Aquatic hyphomycetes in South America and their application as water quality indicators

Hifomicetos acuáticos en América del Sur y su aplicación como indicadores de calidad de agua

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Abstract

Aquatic hyphomycetes are mainly present in pristine lotic aquatic ecosystems, anamorphic fungi that degrade the plant material in this ecosystem, facilitating the cycling of nutrients in the trophic chain. Hyphomycetes are ecologically very important, given their role as bio-indicators due to their sensitivity or tolerance to different physicochemical changes in the ecosystem. However, the taxonomic, ecological, and molecular descriptions are poorly described in a few studies in tropical regions of South America, except for Bolivia and Paraguay, which have none. Currently, a total of 495 species (184 Ingoldian, 46 Aero aquatic, and 265 transitional) have been reported, led by Brazil with 279 species, 121 of which are Ingoldian, followed by Venezuela with 150 species, including 83 Ingoldian and 8 Aero aquatic. The capture of Ingoldian and aero-aquatic fungi spores had more remarkable similarity with the foam and water methods, unlike transitional fungi, which do not present adequate morphological adaptations for them, being particularly captured by the incubation method of plant material. Nevertheless, there are few studies on environmental quality, mostly carried out in Venezuela. Therefore, this review aims to facilitate the development of new studies in lotic and lentic bodies. In this order, aquatic hyphomycetes should be strengthened as additional bioindicators of environmental quality, promoting the ecologically sustainable use of resources.

Key words: ingoldian fungi; aero-aquatic fungi; transitional fungi, bioindicator, environmental quality

Resumen

Principalmente en ecosistemas acuáticos loticos pristinos están presentes los hifomicetos acuáticos, hongos anamorficos que degradan el material vegetal en el mismo, facilitando el ciclaje de nutrientes en la cadena trofica. Son muy importantes ecológicamente, dado su rol biondicador debido a la sensibilidad o tolerancia a diferentes cambios fisicoquímicos del ecosistema, sin embargo, son pocos los estudios taxonómicos y ecológicos en la región tropical como lo es Suramerica, donde se reportan estudios en todos los paises, excepto Bolivia y Paraguay, registrando un total de 495 especies (184 Ingoldianas, 46 Aero acuáticas y 265 transicionales), liderado por Brasil con 279 especies, 121 de las cuales son Ingoldianas, seguido de Venezuela con 150 especies, incluyendo 83 Ingoldianas y 8 Aero acuáticas. La captación de esporas de hongos Ingoldianos y aero acuaticos tuvo mayor similitud con los metodos de espuma y agua, a diferencia de los hongos transicionales, que no presentan adapaciones morfologicas adecuadas para estos, captándose particularmente por el método de incubación de material vegetal. No obstante, son pocos los trabajos en calidad ambiental, en su mayoría realizados en Venezuela. Por lo cual, esta revisión busca facilitar el desarrollo de nuevos estudios al respecto en la región, tanto en cuerpos loticos como lenticos, a fin de afianzar a los hifomicetos acuáticos, como adicionales bioindicadores de calidad ambiental, impulsando el uso ecológicamente sustentable de los recursos.

Palabras clave: hongos ingoldianos, hongos aero-acuáticos, hongos transicionales, bioindicador, calidad ambiental

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Introduction

De Wildeman (1893, 1894, and 1895; Duarte *et al.,* 2016) was the first to identify the typical spores of aquatic hyphomycetes, describing genera such as Clavariopsis, Lemonniera, and Tetracladium; however, almost five decades later, Ingold was another pioneer, to study aquatic hyphomycetes in a lotic ecosystem with moderate turbulence (rivers and streams) of clean water. The reports described samples such as water, foam, and decomposing plant material (1942; 1943ab; 1944, 1975), where it was observed conidia, mainly tetra-radiate and in minority proportion of spherical, coiled, fusiform, and sigmoid shapes. These fungal microorganisms are essential in aquatic ecosystems since they constitute a preponderant trophic link in the flow of nutrients and energy to higher trophic levels. The hyphomycetes are potential water quality bioindicators based on their physicochemical and microbiological characteristics (Bärlocher, 2000). Therefore, it is relevant to continue diversity studies of these aquatic fungi and the industrial biotechnological role and bioremediation, including the different kinds of hydrolytic enzymes synthesized (Fernandez *et al.*, 2010; Fernandez and Smits, 2015).

In this order, many researchers study biodiversity worldwide (Rajashekhar and Kaveriappa, 2003) and community dynamics of aquatic hyphomycetes in lotic ecosystems (Bärlocher and Kendrick, 1974). Since the hyphomycetes are considered fundamental decomposers of organic matter submerged in rivers (Bärlocher 1992 a,b,c), by colonizing leaves litter that falls into the water currents; in this way, the hyphomycetes act as an essential trophic bridge between the submerged leaves and the detritivorous invertebrates in the system (Bärlocher, 2000). In this ecosystem, the asexual spores released from leaves and the conidiophores developed on the leaf surface; this is one of the diagnostic elements for the identification of fungal community structure (Bärlocher, 2000).

