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Inland Water Fungi in the Anthropocene: Current and Future Perspectives[☆]

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Introduction

Fungi and fungi-like organisms (such as oomycetes) are key components of aquatic ecosystems, with parasitic and/or saprophytic lifestyles that influence biodiversity, food web dynamics, and the cycling of organic matter, nutrients, and energy within ecosystems. Yet, they represent an understudied group of aquatic microorganisms, largely neglected by aquatic microbial ecologists. In fact, historically *mycology* was separated from microbial ecology in all aquatic sciences. Studies of fungi are of great ecological and biotechnological interest because fungi have a large variety of polymer-degrading enzymes and detoxification mechanisms. However, the dramatic increase in the human population worldwide and subsequent increasing urban development and anthropogenic pollution has led to a severe modification of inland waters, with adverse effects on fungi. In this article, we highlight the multiple metabolic capacities and adaptive behavior of aquatic fungi to cope with these rapid environmental changes in the **Anthropocene**. We provide an overview of emerging topics in the field of aquatic **mycology** that are, to a great extent, related to the anthropogenic modification of inland waters, in particular **emerging pollutants**, including microplastics.

Diversity and ecology of aquatic fungi and fungi-like organisms

In general, fungi and fungi-like organisms (not necessarily the aquatic ones) have been phylogenetically and taxonomically separated (**Fig. 1**). However, several basic differences make it hard to treat all fungi the same. Therefore, the formal taxonomy-based classification system coexists with the “informal” ecology-based system which is polyphyletic. Thus, many classifications of aquatic fungi have been adopted (**Goh and Hyde, 1996**; Shearer et al., 2007a,b).

Aquatic fungi

A recent estimate based on molecular evidence suggests a global fungal diversity of about 1.5 million species (**Hawksworth and Lücking, 2017**). Aquatic fungi form a taxonomically and morphologically diverse group in freshwater, brackish, and marine habitats. In parallel to their diverse lifestyles, community composition and abundance of fungi vary considerably with their aquatic habitats (**Wurzbacher et al., 2010**). Interestingly, about 96% of all fungal taxa have been recorded in temperate regions and fewer in tropical and subtropical regions (**Rossmann, 1994**; **Hawksworth, 2001**; Duarte et al., 2016; Hyde et al., 2016). Therefore, the “true” number of fungi should be much higher, i.e., 2.2–3.8 million species, because a substantial fraction of the global fungal diversity has not been explored in-depth (**Grossart et al., 2019**).

The number of isolated and described fungal taxa is much lower than global estimates, including only 120,000–143,273 species (**Fungorum, 2018**; **Wijayawardene et al., 2017**). The majority of fungal species are related to the two phyla Ascomycota and Basidiomycota (ca. 96,000 species), which form the subkingdom Dikarya. Our current knowledge of fungal diversity is quite limited (**Tedersoo et al., 2014**), particularly in aquatic systems where the number of described species is low (ca. 3000–4000 species) as compared to terrestrial fungi (**Jones et al., 2014**). Consequently, the number of newly discovered fungal species in aquatic systems is predicted to increase (**Voigt and Kirk, 2011**).

Gessner and Van Ryckegem (2003) suggested that there are ca. 20,000 different species of freshwater fungi, yet only ~5% of the estimated fungal species have been described. The estimated number of species documented from different habitats and substrates include 622 fungal species of ascomycetes, 600 hyphomycetous fungal species from *Phragmites* litter (**Gessner and Van Ryckegem, 2003**), 531 asexual fungal species, 317 species on peat swamp (**Tsui et al., 2001**; **Sivichai et al. 2002**), and 183 trichomycetes. Also, zoosporic fungi comprise more than 500 species of chytrids and members of fungal-like organisms (**Jones et al., 2014**). All other fungal groups, however, are poorly described, including freshwater lichens with about 270 lichenicolous fungi and lichens, 226 fungal species on aquatic plants described as dark septate endophytes or endomycorrhizae, and 40 species of parasitic fungi. In particular, basidiomycetes are poorly

[☆] This article was reviewed for the Encyclopedia of Inland Waters, Second Edition by Section Editor Kendra Cheruvilil.

