



REVIEW

Aquatic hyphomycetes beyond their preferred habitats and ecosystem services

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Abstract

Freshwater aquatic hyphomycetes play a crucial role in global nutrient cycling, mineral balancing, and productivity in flowing water systems. These fungi are keys to several ecological functions in various aquatic systems. They regulate organic waste breakdown, support nutrient recycling, and produce biologically active compounds. Remarkably, they can deliver these ecological services even in unconventional or severe environments due to their adaptive capabilities. Their resilience is further underscored by their presence in extreme habitats and their knack for colonizing distinctive materials. These fungi process exotic plant detritus, combat eutrophication, thrive in polluted habitats, protect plants by suppressing pathogens, enhance plant growth, solubilize phosphate, produce bioactive natural products, and degrade xenobiotics. For such processes, both ascomycetous and basidiomycetous fungi play a key role in litter breakdown in rivers, lakes, and other water bodies. Although aquatic hyphomycetes are a polyphyletic group belonging to *Eumycota*, there is a knowledge gap on the occurrence and functions of aquatic hyphomycetes outside the water column. Thus, this review addresses the occurrence, colonization, and ecosystem services of aquatic hyphomycetes under unusual or unexpected conditions, with specific examples.

Keywords: Adaptation, Colonization, Ecosystem Services, Freshwater, Ingoldian Fungi, Unusual Habitats



1. Introduction

The sustenance of life on earth is dependent on various ecosystem services, which are directly linked with economic, regulatory, and cultural services. These services, crucial to human well-being, are believed to be impacted by both climate change and human activities (Arias-Real et al. 2023, Seena et al. 2023). With their ubiquitous presence, fungi owe their widespread distribution to their remarkable ability to inhabit diverse ecological niches. Their presence spans a range of scales, from broad geographic regions and ecosystems to specific locations and habitats (Fierer 2008, Döll and Zhang 2010, Cantrell et al. 2011). The fungal ecological niches extend far beyond traditional perceptions, encompassing a variety of unexpected habitats due to their multifaceted diversity (Selosse et al. 2018). Freshwater sources (which are 3 % of the water on the planet Earth) are precious for the sustenance of life on Earth, and safeguarding their pristine conditions assumes prime importance (Barros and Seena 2022). Climate change and human activities exert a direct or indirect effect on the ecosystem services of freshwater fungi, varying with their geographic location and proximity to human settlements (Ferreira and Chauvet 2011, Bärlocher 2016, Ferreira and Voronina 2016). Despite these challenges, freshwater ecosystems possess intrinsic abilities to adapt to frequent disturbances, with their response depending on the severity of the disruptions (Döll and Zhang 2010).

Aquatic fungi are ubiquitous in various freshwater and marine ecosystems owing to their morphological, ecological, and phylogenetic diversity. These were first observed by Ingold (1942), who reported their presence in the decaying leaves of running water. Till now, there are more than 1,00,000 fungi known from aquatic ecosystems belonging to more than 3000 species (Bärlocher and Boddy 2016). However, they have been poorly characterized in terms of their contributions to ecosystem processes (Grossart and Rojas-Jimenez 2016, Grossart et al. 2019). The most important group of organisms that exist in freshwater are aquatic fungi, which can involve themselves in detritus processing to fulfil energy flow to higher trophic levels (Sridhar and Bärlocher 2000). In freshwater ecosystems, the primary source of energy is derived from organic matter originating from adjacent land habitats, like riparian vegetation, and from terrestrial runoff. Aquatic fungi play a crucial role in carbon sequestration within these environments, profoundly impacting biogeochemical and nutrient cycles. This influence is a function of their diversity and their enzymatic activities (Chandrashekar and Kaveriappa 1991, Solé et al. 2012, Heeger et al. 2021). Aquatic fungi are capable of enriching organic matter with proteins, enzymes, lipids, and bioactive compounds (Krauss et al. 2011). Owing to the enrichment of plant detritus, invertebrates and vertebrates are attracted to nourishing the processed detritus.

Aquatic hyphomycetes are the most diverse, functional, and indispensable biota in freshwater streams and rivers worldwide (Duarte et al. 2016). Their occurrence was highest at the cooler mid-latitudes (Barreto et al. 2023). Aquatic fungi are exceptionally adapted to flowing waters, as evidenced by their diverse and unique conidial morphologies, including scolecoïd and stauroid forms (Seena et al. 2022) (Figure 1). They act as primary colonizers, converting plant detritus into biomass that is palatable for aquatic invertebrates, thereby enhancing the flow of energy to higher trophic levels (Bärlocher and Sridhar 2014). Recently, Anderson et al. (2022) introduced a multilingual and multiformat education toolkit for aquatic fungi to attract the attention of investigators. Although information on the occurrence and functions of aquatic hyphomycetes in

lotic habitats is available, their presence and ecosystem services outside the lotic habitats are meagre. To comprehend the ecosystem services of aquatic hyphomycetes in atypical environments, this review addresses two key aspects: 1) their capacity to thrive or endure in unique habitats; and 2) their colonization and persistence on unfamiliar substrates. This review also delves into the ecosystem services of aquatic hyphomycetes in unconventional habitats with selected examples.