Most significant aquatic hyphomycete species worldwide occur in temperate and cold regions (Jabiol *et al.*, 2013). However, with great effort in the tropical areas, it is one with the most remarkable biological diversity (Bärlocher, 1992 a,b,c; Santos and Betancourt, 1997; Schoenlein-Crusius and Grandi, 2003; Smits *et al.,* 2007). Thus, this bibliographic review seeks to complete the register of aquatic hyphomycetes in Latin America and the Caribbean. Afterward, the publication of the register of the Mexican region and Central America and the Caribbean (Fernandez and Smits, 2023a) to update the South American register made more than three decades ago (Schoenlein-Crusius and Grandi, 2003), encouraging the execution of more and novel research on these organisms in this biodiverse Earth.

Therefore, in this work, the data was systematized documentary, essentially through the search for scientific articles from indexed journals and theses, which taxonomically and ecologically recorded the species of aquatic hyphomycetes found in lotic and lentic systems in the subregion of "South America.", coupled with the type of sample and the parameters that will relate them to the environmental quality in said bodies of water. In this sense, the "*Google Scholar*" database (https://scholar.google.es) was mainly carried during 5 years (2020-2024), using the words aquatic fungi (freshwater fungi), aquatic hyphomycetes (aquatic hyphomycetes), Ingoldian Fungi, water quality and the names of the countries of the Latin American subregion described above. The updated nomenclature was validated through the data banks Mycobank (http://mycobankorg) and Index Fungorum (http://indexfungorum.org). Finally, the Jaccard index was used to perform a simple and quick meta-analysis of the similarity and diversity of aquatic hyphomycetes depending on the ecological group (Ingoldian, Aero-aquatic, and transient fungi) and the sample collection methods (water, foam, and Sumerged of wet plant remains).

Aquatic hyphomycetes

They are a phylogenetically heterogeneous and artificial group of aquatic fungi, known principally as anamorphic fungi, which are taxonomically classified in the Dikarya subkingdom, primarily as species of the Phylum Ascomycota, in a low percentage in the Phylum Basidiomycota (Shearer *et al.*, 2007), whose identification is classically carried out by the morphology of the spores; however, the rapid and accurate identification of the aquatic hyphomycetes is mainly performed with PCR molecular markers, such as the ITS (Internal Transcribed Spacer) hypervariable mitochondrial regions (Duarte *et al.,* 2022).

These fungal organisms exert an important trophic link between the submerged leaves and the macroinvertebrates of the lotic system by colonizing the deciduous leaves that reach the water courses, thus allowing the cycling of nutrients and energy at higher trophic levels (Bärlocher, 2000). However, some researchers classify these fungi ecologically, recently cataloging them into three groups: Ingoldian (I) in honor of the researcher Ingold, who studied them extensively, as they are exclusive to the aquatic environment, whose hyaline spores are hydrodynamic (tetraradiated and sigmoid); aero-aquatic (A), which grow vegetatively (mycelium only) under conditions submerged in water but spread upon contact with air, from helical-shaped spores; transitional (T), which are facultative, growing in both the aquatic and terrestrial environment, in submerged material (wood or leaf litter), with pigmented spores (dematiaceae) of various shapes (Fernandez and Smits, 2023a).

The capture techniques are mainly of three types: (a) filtered water (Millipore 0.45 µm), which is the most commonly used in these studies because it allows for the capture of spores regardless of substrate type or seasonality; (b) plant debris, incubated either in situ or in vitro, depending on the colonization preferences of fungal species in relation to the morphological and chemical characteristics of the substrate; and (c) foam that accumulates in the backwaters of water bodies, where bubbles trap spores. However, the presence of this foam may decrease during droughts due to reduced turbulence or be eliminated by rainfall (Fernandez and Smits, 2015).

Ecological functionality of aquatic hyphomycetes

The decomposition of plant material, particularly in lotic systems, is a highly dynamic and multifactorial process. It varies in terms of fungal biomass, species diversity, sporulation frequency, and enzymatic activity within the community structure of aquatic hyphomycetes. These dynamics are influenced by a range of factors, including geographical (e.g., latitude, altitude), climatological (e.g., seasonality), physico-chemical (e.g., nutrient levels, conductivity, temperature, pH, oxygen concentration, turbidity, sedimentation), and biological variables (e.g., plant substrate type, bacterial interactions), as well as intra- and interspecific interactions. The presence of both frequent and rare fungal species depends on the specific context. Generally, species richness and diversity are higher in undisturbed environments, where intact nutrient and energy cycles support the establishment of biomonitoring systems aimed at conservation (Fernandez and Smits, 2015).