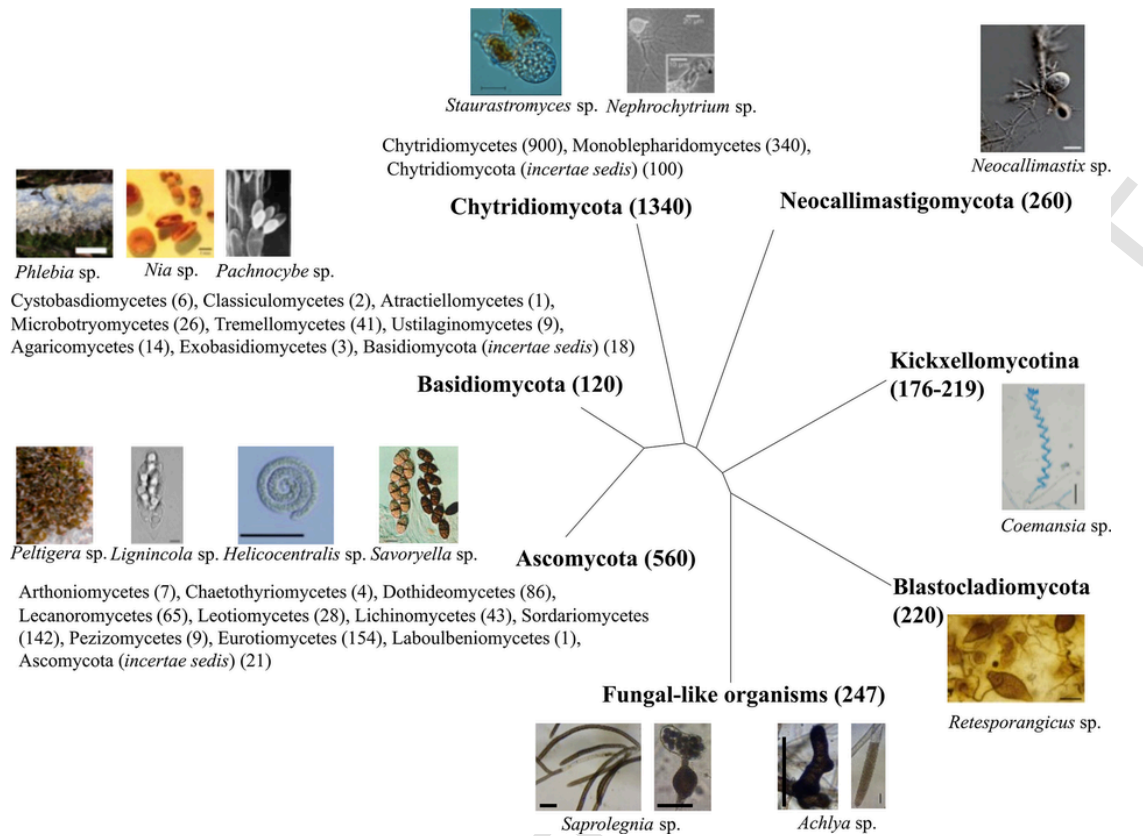


Fig. 1 Phylogeny of freshwater fungi and fungi-like organisms. The morphological and phylogenetic diversity of freshwater fungi and fungi-like organisms is illustrated. The numbers in parentheses stand for the currently identified species within each taxon. Ascomycetes are associated with dead stems and leaves of herbaceous and woody plants. They are mainly responsible for breaking down the lignocellulose constituents of plant cell walls. In contrast to their terrestrial diversity, freshwater Basidiomycota are less abundant. They colonize leaves and twigs in streams and rivers. They are known for basidiomata reduction, the passive release of basidiospores, and the production of branched conidia. Recently, the importance of true zoosporic fungi, including Chytridiomycota, Neocallimastigomycota, Kickxellomycotina, and Blastocladiomycota, has been highlighted. This is mainly due to increased awareness (both in morphology and phylogeny) for yet undescribed taxa (**dark matter fungi**). Many species are parasites and influence food web structure in freshwater ecosystems. Finally, fungi-like organisms, also known as “water molds,” are some of the most devastating aquatic animal pathogens, responsible for massive mortalities of crabs, fishes, amphibians, etc.

documented in freshwater ecosystems, with only 41 non-yeast basidiomycetes and 74 basidiomycetous yeasts. The overall documented species richness of freshwater fungi (< 4200 species) suggests that there are still many freshwater habitats and substrates to be surveyed (Jones et al., 2014).

In aquatic systems, three major types of fungi can be found depending on their growth and adaptation abilities in aquatic ecosystems: (I) terrestrial fungi that are often passively introduced into the water via high loads of fungal propagules from inflowing streams, rainwater runoff, and wind. This fungal group is known as **transient fungi** (versatile immigrants), which exhibit no activity in water - presumably due to unfavorable aquatic conditions or interactions with organisms (Dix and Webster, 1995; Voronin, 2014). (II) Partially adapted aquatic fungi that may be amphibious with one stage of their life cycle underwater and another stage dispersed in air-water boundaries (**aero-aquatic hyphomycetes**; Dix and Webster, 1995; Park, 1972 or periodic immigrants). (III) Fully adapted aquatic fungi (indwellers including Ingoldian fungi; Ingold, 1942) that can maintain their biomass in aquatic ecosystems with constant activity from year to year. They utilize substrates and nutrients available in water bodies, and most are capable of sporulating directly in water (Grossart et al., 2019).