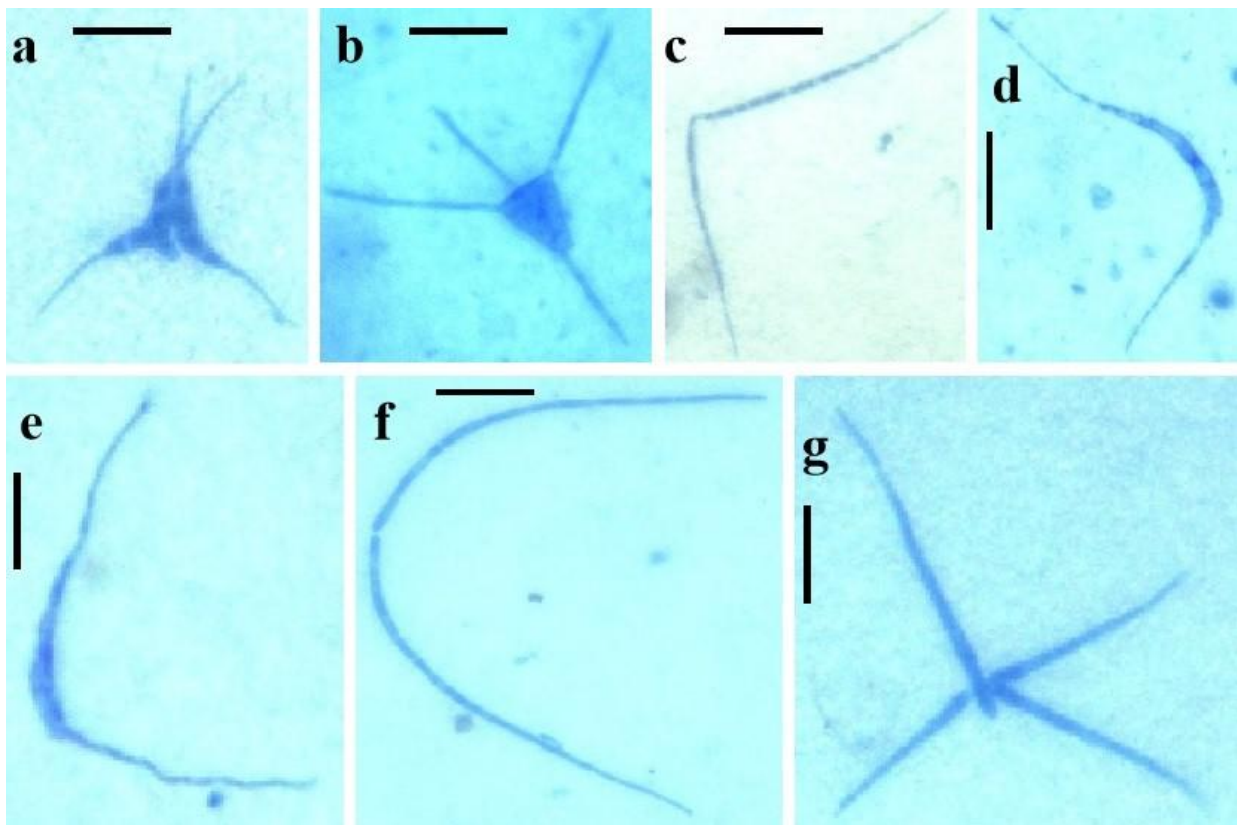


Figure 1: Stauroid and scolecoid conidia of aquatic hyphomycetes found in stemflow and throughfall of trees in southwest India: a, *Campylospora chaetocladia*; b, *Clavariana aquatica*; c, *Condylospora spumigena*; d, *Lunulospora curvula*; e, *Lunulospora cymbiformis*; f, *Synnematophora constricta*; g, *Triscelophorus acuminatus* (Scale bar: 20 μm)

2. Occurrence of aquatic hyphomycetes in unusual habitats

Originally, aquatic hyphomycetes were primarily associated with pristine flowing water (i.e., lotic) habitats. However, accumulating data has revealed their consistent presence and roles in a range of environments beyond their preferred lotic settings. These include brackish waters, canopies, still-water (i.e., lentic) habitats, and even terrestrial environments (Chauvet et al. 2016) (Table 1). There is evidence pointing towards their presence and functions in terrestrial settings being a result of mutualistic relationships with plants and their sexual phases (Selosse et al. 2008). Furthermore, there are documented instances of these fungi thriving in unconventional or stressed environments, including polluted or saline waters, intermittent water sources, and even within the intestines of aquatic animals (Figure 2).

Table 1. Occurrence of aquatic hyphomycetes in selected unusual habitats

Habitat	Selected reference
Polluted groundwater	Krauss et al. 2003
Salinity	Kirk 1969, Sridhar and Kaveriappa 1988, Maamri et al. 2006
Salinization	Canhoto et al. 2017, 2021
Low temperature	Bärlocher and Kendrick 1974, Ceczuga and Orłowska 1998, 1999
High temperature	Chandrashekar et al. 1991, Rajashekhar and Kaveriappa 1996, 2000, Ferreira and Chauvet 2011, Fenoy et al. 2021
Intermittent	Ghate and Sridhar 2015, LeRoy 2019, Simões et al. 2021
Acidic pH	Bärlocher 1987, Thompson and Bärlocher 1989, Raviraja et al. 1998a, Cornut et al. 2012
Alkaline pH	Vass et al. 2013
Intestine	Bärlocher 1981, Sridhar and Sudheep 2011a, Sridhar et al. 2011

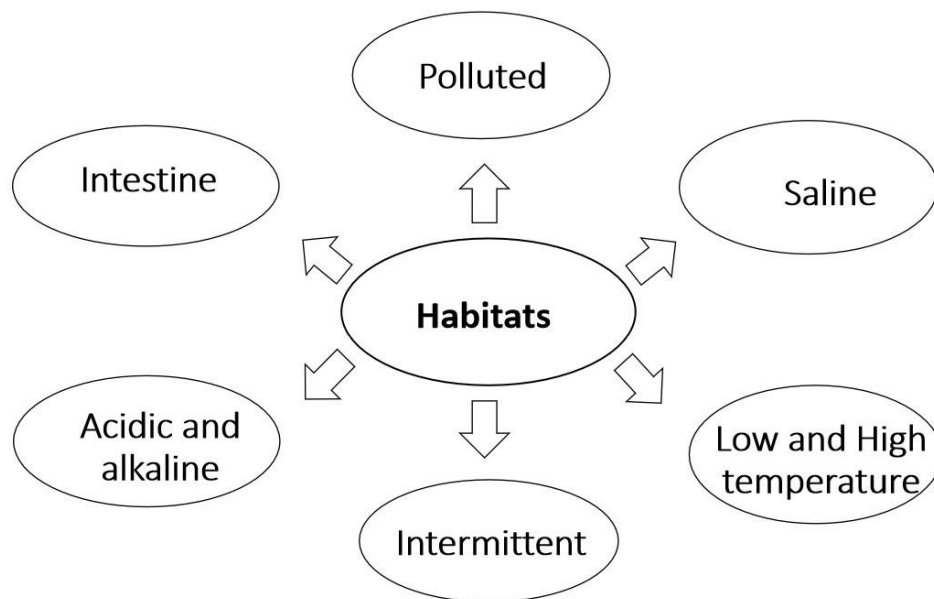


Figure 2: Occurrence of aquatic hyphomycetes in different habitats other than the lotic habitats