Record of aquatic hyphomycetes in South America

Despite the limited number of published studies on this group of fungi in South America, a total of 495 species belonging to 218 genera have been reported to date. Of these, 487 species belong to the phylum Ascomycota and 8 to Basidiomycota, reaffirming the dominance of ascomycetes, which comprise 98.4% of these fungal organisms in lotic systems. These species are distributed across 66 families, including: Acrodictyaceae (2), Acrogenosporaceae (1), Aliquandostipitaceae (9), Amniculicolaceae (11), Annulatascaceae (1), Amphisphaeriaceae (1), Arthrobotryaceae (5), Beltraniaceae (8), Bloxamiaceae (1), Calloriaceae (7), Capnodiaceae (5), Cancellidiaceae (2), Castanediellaceae (1), Ceratocystidaceae (1), Chaetomellaceae (2), Chaetosphaeriaceae (38), Cladosporiaceae (1), Coniocessiaceae (2), Cordanaceae (1), Cylindrosympodiaceae (1), Dermateaceae (4), Didymellaceae (1), Discinellaceae (18), Dissoconiaceae (1), Dothidotthiaceae (3), Distoseptisporiaceae (1), Dyctiosporiaceae (2), Extremaceae (1), Gelatinodiscaceae (1), Gyrotrichaceae (3), Halosphaeriaceae (12), Helotiaceae (21), Helminthosphaeriaceae (7), Herpotrichiellaceae (3), Hyaloscyphaceae (8), Hydrocinaceae (4), Hyphomycetaceae (4), Leotiaceae (9), Longipedicellataceae (1), Lunulosporaceae (3), Massarinaceae (1), Melanommataceae (12), Meruliaceae (1), Microthyriaceae (6), Muyocopronaceae (1), Mytilinidiaceae (1), Nectriaceae (9), Orbiliaceae (24), Pezizellaceae (1), Pleomassariaceae (2), Pleurotheciaceae (1), Pyriculariaceae (1), Pyronemataceae (2), Reticulascaceae (2), Savoryellaceae (1), Sporidesmiaceae (16), Teratosphaeriaceae (7), Torulaceae (1), Trichosphaeriaceae (1), Tricladiaceae (16), Tubeufiaceae (20), Venturiaceae (4), Vermiculariopsiellaceae (2), Vibrisseaceae (1), Wiesneriomycetaceae (10) and Zygosporiaceae (2). As well as those Incertae sedis for being defined as a taxonomic category within this Phylum (116), subclass Hypocreomycetidae (5), or the orders Hypocreales (3) and Sordariales (3). On the other hand, in the Phylum Basidiomycota, five families were found: Camptobasidiaceae (1), Classiculaceae (1), Dacrymycetaceae (1), Hydnaceaceaceae (1) and Niaceae (1), as well as those Incertae sedis for defining a taxonomic category within the subclass Agaricomycetes (2). Additionally, according to the ecological classification described by Fernandez and Smits (2023a), the species found were grouped into 184 Ingoldian, 46 Aero aquatic, and 265 transitional (Anexo 1).

Therefore, out of 14 South American countries, only two (Bolivia and Paraguay) found no records of species of aquatic hyphomycetes in freshwater ecosystems. The highest number of reports were found in Argentina (124), Brazil (279), Venezuela (150), and Chile (87), followed by more than ten species reported in Colombia (57), Peru (55), Ecuador (11), and Uruguay (19) in contrast to Guyana (1), French Guyana (5), and Suriname (1) where reports were scarce (Anexo 1). Altogether, reflect and suggest the intensity of research work with these fungal organisms in such a biodiverse planet region. In this regard, Argentina, Brazil, Chile, and Venezuela were where more works had been published, suggesting that one of the reasons is due to the more significant number of institutions and researchers with financial support for it, an aspect not found in countries such as Bolivia (Pacasa, 2018) and Paraguay (Marchi *et al.*, 2018). Bolivia and Paraguay are presumed to have high fungal biodiversity, but the few mycologists are not dedicated to the taxonomic identification of these fungi in various biomes in their countries, focused mainly on the identification of macroscopic fungi of agricultural interest; therefore, the implementation of more research projects throughout the subregion should be encouraged, particularly in countries with fewer records in order to increase the data and knowledge of these species of aquatic fungi.

Regarding the ecological classification of these aquatic hyphomycetes, only records of the aero-aquatic type were found in decomposing plant samples in humid forests in Guyana and Suriname, probably because the low number of studies published in those countries, while in French Guyana, using only this type of sample, a lower percentage (20 %) of aero-aquatic hyphomycetes and a higher percentage (80 %) of transitional hyphomycetes were reported, since this semi-aquatic environment favors the development of these type hyphomycetes. Moreover, Argentina has 57 % transitional hyphomycetes, and 31 % of Ingoldian hyphomycetes were found using 91 % of plant samples. Similarly, based on only this sample submerged in Ecuadorian and Uruguayan rivers, a higher percentage of Ingoldian hyphomycetes was described, respectively 55 % for Ecuador and 89 % for Uruguay (figure 1a,b).