Based on their morphology and lifestyle including different functional behaviors (independent of phylogeny), aquatic fungi are further separated into six major groups (Wurzbacher et al., 2010):

1. *Aquatic hyphomycetes* are recorded on decaying leaves and lignocellulosic debris in freshwater ecosystems worldwide. Aquatic **hyphomycetes** (Nilsson, 1964), also known as amphibious **hyphomycetes** (Michaelides and Kendrick, 1978), comprise **anamorphic** fungal taxa of ascomycetes and basidiomycetes (Shearer et al., 2007a,b) that are specifically adapted to aquatic habitats via their reproductive systems by producing their spores in relatively large multiradial (often tetradial), sigmoid or spherical

- conidia with tips usually covered with sticky mucilage (Read et al., 1992) to facilitate attachment to and colonization of a specific substrate. Aquatic **hyphomycetes** are categorized into two ecological groups according to their reproductive behavior (Goh and Hyde, 1996): (a) the **Ingoldian fungi** (Ingold, 1942) are characterized by their ability for sporulation on plant materials underwater and (b) the **aero-aquatic fungi** that do not sporulate underwater but need air exposure for sporulation to complete their life cycle (Wurzbacher et al., 2010). On the other hand, Goh (2003) provides another common group of aquatic hyphomycetes, i.e., transparent fungi with asexual reproduction (mitosporic) and dark conidia (coelomycetes) that have been recorded from various freshwater habitats. However, their conidial structure is not as well adapted for the aquatic ecosystems as the **Ingoldian** and **aero-aquatic hyphomycetes** (Goh and Hyde, 1996). These fungi include two ecological groups, namely, indwellers that are present only in freshwater environments (e.g., *Aquaphila*, *Canalisporium*, *Camposporidium*) and immigrants that occur in both terrestrial and freshwater environments (e.g., *Acrodictys*, *Acrogenospora*, *Arthrobotrys*) (Park, 1972).
2. **True zoosporic fungi** currently include phyla Chytridiomycota, Neocallimastigomycota, Kickxellomycotina, and Blastocladiomycota. They commonly occur as saprobes in the degradation of particulate organic matter of dead animals, pollen grains and plant litter as well as parasites of vertebrate animals, e.g., frogs, zooplankton and phytoplankton, or as symbionts in the mammalian digestive system. Consequently, zoosporic fungi have significant ecological roles in nutrient cycling and regulation of the populations of phytoplankton in aquatic ecosystems and also cause some economically important plant and animal diseases (Gleason et al., 2017). True zoosporic fungi typically occur in the pelagic zone of standing waters (Wurzbacher et al., 2010) and their reproductive units display primary adaptations to an aquatic lifestyle in the form of unflagellated motile zoospores (Wong et al., 1998).
 3. **Aquatic ascomycetes and basidiomycetes** (**teleomorphic** stage; develops sexual reproductive units including ascospores characteristic for ascomycetes and basidiospores for basidiomycetes) are microscopic fungi that decompose submerged woody material that falls into aquatic habitats. Since the 1990s, several studies concerning freshwater ascomycetes have been performed increasing the number of described species from 370 (Shearer, 1993) to 622 species (Cai et al., 2014; Shearer et al., 2014). Currently, about 675 species related to freshwater ascomycetes have been characterized and comprise several taxonomic groups (i.e., dothideomycetes, sordariomycetes, and leotiomycetes) ubiquitously found in freshwater on submerged and exposed woody debris (Jones and Pang, 2012; Shearer et al., 2014). The majority of freshwater ascomycetes form microscopic ascocmata (less than 0.5 mm) and contain structurally water-adapted ascospores characterized by several sheaths or wall ornamentations covered by a gel-like sticky material that supports spore dispersal and attachment (Digby and Goos, 1987).
 4. **Yeasts** are unicellular fungi with spherical or oval-shaped cells, representing a diverse group belonging to ascomycetes and basidiomycetes (Shearer et al., 2007a,b) that are found mainly in the pelagic zone of freshwater habitats (Wurzbacher et al., 2010) and the pelagic and estuarine habitats of marine systems. Our understanding of their ecology and functions in aquatic ecosystems is still limited (Wurzbacher et al., 2010). However, they may play a similar role as heterotrophic bacteria generally referred to as the main (micro)organisms taking up and re-mineralizing dissolved organic matter.
 5. **Glomeromycota** represent another under-studied group of aquatic fungi with little information on their ecology, composition and role in aquatic ecosystems (Goh and Hyde, 1996). The majority of glomeromycetes is terrestrial, except for aquatic trichomycetes (Shearer et al., 2007a,b), and form a polyphyletic group which grows parasitically or mutualistically (order Harpellales) together with aquatic arthropods (Hibbett et al., 2007; Jobard et al., 2010). In addition, Glomeromycota are comprised of ecologically beneficial mycorrhizal fungi forming symbionts with the roots of aquatic macrophytes. These mycorrhizal fungi are characterized by the formation of special structures (vascular and/or arbuscular structures) inside the plant roots providing the plant with nutrients, e.g., phosphorus in nutrient-limited aquatic ecosystems (Wurzbacher et al., 2011).
 6. **Fungi-like organisms** (Oomycetes, Straminipila) are well-documented (Wong et al., 1998) and considered the most ubiquitous aquatic “fungal” group characterized by biflagellate heterokont (two unequal flagella) zoospores (Dick, 1989; Shearer et al., 2007a,b). Although Straminipila (hyphochytriomycota, Oomycota, and labyrinthulomycota) share similar morphological and physiological traits with true fungi (chytridiomycota, rosellomycota, and aphelida), their ecological functions and trophic strategies appoint them as false fungi (Alexopoulos et al. 1996; Beakes et al. 2014; Karpov et al. 2014).