The occurrence of several aquatic hyphomycetes has been reported in polluted aquatic habitats, including sewage, animal waste, contaminated starch factory effluents, coal-mine effluents, and xenobiotic polluted sites (Sridhar and Raviraja 2001, Khallil et al. 2023). Many species are repeatedly found in water bodies polluted by sewage (e.g., *Alatospora acuminata*, *Anguillospora longissima*, *Clavariopsis aquatica*, *Flagellospora curvula*, *Nectria lugdunensis*, *Tetracladium marchalianum* and *T. setigerum*) and organic wastes (e.g., *Clavariopsis aquatica* and *Lunulospora curvula*) (Sridhar and Raviraja 2001). Many polluted aquatic habitats reduce the species richness of aquatic hyphomycetes by 0–100 %. The reduction in species diversity is contingent upon their



presence in organic debris (such as leaf litter and seeds) or in drift (including water and foam) (Sridhar and Raviraja 2001). When sterile leaves were incubated in groundwater contaminated with heavy metals and xenobiotics, a notable diversity of aquatic hyphomycetes was observed (Krauss et al. 2003, Calabon et al. 2023). While numerous aquatic hyphomycete species are sensitive to pollutants, certain species have evolved a tolerance for adapted environments altered by pollutants such as organic matter and heavy metals. Examples of such species include *C. aquatica*, *N. lugdunensis* and *T. marchalianum* (Dalton and Smith 1970, Krauss et al. 2003, Sridhar et al. 2005, Augustin et al. 2006, Solé et al. 2008b, Sridhar et al. 2008, Solé et al. 2012, Ferreira et al. 2014). Although the street runoff is polluted in southwest India, four aquatic hyphomycetes (*Alatospora acuminata*, *Anguillospora crassa*, *Flagellospora curvula*, and *Helicomyces roseus*) were dominant, indicating their tolerance to urban pollution (Ghate and Sridhar 2018). The observed variability, whether in the form of sensitivity or tolerance, in disturbed environments makes numerous species of aquatic hyphomycetes suitable as bioindicators for human-induced stress in aquatic ecosystems (Solé et al. 2008a). It would be interesting to study in detail their bioremediation properties like pollutant degrading or adsorption capabilities, especially with the scope of utilization in urban waste treatment plants.

The occurrence, diversity, and functions of aquatic hyphomycetes in some aquatic habitats (saline and low oxygen) are scanty. Hence, their detection in these settings cannot be reliably achieved using traditional methods (Pascoal and Cássio 2004, Fuentes-Cid et al. 2014). Leaf processing continues by aquatic hyphomycetes with moderate salinity ranges between 3 and 14 % (Maamri et al. 2006). Interestingly, in a seasonal study conducted on an estuary in southwest India, the occurrence of several aquatic hyphomycetes on leaf litter during the monsoon season and a few during the summer season was reported (Sridhar and Kaveriappa 1988). Sporulation of many species of aquatic hyphomycetes was reported in the salinity range of 3.4–17 ppt. As the reproduction of aquatic hyphomycetes is more sensitive to salinity than their biomass, it is possible that they can survive higher saline conditions in the mycelial stage (Bärlocher 1992). Similarly, in a recent study, occurrence and leaf litter processing by aquatic hyphomycetes have been reported in salinized stream conditions (Canhoto et al. 2017, 2021).

In temperate regions, aquatic hyphomycetes are less inhibited at water temperatures near 0 °C (Bärlocher and Kendrick 1974). Although their peak sporulation is observed in the range of 15–25 °C, their sporulation peaks at lower temperatures (Dang et al. 2009). Interestingly, species from temperate zones endure longer freezing durations compared to their tropical counterparts, while the reverse seems to be the case under elevated temperatures (Sridhar and Bärlocher 1993a). Aquatic hyphomycetes are believed to have evolved mechanisms to withstand the variable nature of temperature extremes. These adaptations significantly influence their roles and functions within aquatic ecosystems (Tomczyk et al. 2023). Notably, the upper limit of water temperatures in temperate streams often corresponds to the lower limit in tropical streams (Sridhar et al. 1992). Some species of aquatic hyphomycetes were recorded in thermal springs at temperatures ranging between 34 °C and 36 °C in southwestern India (Chandrashekar et al. 1991, Rajashekar and Kaveriappa 1996). Temperature increases in streams severely affect the assemblage of aquatic hyphomycetes and speed up the rate of litter decomposition (Ferreira and Chauvet 2011).



Although the β -diversity of aquatic hyphomycetes increased with temperature elevation, it showed a negative effect on their functional roles (Fenoy et al. 2021). Thus, temperature extremes alter the functioning of stream ecosystems, including decomposition and nutrient cycling (Pérez et al. 2021, Arias-Real 2022, Gentilin-Avanci et al. 2022).

Intermittency is often seen in freshwater bodies, which has been considered one of the environmental stresses that have an impact on lotic biota as well as their ecological functions (e.g., organic matter mineralization) (LeRoy 2019, Graça et al. 2023, Simões et al. 2023). Simões et al. (2021) argued that native riparian vegetation can regulate stream temperature increases and, in turn, protect aquatic bodies from the severity of intermittence. Assessment of aquatic hyphomycetes in the sediments of nine temporary streams in southwest India showed the dominance of *Anguillospora longissima*, *Cylindrocarpon* sp. and *Flagellospora curvula* during the summer and monsoon seasons (Ghate and Sridhar 2015). The results showed that conidial biomass is dependent on the organic matter in streambed sediments and that scolecoïd conidia have higher dispersal ability than stauroïd conidia in sediments.