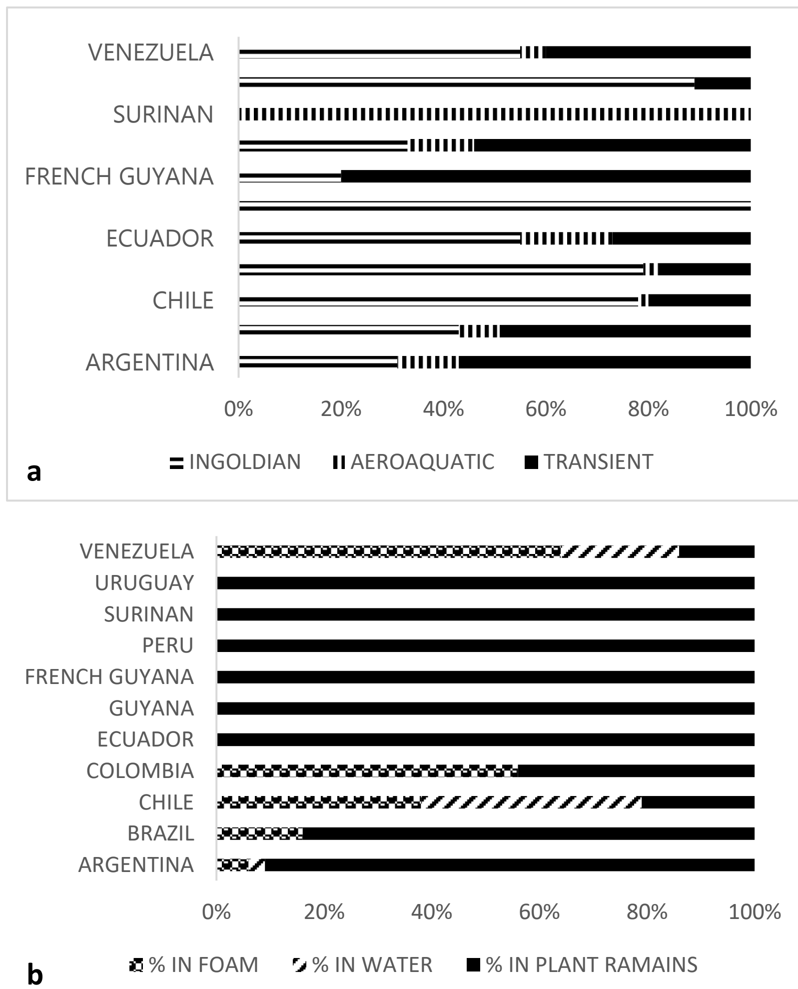

Figure 1. Aquatic hyphomycetes in South America. a. Type of fungus. b. Type of sample.

On the other hand, Chile (CH) and Colombia (CO) reported higher percentages of Ingoldian species (CH: 78 %; CO: 79 %), followed by transitional species (CH: 20 %; CO: 18 %) and aero-aquatic species (CH: 2 %; CO: 3 %) by using 38 % and 56 % of foam samples for Chile and Colombia, respectively, as well as 41% of water samples for Chile, reaffirming the fact that these two types of samples capture the typical aquatic fungal species in lotic systems. In contrast, studies in Argentine rivers have been carried out in a higher percentage (90 %) with submerged plant samples and very little with foam (7 %) and water (3 %), obtaining 59 % of transitional hyphomycetes, followed by 28 % of Ingoldian hyphomycetes and 13 % of aero-aquatic hyphomycetes, confirming that with plant material the incidence of transitional fungi is higher (figure 1a, b).

In the Brazilian context, most of the research has focused on submerged plant material (84 %), either naturally present or incubated for a specific period, while the remaining 16 % has involved natural foam. The findings are distributed as follows: 43 % of Ingoldian species, 8 % of aero-aquatic species, and 49 % of transitional species. This distribution is likely influenced by the method used to collect decomposing plant material. The decomposing plant material typically consists of leaf litter semi-submerged in river backwaters or incubated in leaf discs for a set period, resulting in 51 % of species being exclusive to aquatic hyphomycetes (Ingoldian and aero-aquatic). It is important to note that Brazil has the highest number of aquatic hyphomycetes (279) in South America, including 121 Ingoldian species (figure 1ª,b).

Lastly, in Venezuela, despite having more than 15 years with greater research intensity with aquatic hyphomycetes, using the three types of samples (plant remains, water, and foam), it is currently in second place in reports from the American subcontinent, with 150 species, of which 83 are Ingoldian (55 %), eight are aero-aquatic (5 %), and 59 are transitional (40 %). It is important to highlight that the highest percentage of these fungi was collected through the natural foam (64 %) and water (22 %), systems traditionally used by pioneer researchers with typical aquatic hyphomycetes (Ingoldian and aero-aquatic) (figure 1a,b).

Regarding the percentage of similarity of the spore capture method according to the ecological group of aquatic hyphomycetes, we found a greater similarity (35.4 %) with the water and foam method if we evaluated the aquatic hyphomycetes without discriminating by group. However, when analyzing by ecological group, we found an interesting contrast with Ingoldian fungi, with a high similarity (41 %) with the submerged with wet plant remains and foam method, followed by the water method with the foam method with 40 %. In the case of aero-aquatic fungi, the most significant similarity was between the foam and water method, with 60 % being very low (4.9-9.8 %) when comparing the submerged with wet plant method with the foam and water method, a similar response with transient fungi, but with 20 % similarity between the foam and water method (table 1). These findings reinforce the proposition that the morphological characteristic of the spore is decisive for its capture according to the method, with the foam and water methods being the ideal ones to capture the majority of aquatic hyphomycetes, particularly the Ingoldians, and aero-aquatics, which present adequate hydrodynamic buoyancy structures, unlike the transient fungi that are captured more frequently with the plant material incubation method, since they do not have morphological adaptations for their buoyancy; and dispersion in water and, therefore are difficult to capture using the natural foam or water technique; generally, they can be observed in plant material incubated in vitro (Fiuza *et al.*, 2017b).

Assessment of aquatic hyphomycetes as bioindicators of environmental quality

Correspondingly, taxonomic studies of these fungal organisms and their use as bioindicators remain limited and sporadic, despite their recognition for over a decade as effective ecological markers in riverine systems. They have been employed to assess environmental quality in both lotic and lentic ecosystems, using indicators such as species richness, spore production, and the presence of sensitive or tolerant species (Solé *et al.*, 2008). The role of aquatic fungi as bioindicators is based on the premise that the composition and function of their assemblages shift in response to anthropogenic and natural disturbances (Bärlocher, 2016). For instance, reductions in species richness and conidial concentrations have been observed in environments affected by elevated salinity (Tsui *et al.*, 2016) or the presence of fungicides (Cornejo *et al.*, 2021), compared to pristine waters or areas along the same river with differing levels of impact. To date, only fourteen studies have been reported, distributed chronologically by country: four in Venezuela, four in Brazil, three in Argentina, and one each in Chile, Colombia, and Ecuador. This limited number of studies is likely due to a general lack of interest in exploring aquatic fungi as potential indicators of environmental quality.

