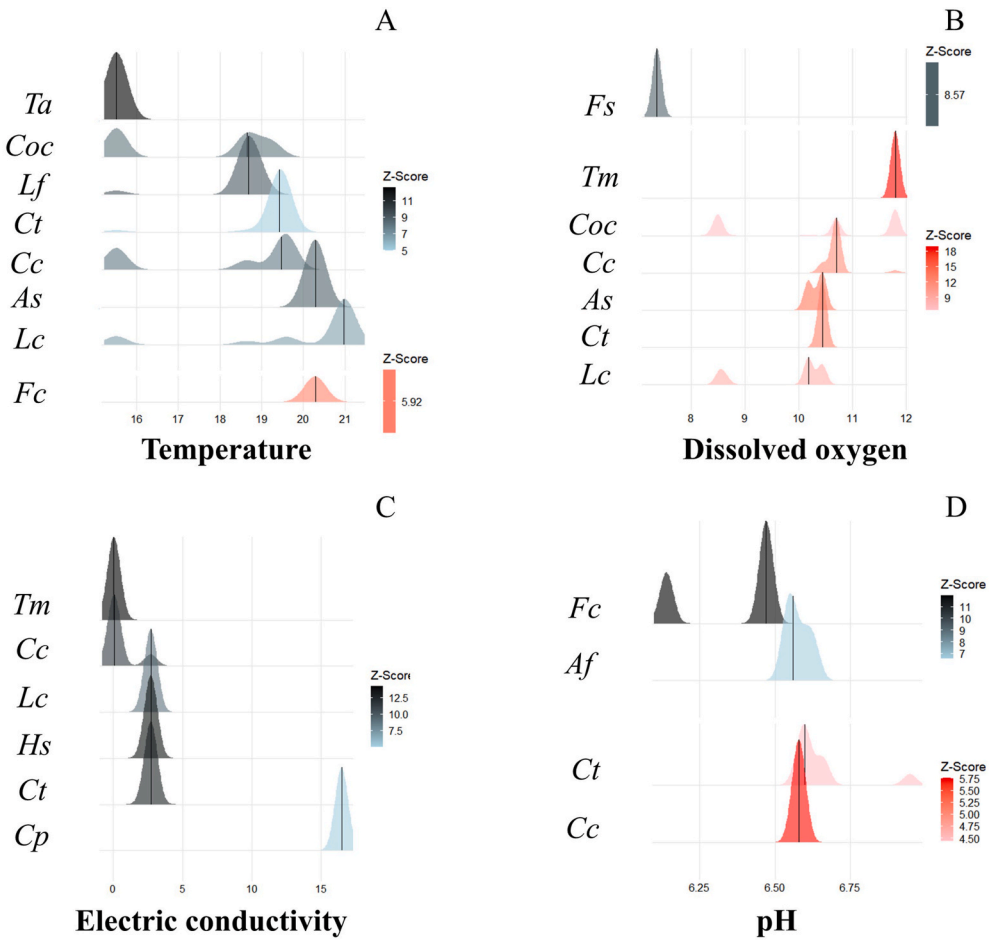

Fig. 4. Results of TITAN showing values of largest indicator z-scores in aquatic hyphomycete communities change points by probability density function of the nBoot bootstrapped replicates (n = 500) along the subtropical-tropical gradient by (A) temperature, (B) dissolved oxygen, (C) electrical conductivity, and (D) pH. Taxa names are arranged discretely along the y-axis based on the rank order of the central tendency of the probability density function for z- (dark colors were negative, decliners) and z+ (red colors positive, increases), respectively. Cp = *Campilosporium pellucidum*, As = *Aquanectria submersa*, Fc = *Flagellospora curvula*, Lc = *Lunulospora curvula*, Ct = *Clavatopospora tentacula*, Af = *Anguillospora filiformis*, Ca = *Culicidospora aquatica*, Al = *Anguillospora longissima*, Lp = *Lemoniera pseufloscula*, Lf = *Lemoniera filiformis*, Ta = *Tricelosphorus acuminatus*, Tm = *Tricelosphorus monosporus*, Cc = *Campilospora chaetocladia*, Coc = *Colispora curvula*.