Aquatic hyphomycetes are usually abundant in broad pH ranges (5–7) but decrease in other acidic and alkaline pH ranges (Bärlocher 1987, Raviraja et al. 1998a). The loss of litter weight attains a peak in the pH range of 4–6 (Thompson and Bärlocher 1989, Rosset and Bärlocher 1985). Acidic conditions resulted in decreased decomposition rates in benthic as well as hyporheic zones (Corunt et al. 2012). Industrial waste wiped out the biota in Hungary's Toma stream, which exhibited an alkaline pH of 12.8 (Vass et al. 2013). When four kinds of leaf litter were incubated in the Toma stream, they were colonized by 26 species of aquatic hyphomycetes. Notably, *Necrria lugdunensis*, *Tetracladium marchalianum*, and *Tricladium* sp. were dominant. However, the overall species count was lower compared to a benchmark site (Vass et al. 2013). Similarly, the runoff water from the catchment area, rich in chemical fertilizers and pesticides, is affecting the diversity of aquatic hyphomycetes in river beds, including tributaries of rivers.

The incidence of aquatic hyphomycetes in the guts of stream invertebrates and vertebrates is not surprising. Many aquatic hyphomycetes pass through the gut of *Gammarus pulex* (Bärlocher 1981). Sridhar et al. (2011) demonstrated evidence of the survival of aquatic hyphomycetes within the digestive systems of *Gammarus tigrinus* and *Hyella azteca*. Fecal samples from three common Cyprinidae fish species in a freshwater stream in southwest India revealed a prominent presence of six distinct aquatic hyphomycetes (*Anguillospora longissima*, *Cylindrocarpon* sp., *Flagellospora curvula*, *Triscelophorus acuminatus*, *T. konajensis*, and *T. monosporus*) (Sridhar and Sudheep 2011a). The possibility of these fish facilitating the upstream transfer of aquatic hyphomycetes, especially since some are known to swim against the current, should be considered (Liao 2007).

Even though studies are being undertaken on the fungal diversity of aquatic hyphomycetes in various marine and aquatic ecosystems, there is a need to focus on artificial habitats like wells, dams, and canals, which provide unique conditions for adaptation (Sridhar 2020). Moreover, the destruction of diversity caused by man-made events like mass bathing during Kumbh (a holy bathing ritual as per Hindu mythology), destruction of catchment areas, extinction or reduction in



the population of fish, and unique and extreme habitats like hot water springs in Odisha (Lonar, Pangong, and Loktak lakes) are areas that need attention with regard to aquatic fungal diversity and their ecological function.

3. Colonization on unusual substrates by aquatic hyphomycetes

Aquatic hyphomycetes have a remarkable ability to adapt to harsh conditions, often seeking refuge in various environments such as wood, live roots, soil, and sediments, among others (Table 2). Parallel to their presence in unconventional ecological niches, they can also be found colonizing substrates other than their favoured submerged leaf litter typically found in freshwater streams. Examples of such substrates include wood, live roots, soil, tree canopies, and land-based litter (Figure 3). Although woody litter is a common substrate in streams, not much is known about its colonization by aquatic hyphomycetes. Persistent wood in freshwater is highly valuable for distinguishing the perfect state of aquatic hyphomycetes (Webster 1992). Shearer (1992) compiled the reports for up to 86 species (in 46 genera) of aquatic hyphomycetes on woody debris in freshwaters and terrestrial habitats. In a study conducted by Sridhar et al. (2010), naturally submerged woody litter in 12 high-altitude streams in the Western Ghats of India yielded many aquatic hyphomycetes. Incubation experiments, both damp and in bubble chambers, showed that *Anguillospora longissima*, *Flagellospora curvula*, *F. penicillioides*, and *Lunulospora curvula* were particularly prevalent in both the bark and cambium. Additionally, species such as *Alatospora acuminata*, *Anguillospora crassa*, *Clavariopsis aquatica*, and *Tetracladium marchalianum* were frequently encountered on woody litter. Among these anamorphs, *Anguillospora crassa*, *A. longissima*, *Clavariopsis aquatica*, and *Flagellospora penicillioides* are known with their respective teleomorphs, *Mollisa uda*, *Massarina* sp., *Massarina* sp. and *Nectria penicillioides* (Webster 1992). Interestingly, all these mentioned species, including *Tetracladium marchalianum*, exhibit robust exo-enzymatic abilities (Shearer 1992, Raja et al. 2018, El-Elimat et al. 2021). A separate study delved into the colonization of aquatic hyphomycetes in air-dried woody debris that was submerged in a southwestern stream (Sudheep and Sridhar 2013). During bubble chamber incubation experiments involving wood materials, *Lunulospora curvula*, and *Triscelophorus acuminatus* were dominant. The spatial distribution of aquatic hyphomycetes in naturally submerged hard and soft woody materials revealed the occurrence of 10 and 26 species, respectively (Sridhar and Sudheep 2011b). Furthermore, it was noted that lignicolous fungi predominantly inhabited hardwoods, while aquatic hyphomycetes were more prevalent in softwoods.

Submerged roots in streams are potential sites of colonization by aquatic hyphomycetes. Roots of many streamside Angiosperms, Gymnosperms, and Pteridophytes are targets for colonization by aquatic hyphomycetes (Sridhar and Bärlocher 1992, Raviraja et al. 1996, Sati and Belwal 2005, Sati et al. 2009, Ghate and Sridhar 2017). Aquatic hyphomycetes derive multiple benefits by colonizing roots exposed to stream environments. The periodic turnover of these roots also offers them nutritional advantages. Furthermore, roots serve as shelters, protecting the fungi from aquatic predators and preventing their downstream dispersal. This strategic positioning also enables them to cope with intermittent challenges such as droughts or stream contaminants. Additionally, the