Table 1. Jaccard's percent similarity of aquatic hyphomycete species (total, Ingoldian, aero-aquatic, and transient) recorded using three spore collection methods in South America. Spore collection methods: SWPR – Submerged with wet plant remains; F – Foam; W – Water.

Total aquatic hyphomycetes	**SWPR**	**F**	**W**
SWPR	100	28,7	17,9
F	28,7	100	35,4
W	17,9	35,4	100
Ingoldian fungi			
SWPR	100	41	27,3
F	41	100	40,4
W	27,3	40	100
Aero-aquatic fungi			
SWPR	100	9,8	4,9
F	9,8	100	60
W	4,9	60	100
Transient fungi			
SWPR	100	17.1	8,3
F	17,1	100	20
W	8,3	20	100

In Argentina, in the Santiago River area, which is heavily impacted by residential and industrial sewage, fungi were studied on submerged plant debris. Among the 72 fungal species recorded, 82 % were classified as "geofungi" or transitional forms (as defined in this study), 15 % as aero-aquatic fungi, and only 3 % as Ingoldian fungi. The transitional group was the most frequent, while the latter two groups, which are typically dominant in uncontaminated aquatic environments, were notably diminished. The most frequently occurring species within the transitional group included *Camposporium antennatum*, *Camposporium pellucidum*, *Dactylaria appendiculata*, *Dactylaria longidentata*, *Dictyosporium elegans*, *Helicosporium griseum*, *Sporidesmium filirostralum*, *Sporidesmium hyalospermum*, and *Tetraploa aristata*. Among the Ingoldian fungi, only *Isthmolongispora asymetrica* and *Lateriramulosa biinflata* were detected, both at low frequencies (Arambarri *et al.*, 1992). These results suggest that transitional fungi are more tolerant to pollution and that this group, as a whole, may serve as a bioindicator of disturbance, as evidenced by the altered proportion and frequency of transitional versus Ingoldian species.

Subsequently, Tarda et al. (2019) evaluated four tributary streams of the Río de la Plata estuary in Argentina: two located in rural areas dedicated to cattle grazing (Cajaravillas and Chubichaminí) and two in suburban areas used for agriculture (Carnaval and Gato). A distinct assemblage of Ingoldian and transitional dematiaceous hyphomycetes was found when incubating leaf sections of *Typha latifolia*, depending on the level of environmental impact of each water body. In the water samples, Ingoldian and transitional fungi represented 30% and 70% of the assemblage, respectively. Sporulation rate, fungal diversity, and richness were higher in water bodies of lower environmental quality. The most frequent species were *Anguillospora longissima*, *Arthrinium* sp., *Margaritispora aquatica*, and *Tricellula botryosa*.

It is important to note that transitional hyphomycetes, such as *Brachysporium* sp., *Sporidesmium* sp., and *Tetraploa abortiva*, were associated with water bodies characterized by high nutrient levels (nitrogen and phosphorus) and elevated temperatures. In contrast, Ingoldian hyphomycetes such as *Amniculicola longissima*, *Alatospora acuminata*, *Flabellospora* sp., and *Margaritispora aquatica* were more frequently found in waters with higher pH and dissolved oxygen concentrations. These findings support the idea that such fungi can serve as indicators of environmental change in rivers influenced by different land use practices in adjacent areas.

Finally, Kravetz et al. (2023) evaluated water quality indices in the Gutiérrez Stream, a tributary of the Luján River (Luján City, Buenos Aires, Argentina), considering nutrient concentrations (nitrates, ammonium, and chlorides), physicochemical parameters (dissolved oxygen, pH, temperature, conductivity, BOD, and COD), and biological indicators such as biofilm algae and aquatic hyphomycetes. The fungal community was assessed using dry leaflets of Gleditsia triacanthos (black acacia), an abundant woody species in local water bodies, incubated both in situ and in vitro. Sampling was conducted at two upstream sites (Site I: no environmental impact; Site II: transitional conditions) and three downstream sites located at the entrance of a canal that receives effluents from textile industries, each with distinct ecological characteristics.

The richness of aquatic hyphomycetes was significantly higher at the undisturbed site, with 11 of the 16 recorded fungal species found exclusively in that location. These included *Alatospora acuminata*, *Amniculicola longissima*, *Anguillospora crassa*, *Anguillospora filiformis*, *Anguillospora pseudolongissima*, *Aquanectria penicillioides*, *Camptobasidium hydrophilum*, *Flagellospora curvula*, *Lunulospora curvula*, *Lunulospora cymbiformis*, and *Sigmoidea prolifera*. The sporulation rate at this site reached 1447 conidia/mL. In contrast, in the downstream impacted areas, the number of fungal species ranged from 3 to 8. Species found exclusively in these sites included *Camposporium pellucidum*, *Neotorula aquatica*, *Sigmoidea aurantiaca*, *Trichocladium angelicum*, and *Vargamyces aquaticus*, with sporulation rates ranging from 20.47 to 197.75 conidia/mL.