4.1. Aquatic hyphomycete responses to environmental variables

The structures and compositions of the aquatic hyphomycete communities differed locally and seasonally. However, two species were dominant at all stream sites. *Lunulospora curvula* and *Anguillospora longuissima* are considered common species in both temperate (Gessner et al., 1993; Pérez et al., 2018; Gossiaux et al., 2019) and tropical streams (Smits et al., 2007; Fiuza and Gusmão 2013; Sales et al., 2015; Schoenlein-Crusius et al., 2015; Fiuza et al., 2017, 2022; Del Cid et al., 2019). The higher diversity of aquatic hyphomycete communities in subtropical streams might be related to the similar environmental conditions present, such as high altitudes and low temperatures (Graça et al., 2016).

Sporulation rates decreased with temperature, supporting the preference of aquatic hyphomycetes for low temperatures (Krauss et al., 2011; Gonçalves et al., 2013; Bärlocher and Boddy, 2016). According to Seena et al. (2019), water temperatures influence the distribution and diversity of fungal decomposers, as well as community composition. In addition, interspecific interactions among aquatic hyphomycete species may affect their response to temperature (Suberkropp, 1984). Among the species that exhibited relationships with temperature, *Flagellospora curvula* was the only one that was not affected by increased temperature. Because this species is adapted to higher temperatures, it is considered a cosmopolitan species and occurs in both tropical and temperate regions (Sridhar et al., 2010; Fiuza et al., 2017).

Although some aquatic hyphomycete species can grow under anaerobic conditions (Field and Webster, 1983), in the present study, seven species were related to dissolved oxygen levels. Among them, only *F. curvula* did not produce greater numbers of spores with increasing dissolved oxygen levels. These results corroborate those found by Medeiros et al. (2009), who reported *F. curvula* as one of the rare species that survived under low dissolved oxygen levels. The negative influence of electrical conductivity on the activities of some aquatic hyphomycete species might be related to the fact that this parameter decreases their reproduction rates (Sales et al., 2015) and, consequently, their participation in leaf litter decomposition (Breda et al., 2021).

Low pH values can act as physiological stressors in aquatic communities. Decreases in water pH favor acid-tolerant fungi and cause reductions in species richness (Sales et al., 2015; Tolkkinen et al., 2015; Ortiz-Vera et al., 2018) because most species prefer slightly acidic waters (Rosset and Bärlocher, 1985). While *Anguillospora filiformis* and *F. curvula* were favored by low pH values, *Campylospora chaetocladia* and *Clavatospora tentacula* were not favored or were even inhibited. Our results can, therefore, indicate the natural niche of each aquatic hyphomycete species along the pH gradient.

5. Conclusion

This study revealed that aquatic hyphomycete communities had higher diversity in forest low-order streams located at higher latitudes. In tropical sites, where streams have higher temperatures, aquatic hyphomycetes have low diversity. Despite this, the influences of these communities on leaf decomposition did not differ between tropical and subtropical sites. Other environmental factors, such as dissolved oxygen, electrical conductivity, and pH, influenced the diversity and structure of aquatic hyphomycete communities. Furthermore, several species had specific responses to these environmental factors, which demonstrates the high sensitivity of aquatic hyphomycetes to environmental changes. Therefore, it is necessary to carry out more studies to evaluate the role of aquatic hyphomycetes in organic matter processing in tropical regions

to expand the knowledge of these important decomposers in the energy flow and nutrient cycling of forest streams.

Author contributions

LUH conceptualized the experiment. RSR performed the statistical analyses. LUH, RSR, JFGJ, MSM, YM, RCL, AOM, and GGB performed the experiments. All authors were involved in the interpretation of the results and in the manuscript and the writing was led by GGB and AOM.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2022.101223.

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