Table 2. Colonization of aquatic hyphomycetes in selected unusual substrates

Substrate	Selected reference
Submerged wood	Shearer 1992, Sridhar et al. 2010, Sridhar and Sudheep 2011b, Sudheep and Sridhar 2011, 2013
Submerged roots	Sridhar and Bärlocher 1992, Raviraja et al. 1996, Sati and Belwal 2005, Sati et al. 2009, Ghate and Sridhar 2017, Koranga and Sati 2023
Sediments	Sridhar et al. 2008, Sudheep and Sridhar 2012, Ghate and Sridhar 2015, Karun et al. 2016, Martinez et al. 2020
Soil	Bessey 1939, Waid 1954, Gams et al. 1969
Terrestrial leaf litter	Sridhar and Kaveriappa 1987, Sridhar and Bärlocher 1993b, Sridhar et al. 2020
Terrestrial woody litter	Sharathchandra and Sridhar 2020
Tree canopy	Sridhar 2009, Révay and Gönczöl 2011, Chauvet et al. 2016, Magyar et al. 2021, Sharathchandra and Sridhar 2022

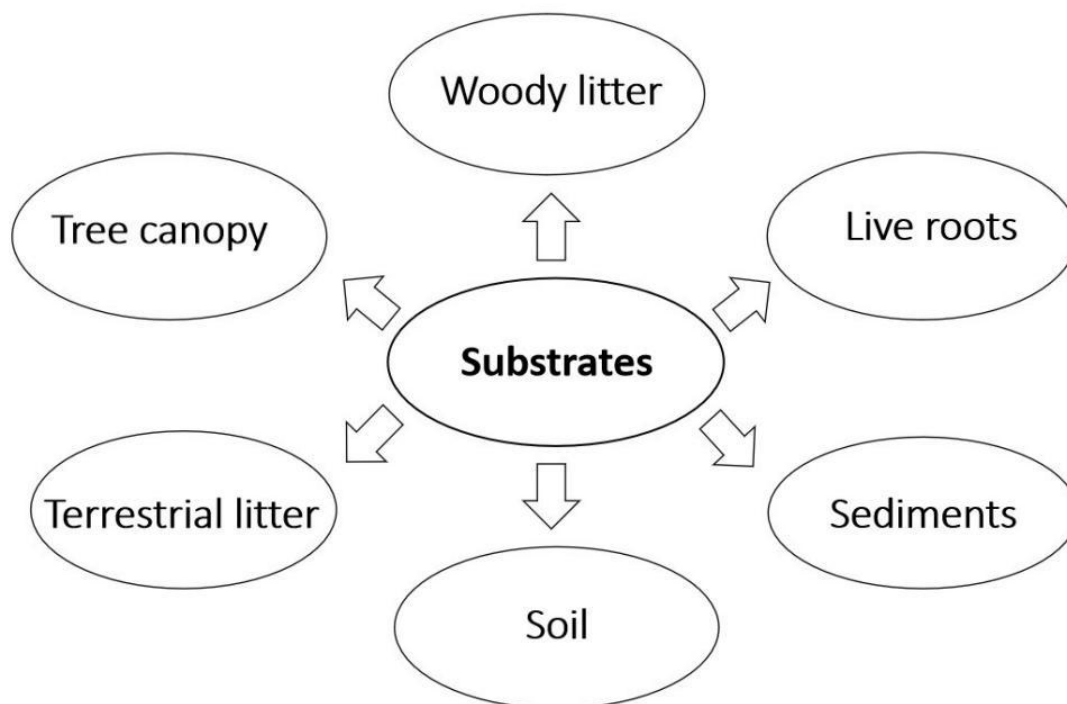


Figure 3: Colonization of aquatic hyphomycetes on substrates other than leaf litter

presence of endophytic aquatic hyphomycetes on plant roots is advantageous for the plants themselves due to the fungal production of bioactive compounds that guard against pathogenic microbes and herbivores. Another potential ecological niche for aquatic hyphomycetes that could be extrapolated to streams is the aquatic fern (Sati and Belwal 2005, Sati et al. 2009). Our



understanding of the mutualism of aquatic hyphomycetes in aquatic ecosystems is still in its infancy.

Stream sediments provide a habitat for aquatic hyphomycetes, offering them refuge from predators and drought conditions. Their growth, sporulation, and accumulation in these sediments further promote their dispersion into the groundwater. Only a limited number of studies have investigated the presence and role of aquatic hyphomycetes within stream sediments (Sudheep and Sridhar 2012, Ghate and Sridhar 2015, Martinez et al. 2020). Stream sediments are the sites of the accumulation of various pollutants, and it is interesting to track the competence of aquatic hyphomycetes to cope with such contaminants in the sediments. They may transform some of the pollutants with the help of their potential extracellular enzymes, organic acids, and other secondary metabolites. A few reports are available on the incidence of aquatic hyphomycetes in terrestrial soil as well as terrestrial roots (Sridhar and Bärlocher 1993b). Regarding the adaptation and functionality of aquatic hyphomycetes in soil or root systems, their role in plant protection and growth enhancement is of significant importance (Sati and Pant 2020, Pant and Sati 2021).

The incidence of aquatic hyphomycetes in terrestrial litter has been reported in several instances (Sridhar and Bärlocher 1993b). Some recent studies have also repeatedly documented aquatic hyphomycetes in terrestrial leaves as well as woody litter (Sridhar et al. 2020, Sharathchandra and Sridhar 2020). Similarly, a wide range of aquatic hyphomycetes have been adapted to occur in tree canopies (Sridhar 2009, Révay and Gönczöl 2011, Chauvet et al. 2016). Based on these reports on the existence of aquatic hyphomycetes in terrestrial conditions, it can be inferred that these fungi have strong sexual and asexual morphs to survive and disseminate outside their usual aquatic habitats.

4. Adaptation and ecosystem services of aquatic hyphomycetes

Aquatic hyphomycetes can provide ecosystem services beyond their typical lotic environments due to their adaptability to colonize diverse substrates across varied ecological niches (Table 3). Increasing evidence from field, mesocosm, and microcosm studies points to the presence of aquatic hyphomycetes in atypical habitats. Their prevalence and associated ecosystem services in these so-called extreme habitats or varied substrates appear to be surprising compared to their favoured flowing freshwater environments (Figure 4). Evidence supporting the involvement of aquatic hyphomycetes in plant detritus turnover, mineralization, and energy transfer to the upper trophic levels in aquatic habitats will also be extended to terrestrial, sedimentary, and groundwater habitats (Chauvet et al. 2016).