Only two species, *Aquanectria penicillioides* and *Flagellospora curvula*, were detected across all study sites, indicating a higher tolerance to elevated levels of salts (ammonium, chlorides, and phosphates) discharged by nearby industries. However, their sporulation rates decreased significantly in impacted sites. In contrast, *Alatospora acuminata* and *Anguillospora crassa* were exclusive to the undisturbed site and are considered sensitive to contamination. These results provide a valuable baseline and suggest that the combined use of fungal and chemical-biological indicators enhances the sensitivity of water quality assessments by allowing for a more comprehensive evaluation of contamination effects.

On Brazil's southern Atlantic slope, twelve third-order rivers and tributaries of the Uruguay River were evaluated. These water bodies are bordered by natural vegetation dominated by the tree species *Araucaria angustifolia* and exhibit varying degrees of environmental disturbance due to agricultural, industrial, or domestic activities from surrounding rural and urban populations. The composition of aquatic hyphomycetes was studied in relation to physicochemical parameters (pH, conductivity, temperature, turbidity, total solids, and dissolved oxygen) and nutrient concentrations (phosphate, nitrate, nitrite, sulfate, ammonium, chloride, calcium, magnesium, and sodium), using incubated leaf sections of *Nectandra megapotamica* as substrate.

Approximately 12 % (21 species) of the aquatic hyphomycetes previously reported in Brazil were found in this study. This relatively low richness may be attributed to the use of a single plant species instead of a mixed leaf litter substrate or foam. *Lunulospora curvula*, *Flagellospora curvula*, and *Aquanectria submersa* were the dominant species in water columns of rivers 10, 11, and 12, respectively. *Anguillospora* sp., *Campylospora parvula*, and *Mycocentrospora acerina* were exclusive to individual rivers. Notably, *L. curvula* and *F. curvula* together accounted for over 80 % of the total spores counted.

Spore concentration showed species-specific responses to environmental conditions. *Tripospermum myrti* and *Heliscus tentaculus* exhibited higher concentrations in environments with high dissolved oxygen, neutral pH, and low conductivity. Conversely, *Articulospora tetracladia*, *Alatospora acuminata*, and *Campylospora chaetocladia* were associated with elevated ammonium levels, while *Tetracladium marchalianum* and *Anguillospora filiformis* were linked to high nitrate and phosphate concentrations. *L. curvula* was present across a wide range of dissolved oxygen, conductivity, and nutrient levels, suggesting it is a tolerant species.

Overall, the study indicated that electrical conductivity is the most consistent predictor of spore concentration. However, species richness appears to be influenced by a combination of conductivity, dissolved oxygen, and phosphate levels (Breda *et al.*, 2021).

In pristine lotic ecosystems within two forest reserves in northeastern Brazil (Pedra Talhada and Charles Darwin), the diversity of aquatic hyphomycetes was assessed in relation to physicochemical water parameters, including temperature, pH, dissolved oxygen, conductivity, turbidity, phosphate, and nitrate concentrations. The evaluation was based on fungal assemblages recovered from submerged leaf debris.

A total of 53 species were recorded, with the most frequently encountered taxa being *Blodgettia aquatica*, *Blodgettia indica*, *Flagellospora penicillioides, Flagellospora* sp., *Ingoldiella hamata*, *Mycoleptodiscus disciformis*, *Triscelophorus monosporus*, *Wiesneriomyces laurinus*, *Xylomyces acerosisporus*, and *Xylomyces giganteus*. Among the measured environmental variables, dissolved oxygen had a significant influence on fungal diversity. Ingoldian taxa such as *Flagellospora* sp. and *T. monosporus* were more frequently recorded under high dissolved oxygen conditions. However, no species were identified as specific bioindicators of water quality, since the remaining physicochemical parameters were consistent between both sites and within the thresholds established by Brazilian water quality regulations (Rodrigues *et al.*, 2021).

Similarly, Brazilian studies evaluated the diversity of aquatic hyphomycetes by incubating leaf sections of *Nectandra megapotamica* in two subtropical and three tropical rivers. Significant correlations were found between the occurrence of certain species and environmental parameters, supporting the role of these fungi as bioindicators. High temperatures, elevated pH and electrical conductivity, and low dissolved oxygen levels were found to negatively impact fungal sporulation.

Furthermore, the lower species richness observed in tropical rivers (15 species), where the mean annual temperature was higher (21°C) than in subtropical rivers (17.5°C), suggests that moderate temperatures are more favorable for the growth and diversity of aquatic hyphomycetes. However, *Anguillospora longissima* and *Lunulospora curvula* were consistently among the most frequent species across regions, regardless of temperature, season, or geographical location.

While *Flagellospora curvula* appeared tolerant to temperature variation, it exhibited sensitivity to reduced dissolved oxygen levels (7.01–7.71 $mg \cdot L^{-1}$), as evidenced by its decreased conidial production. In contrast, *Aquanectria submersa*, *Colispora curvata*, *Campylospora chaetocladia*, *Clavatospora tentacula*, L. *curvula*, and *Triscelophorus monosporus* displayed increased sporulation at these oxygen levels, suggesting a greater tolerance.

Regarding pH, low values (5.8–6.5) were associated with reduced sporulation, although *Anguillospora filiformis* and *F. curvula* maintained higher conidial concentrations, indicating tolerance. Conversely, *Campylospora chaetocladia* and *Clavatospora tentacula* were considered sensitive, as their growth was inhibited under acidic conditions.

Finally, *Camposporium pellucidum* was the most tolerant species at elevated conductivity levels (33.25–70.00 $\mu S \cdot cm^{-1}$), showing high conidial production. In contrast, *Campylospora chaetocladia*, *Clavatospora tentacula, F. curvula*, *L. curvula*, and *T. monosporus* were identified as sensitive to high conductivity, as indicated by reduced sporulation rates (Gomes *et al.*, 2023).

Likewise, an assessment of diversity indices (α, β, and γ) of aquatic hyphomycetes was conducted in tributary streams of the Ribeira River within the Campos Gerais National Park in southern Brazil. The study included eight streams located in pristine areas of native forest and eight streams in areas affected by agricultural activities, which were characterized by elevated nutrient pollution levels, particularly phosphorus. High fungal richness was recorded across all sampling sites, regardless of the degree of anthropogenic disturbance. No significant differences were observed in any of the diversity indices analyzed, and no fungal species were identified as bioindicators. The underlying causes of this pattern remain unclear and warrant further investigation (Ratz *et al.*, 2024).

In Chile, the composition and frequency of aquatic hyphomycetes were assessed in two contrasting zones, one pristine and one anthropogenically disturbed, along the Damas River, a lotic system bordered either by natural riparian vegetation in the undisturbed site or by urban development in the disturbed site. Although the specific source of pollution in the impacted area was not detailed, it was associated with reduced dissolved oxygen concentrations. Leaves of *Salix babylonica* were incubated in situ for 20 days to facilitate fungal colonization. A total of 17 species were recorded in the pristine area. Among these, the most frequent taxa, with more than 75 percent occurrence, were *Clavariopsis aquatica*, *Lemonniera aquatica*, *Tetracladium marchalianum*, and *Triscelophorus acuminatus*. Intermediate-frequency species, with 25 to 75 percent occurrence, included *Anguillospora* sp., *Campylospora chaetocladia*, *Clavatospora longibrachiata, Lunulospora curvula*, and *Tetrachaetum elegans*, while rare taxa, with less than 25 percent occurrence, comprised *Alatospora acuminata*, *Flagellospora curvula*, *Flagellospora penicillioides*, *Heliscus submersus*, *Mycocentrospora acerina*, *Mycocentrospora angulata*, *Scorpiosporium gracile*, and *Tricladium chaetocladium*. In contrast, only four of these species, namely *T. acuminatus*, *C. chaetocladia, C. longibrachiata*, and *C. aquatica*, were detected at the disturbed site, all at markedly reduced frequencies. *T. acuminatus* was the most frequent taxon in the impacted zone. Notably, *L. aquatica* and *T. marchalianum*, which were highly frequent in the pristine area, were absent from the polluted site, suggesting their sensitivity to environmental degradation (Burgos and Castillo, 1986).

In Colombia, the Ingoldian aquatic hyphomycetes percentage of sigmoid and tetraradiate types were evaluated in two areas (upstream "without impact"; downstream "with impact") of the Acaciítas river (Acacías, Meta-Colombia), with different degrees of environmental impact (type not specified), incubating leaf segments of *Inga brachyrachys* and *Matayba* sp., native plants of the riparian zone of the river. The predominant sigmoid species were *Anguillospora pseudolongissima*, *A. penicillioides*, and *Filosporella versimorpha*, while the dominant tetraradiate species were *Triscelophorus acuminatus* and *T. mosnosporus*. The percentage of sigmoid species was significantly higher (64 %) in the affected area, as opposed to the non-impacted area (56.5 %), which suggests that sigmoid species are tolerant to urban pollution, while tetraradiate species are sensitive to it (Kravetz and Pardo, 2020).

In Ecuador, at the Cajas National Park, the diversity of aquatic hyphomycetes in three micro-watersheds (Mat: Matadero; LL: Llaviuco; and Maz: Mazán), from the highest to the lowest degree of environmental impact (Mat>LL>Maz) due to the pasture intensity cultivation. Intense cattle grazing was evaluated by leaf incubation, foam, and water. It was found that the diversity of aquatic hyphomycetes was not affected. Still, the species composition was *Tetracladium marchalianum* and *Heliscus lugdnensis*, tolerant species characterized for being present in greater abundance in the micro-basin with the most significant impact, with high conductivity values and suspended organic matter. On the other hand, in two micro-basins with less disturbance, the diversity increases, as well as the frequency of the species *Alatospora acuminata*, *Articulospora tetracladia* and *Triscelophorus acuminatus*, which are considered indicator species of environmental quality (Guerrero and Urdiales, 2016).

In Venezuela, several studies have been carried out on the relationship between aquatic hyphomycetes and water quality in the Cupira, Chirgua, Vigirima, Borburata, and Patanemo rivers, according to the degree of environmental affectation (headwaters: no impact; downstream: with impact due to agricultural and livestock activities in rural populations) of 2 or more areas of these rivers, establishing potential bioindicator species.