Like many other organisms in aquatic and terrestrial ecosystems, aquatic hyphomycetes are increasingly facing challenges due to climate change, including global warming, intermittent water flow, drought, and changes in riparian vegetation, as well as from human activities (Döll and Zhang 2010). Supportive evidence is accessible on the adaptation and function of aquatic hyphomycetes in many such chaotic situations. The decomposition of exotic plant litter, including introduced, monocultured, and invasive species, has been the subject of research by many authors (e.g., *Acacia* and *Eucalyptus*) (Raviraja et al. 1998b, Pereira and Ferreira 2021, da Silva et al. 2023). The decomposition of eucalypt leaf litter in Brazilian streams was mainly caused by the



Table 3. Selected examples of ecosystem services of aquatic hyphomycetes in usual and unusual habitats

Habitat	Ecosystem service	Selected reference
Natural detritus	Decomposition and energy flow	Suberkropp 1992, Chung and Suberkropp 2009
Exotic detritus	Decomposition and energy flow	Sridhar et al. 1992, Raviraja et al. 1998b, Gomes et al. 2016, Pereira and Ferreira 2021
Eutrophic	Combat eutrophication	Raviraja et al. 1998b, Bärlocher 2005, Sridhar et al. 2009
Polluted	Growth, reproduction, resistance and tolerance	Raviraja et al. 1998b, Raghu et al. 2001, Sridhar and Raviraja 2001, Krauss et al. 2003, Jaeckel et al. 2005, Sridhar et al. 2005, Braha et al. 2007, Duarte et al. 2008, Ehrman et al. 2008, Seena et al. 2020
Soil and or microcosm	Plant protection	Sati and Arya 2010a, Arya and Sati 2011, Sati and Singh 2014, Singh and Sati 2020, Pant and Sati 2021
	Plant growth promotion	Sati and Arya 2010b, Sati and Pant 2020, Pant and Sati 2023
	Phosphate solubilization	Singh and Sati 2017, Sati and Pant 2019
Mesocosm and or microcosm	Natural products	Kaida et al. 2001, Sridhar 2012, Soe et al. 2019, El-Elimat et al. 2021
	Enzymes	Suberkropp and Klug 1976, Chandrashekar and Kaveriappa 1991, Gulis and Stephanovich 1999, Martin et al. 2009, Krauss et al. 2011, Solé et al. 2012, Heeger et al. 2021
	Degradation of xenobiotics	Junghanns et al. 2005, 2008, Augustin et al. 2006, Solé et al. 2008b, Bärlocher et al. 2011
	Plastic nanoparticle tolerance	Seena et al. 2019, Trabulo et al. 2022

dominance of *Anguillospora filiformis* (99.6 %), which indicates such leaf litter in streams decreases the diversity of aquatic hyphomycetes (Gomes et al. 2016). Conversely, in Portugal, Acacia leaf litter has been observed to reduce both the decomposition rate and the aquatic hyphomycete community (Pereira and Ferreira 2021). Tonello et al. (2021) found that the removal of riparian vegetation in the streams of the Atlantic Forest led to an increase in primary production, but this was coupled with a reduction in litter decomposition rates. In Europe, the loss of native alder trees (*Alnus glutinosa*) similarly resulted in slower decomposition rates of other leaf litter (Alonso et al. 2021). Notably, in the Western Ghats, leaf litter from introduced plant species like *Coffea* and *Hevea* supports a higher species richness of aquatic hyphomycetes compared to native