In the Cupira River (San Diego Municipality, Carabobo State), the number of fungal species decreases with contamination; 41 species were found in the upstream, 27 in the intermediate area, and 9 in the downstream zones; the most frequent species in all the evaluated areas with was *Flabellospora crassa*, followed by *Flagellospora curvula*, *Clavatospora tentacula*, *Campylospora* sp., *Helicomyces torquatus*, *Alatospora acuminata*, *Anguillospora crassa*, *Brachiosphaera tropical*, *Camposporium pellucidum*, *Phalangispora constricta*, and *Campylospora chaetocladia*. The species *Alatospora acuminata*, *Campylospora* sp., *Flabellospora acuminata*, and *Helicomyces torquatus* decreased drastically in the downstream zone, indicating that they are sensitive to the downstream contamination, characterized by the high level of total solids and mainly by the raised level of total coliforms and fecal. Although the species *Camposporium pellucidum*, *Clavatospora tentacula*, *Diplocladiella scalaroides*, and *Flagellospora curv*ula increased their frequency, being considered tolerant to the aforementioned environmental stress (Storaci *et al*., 2013).

At the Chirgua River (Bejuma Municipality, Carabobo State), the species decline is observed depending on the environmental disturbance, *Clavatospora tentacula* and *Triscelophorus acuminatus* being the most frequent species in all the areas evaluated. In contrast, the species sensitive to bacterial contamination (fecal and total coliforms) were *Brachiosphaera tropicalis*, *Camposporium antenatum*, *Campylospora filicladia*, *C. parvula*, *Clavatospora tentacula*, *Clavatospora stellata*, *Culicidospora gravida*, *Diplocladiella scalaroides*, *Flabellospora acuminata*, *Helicomyces colligatus*, *Helicomyces* sp., *H. torquatus*, *Phalangispora constricta*, *Tetracladium marchalianum* and *Triscelophorus monosporus*. The tolerant species were *Alatospora acuminata*, *Campylospora chaetocladia*, *Flabellospora crassa*, *Isthmotricladia gombakiensis*, *Tetraploa* cf. *aristata*, and *Triscelophorus acuminatus* (Fernandez *et al*., 2017).

he number of species and the concentration of conidia decreased in correlation with the increase in coliforms (total and fecal) and nitrate levels in the Vigirima River (Guacara Municipality, Carabobo State). The species most sensitive to environmental stress were *Brachiosphaera tropicalis*, *Clavatospora stellata*, *Culicidospora gravida*, *Diplocladiella longibrachiata*, *F. crassa*, and *Tetraploa* cf. *aristata*, whereas the more tolerant species included *Alatospora acuminata*, *Anguillospora longissima*, *C. antenatum*, *C. pellucidum*, *Camposporidium* sp., *Campylospora chaetocladia*, *C. filicladia*, *Clavatospora tentacula*, *Diplocladiella scalaroides*, *Flagellospora curvula*, *Helicomyces torquatus*, and *Triscelophorus monosporus* (Fernandez and Smits, 2020).

Finally, the assessment in the upstream and mouth of two rivers (Borburata and Patanemo) at the northern slope of Venezuela, the tendency of decreasing species richness and the conidia concentration was maintained, but at high levels of conductivity, sulfate, total solids, and total coliforms, aquatic hyphomycetes spores were found only at the Borburata River mouth; those sensitive species were: *Alatospora crassa*, *Anguillospora filiformis*, *Beltrania rhombica*, *Camposporium antenatum*, *Campylospora filicladia*, *Diplocladiella longibrachiata*, *Helicomyces* sp., and *Triscelophorus monosporus*. However, *Brachysporiella setosa* and *Tetraploa aristata* were the tolerant species (Fernandez and Smits, 2021a).

Conclusions: Future Research Perspectives on Aquatic Hyphomycetes in South America

This bibliographic review provides a novel and detailed synthesis of aquatic hyphomycete records by country across South America, organized according to their taxonomic and ecological classification and the spore capture methods employed. The aim is to support future and innovative research on the taxonomy, ecology, and environmental roles of these aquatic fungi, with particular emphasis on their potential as bioindicators, especially in countries where studies are scarce or nonexistent.

The review recommends the use of multiple spore capture methods, in conjunction with the ecological classification of aquatic hyphomycetes presented herein, to ensure the detection of the full spectrum of species present in aquatic ecosystems. This approach would enable more accurate estimations of species diversity and identification of potential bioindicator taxa, thereby contributing to the design of effective conservation programs.

Despite the considerable number of taxonomic and ecological studies conducted in South America, some countries still lack research on aquatic hyphomycetes. Notably, only 14 studies of this kind were found across the region. With the exception of Bolivia and Paraguay, all South American countries have reported the presence of these fungi, totaling 495 species to date: 184 Ingoldian, 46 aero aquatic, and 265 transitional. Brazil reports the highest diversity, with 279 species (including 121 Ingoldian), followed by Venezuela with 150 species (83 Ingoldian and 8 aero aquatic).

This review aims to facilitate the development of future studies on this ecologically significant group of fungi in both lotic and lentic freshwater systems. Such research will enhance the use of aquatic hyphomycetes as bioindicators of environmental quality, complementing traditional indicators and promoting the sustainable management of freshwater resources.

Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

Rafael Fernández Da Silva, Gunta Smits Briedis and María Daniela Artigas Ramirez: Conceptualization, methodological design development, data collection, data analysis, project administration, review, writing, and editing.

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