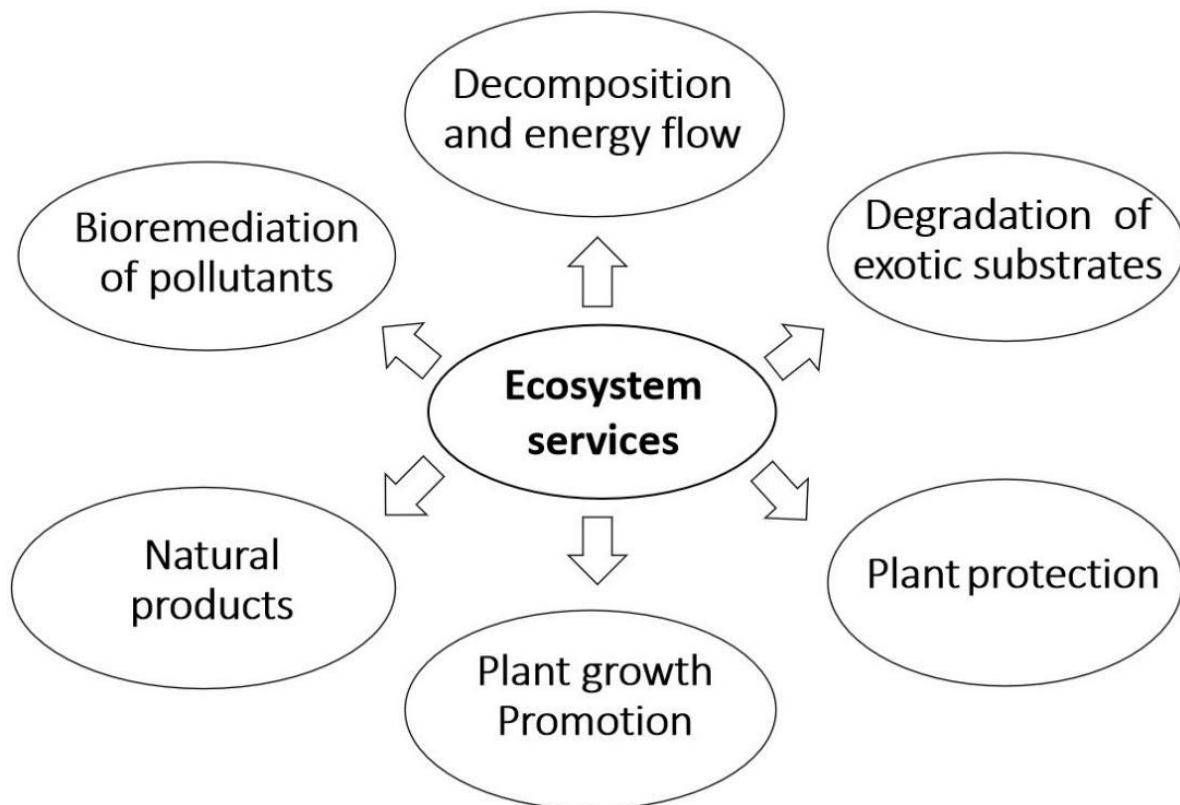


Figure 4: Ecosystem services of aquatic hyphomycetes in unusual habitats

tree species (Sridhar et al. 1992). Essentially, environmental heterogeneity within an ecosystem underpins the relationship between biodiversity and ecosystem services, with species richness exerting a substantial impact on ecosystem services (Albrecht et al. 2021). As a result, the management of riparian tree species emerges as a top priority to optimize aquatic health resources (Larrañaga et al. 2021).

While leaf litter decomposed more rapidly under eutrophic conditions in Portugal, the variety of aquatic hyphomycetes diminished (Sridhar et al. 2009). Conversely, in a eutrophic stream in southwest India, while the decomposition rates of leaves remained unchanged, there was a notable decline in aquatic hyphomycetes (Raviraja et al. 1998b). It has been predicted that depletion of dissolved oxygen or increased pollutants in eutrophic conditions might influence the decline in the diversity of aquatic hyphomycetes (Lecerf and Chauvet 2008, Krauss et al. 2011). In addition, several organic or inorganic constituents in minute quantities in the eutrophic streams might serve as hormetic doses that selectively promote or stimulate the growth and functions of aquatic hyphomycetes (Calabrese and Baldwin 2003, Sridhar and Bärlocher 2011). In the presence of either extremely low or high pollutant concentrations, aquatic hyphomycete communities undergo selective enrichment or selective/total species extirpation, respectively, as documented by Sridhar and Raviraja (2001). Notwithstanding, pollutant-resistant taxa, encompassing core groups,



keystones, and both rare and infrequent species, persist in their ecological functions. Consequently, a reduction in species diversity should not be directly equated with a comprehensive cessation of critical ecological processes such as decomposition and mineralization.

Even though heavy metals (Cd, Cu, and Zn) inhibit the growth and reproduction of aquatic hyphomycetes in hyper-polluted habitats in Central Germany, many of them developed tolerance by producing phytochelatins (e.g., *Articulospora tetracladia*, *Nectria lugdunensis*, and *Tetracladium marchalianum*) (Mirsch et al. 1997, 2001, Krauss et al. 2003, 2011). Some of the aquatic hyphomycetes that exist in heavy metal-hyperpolluted aquatic habitats developed stress responses through long-term exposure, possibly by changing their functional genes in favour of metabolism, survival, and functions (e.g., *Nectria lugdunensis*) (Krauss et al. 2011). Raviraja et al. (1998b) documented similar findings in a stream contaminated with organic pollutants in southwest India. The capacity of aquatic hyphomycetes to either tolerate or evade heavy metals in streams serves as a vital strategy to sidestep the associated toxicity. Several biochemical processes exhibited by aquatic hyphomycetes, such as the production of catalase, sulphate reductase, superoxide dismutase, and glutathione, assist in counteracting the effects of heavy metals in streams, as observed in species like *Heliscus submerses*, *Nectria lugdunensis*, and *Varicosporium elodeae* (Krauss et al. 2011). Seena et al. (2020) have demonstrated the role of amino acids and lipids in managing the metal toxicity of *Neonectria lugdunensis*.

In the Himalayan region, numerous aquatic hyphomycetes, isolated as endophytes from riparian tree roots, exhibit inhibitory effects on pathogenic microbes, promote plant growth and demonstrate phosphate solubilization (see Table 3). Several of these root-associated endophytes displayed suppressive activity against both pathogenic bacteria and fungi. Pot experiments of several plant species (*Capsicum annuum*, *Hibiscus esculentus*, *Solanum melangena*, and *Triticum aestivum*) inoculated with root endophytic aquatic hyphomycetes showed significant growth promotion (Pant and Sati 2023). Similarly, many root endophytes also showed phosphate solubilization in Pikovskaya agar as well as Pikovskaya broth (Singh and Sati 2017, Sati and Pant 2019).

Over the past three decades, several freshwater fungi (mainly ascomycetes) have yielded up to 280 compounds, with 199 of these exhibiting bioactive properties (Gulis and Stephanovich 1999, El-Elimat et al. 2021). Aquatic hyphomycetes are also potential sources of many bioactive metabolites. Several cyclic depsipeptides derived from *Clavariopsis aquatica* showed inhibitory activity against eight plant pathogenic fungi (Soe et al. 2019, Kaida et al. 2001, El-Elimat et al. 2021). A unique antibacterial and antifungal metabolite, termed "anguillosporal", was extracted from *Anguillospora longissima* (Harrigan et al. 1995). Similarly, *Dendrospora tenella* produced bioactive tenellic acids A-D as diphenyl ether derivatives (Oh et al. 1999a). Seven new metabolites (tricladolides A-D and tricladic acids A-C) were reported from *Tricladium castaneicola* (Han et al. 2015). The sexual morph of *Tumulularia aquatica* (*Massarina aquatica*) growing on oak wood also showed antifungal effects and produced bioactive sesquiterpenoids (Fisher et al. 1983, Oh et al. 1999b, 2003). Likewise, an antifungal metabolite, quinaphthin, has been isolated from the aero-aquatic fungus *Helicoon rihonis* (Adriaenssens et al. 1994, Fisher et al. 1988).



Nearly every aquatic hyphomycete can break down the cellulose, hemicellulose, and pectin found in leaf litter. They can produce and modify various xenobiotics using oxidative enzymes akin to those observed in land-based fungi (Krauss et al. 2011). Specific aquatic hyphomycetes, such as *Clavariopsis*, *Nectria*, *Tetracladium*, and *Varicosporum*, when cultivated in a lab setting, have demonstrated the ability to process DDT (dichlorodiphenyltrichloroethane) at minimal concentrations (Hodkinson 1976). However, reproduction of aquatic hyphomycetes declined upon exposure to pentachlorophenol (Sridhar and Raviraja 2001). Krauss et al. (2011) schematically represented the capability of aquatic hyphomycetes involved in the mineralization of xeno-organic pollutants. Laccases responsible for lignin modification were reported by many investigators in aquatic hyphomycetes, especially *Clavariopsis aquatica* (Junghanns et al. 2005, Martin et al. 2007, 2009, Solé et al. 2012). Recently, Heeger et al. (2021) sequenced the genome of *C. aquatica* and found differential expression of genes responsible for the modification of lignocellulose and its constituents (cytochrome P450 monooxygenases, laccases, and peroxidases). Thus, *C. aquatica* serves as a model organism for further investigation in toxicology and bioremediation owing to its capability to detoxify aromatic lignin components and xenobiotics in lotic habitats (Junghanns et al. 2005).

The introduction of heavy metal nanoparticles into aquatic environments hinders the decomposition of organic matter (Pradhan et al. 2011). Yet, when ZnO nanoparticles and acid rain are combined, they lead to an increase in leaf litter decomposition, ranging from 1.2 to 2 times (Du et al. 2022). The presence of silver nanoparticles, either independently or in conjunction with microplastics, interferes with the transformation of organic matter by aquatic hyphomycetes in waterways (Trabulo et al. 2022). While nanoscale microplastics diminish the capacity of aquatic hyphomycetes to break down leaf litter, the rich fungal diversity in aquatic systems appears to somewhat mitigate this effect (Seena et al. 2019).

5. Conclusions and outlook

Aquatic hyphomycetes are indispensable biota involved in several ecosystem services in lotic water bodies. They are successful in many habitats due to their capabilities for colonization, growth, sporulation, dissemination, floatation, and spore germination. They possess the inherent capacity to deal with multiple climatic changes and human perturbations. Although their reproduction is affected by unusual conditions (e.g., temperature, eutrophication, and xenobiotics), their mycelia remain hidden or tolerant to such conditions. Some of the xenobiotics serve as hormetic doses at very low threshold levels. Factors such as temperature, fire, and nutrient enrichment yield comparable effects, notably the accelerated decomposition rates of organic matter, resulting in the rapid exhaustion of nutrient reserves. In response, aquatic hyphomycetes have evolved to circumvent turbulent conditions by finding refuge in more stable environments, such as within woody debris, living roots, and even the intestines of aquatic organisms. Although aquatic hyphomycetes appear to function individually at the outset, they have interspecies networks (as core-group, keystone, cryptic, and infrequent species) and interactions with varied live entities (roots, hydrophytes, lichens, and animals) and dead substrates (woody litter and sediment) in aquatic and semi-aquatic ecosystems. These mutualistic associations and interactions not only offer additional protection but also support their survival in atypical conditions, thereby sustaining ecosystem services. Molecular studies, encompassing genomics and metabolomics,



related to both culturable and non-culturable aquatic hyphomycetes in atypical environments, offer a deeper understanding, enabling a more accurate assessment of their significance.

There are several gaps in our knowledge to understand the ecosystem services of aquatic hyphomycetes in their usual as well as unusual habitats: 1) Metabolic capabilities (secondary metabolites of nutritional, medicinal, agricultural, and industrial significance); 2) Capability of bioremediation of xenobiotics (agricultural chemicals, pollutants, and waste waters); 3) Mutualistic associations (as endophytes with plants, hydrophytes, and lichens); 4) Nutritional composition (amino acids, minerals, fatty acids, vitamins, hormones, and growth factors); 5) Occurrence in ground waters, aquifers, and cave streams suggests their role in purifying drinking waters. There is a need for more focused research on aquatic hyphomycetes, wherein we look for the answers mentioned above. All these areas also want to be visualized considering local habitat level changes, viz., change in salt concentration of the sea due to glacier melting and surplus rainfall in rivers, and change in nitrogen content of river beds due to enhanced fertilizer or sewage input. Moreover, the effects of altitude and latitude, drift and compensatory mechanisms, and transport within and between streams are some of the factors that need to be focused on when working with moving water in relation to aquatic hyphomycetes.

Numerous questions about aquatic hyphomycetes still await answers: 1) How well do aquatic hyphomycetes manage disturbances? 2) Do they offer ecosystem services in compromised habitats or scenarios? 3) Are they capable of recovering from or evading harsh conditions owing to changes in hydrological regimes, including climate change? 4) What backup tactics do they employ to sidestep tumultuous situations? 5) Can they act as indicators reflecting the intensity of disturbances? Recent studies on aquatic hyphomycetes from various regions are gradually providing evidence that may shed light on these queries. Studies like the exploration of the aquatic fungal diversity of rivers while entering urban areas, during their residence in such habitats, and while they leave the urban regions will help to understand the above rationale. Moreover, there is a need for aquaculturists and mycologists to collaborate to understand the effects of pollutants on fish, other fauna, and aquatic fungi and document the gut aquatic fungal diversity. Successional studies would also help to understand the pre- and post-flood diversity of aquatic hyphomycetes and how the species reestablishes itself. It would be interesting to study the colonization of exotic substrates in water bodies like plastics, rubber, tyres, and cloth by aquatic hyphomycetes.

Globally, ten major disturbances lead to a decline in biodiversity, and out of these, seven notably impact freshwater ecosystems (Malmqvist and Rundle 2002, Rockström et al. 2009). Due to human activities, restoring ecosystems for sustained productivity has become a pressing concern in today's context. To leverage and optimize the benefits of aquatic hyphomycetes in freshwater, it is crucial to conduct ecological risk assessments and restore their native conditions, ensuring their functional integrity in the context of current climate change. The fungal hyphomycetes seem to be the least privileged organisms in aquatic systems. However, they may be the most important ones as far as eco-function is concerned, as we have observed in other habitats and ecosystems.



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