Although cultivation is often biased, e.g., by sample handling and the choice of media, more fungal isolates from aquatic ecosystems are required to better characterize their genetics, physiology, and ecological role (Grossart et al., 2019). Yet, it remains difficult to characterize and estimate total fungal diversity at any given sampling site, often due to the lack of experience and qualified staff and suitable identification manuals, especially in tropical regions. There is a great demand to provide new techniques and strategies to isolate and assess fungal diversity and enable realistic site estimates for conservation purposes (Cannon, 1997 and Hawksworth, 2001). The application of different isolation techniques to the same waterbody may yield entirely different fungal communities (Abdel-Raheem, 2004; Sridhar et al., 2010). Whereas direct observation techniques can be used for investigations of growth of **zoosporic fungi**, aquatic **hyphomycetes**, and **teleomorphic** fungi on different substrates (Müller-Haackel and Marvanová, 1979; Sparrow, 1968), the baiting technique is commonly used for isolation of **zoosporic fungi** and aquatic **hyphomycetes** from water samples using specific baits such as boiled sesame and hemp seeds (for oomycetes, fungal-like organisms), phytoplankton, pollen grains, and snakeskin (for chytrids) and plant leaves (for aquatic **hyphomycetes**) (Shearer and Von Bodman, 1983; Shearer, 1972; Sparrow, 1968). Furthermore, the moist chamber technique can be employed to isolate **teleomorphic** fungi using woody blocks (Shearer and Von Bodman, 1983; Shearer, 1972). Finally, yeasts can be obtained by dilution plating of water or sediment on specific media (Fell, 2001; Kumar et al., 2011). Although most aquatic fungi remain uncultivated, new methods, baits, and media may isolate the entire fungal community in aquatic systems.

The phylogenetic relationship of aquatic fungi, including Ascomycota, Basidiomycota, Chytridiomycota, Neocallimastigomycota, Kickxellomycotina, Blastocladiomycota, and fungi-like organisms is given in Fig. 1. Recently, a new and surprisingly large fungal diversity has been discovered in aquatic habitats using molecular tools. These so-called **dark matter fungi** are mainly related to the early branches of the fungal tree, i.e., Aphelida, Rozellomycota, and Chytridiomycota (Grossart et al., 2016). Thus, considerable efforts to discover and evaluate their ecology and ecophylogenetics are needed. For example, their role as parasites or saprotrophs still needs to be identified and quantified (e.g., Banos et al., 2020). Whereas parasites exploit their living host for nutrition, saprotrophs use an array of excreted (extracellular) enzymes to digest their dead nutritional substrate directly (e.g., dead organism or other nonliving organic matter).

Current conceptual models indicate a multitude of different processes by which aquatic fungi transform and incorporate **allochthonous** and **autochthonous organic matter** into organismic biomass and transfer it to higher trophic levels. Recently, three major processes have been identified to describe the different ecological roles of fungi in the aquatic realm (Grossart et al., 2019): (i) **mycoloop**, (ii) **mycoflux**, and (iii) **benthic shunt**.

The **mycoloop** has been well described (Kagami et al., 2007, 2014) and refers to parasitic fungi that render inedible phytoplankton available to zooplankton grazers by producing zoospores or by fragmentation of large phytoplankton cells. The **mycoflux** relates to the important role of fungal interactions in organic matter and organisms that result in aggregation or disintegration of sinking organic particles, including living organisms and dead cell debris (Grossart et al., 2019). Most consequences of the mycoflux are still unknown, but we propose that they significantly affect the efficiency of the aquatic carbon pump and hence carbon sequestration. The **benthic shunt** describes how fungal colonization of (mainly terrestrial) organic litter and the formation of fungal biomass allows for an efficient transfer of this organic matter to macrozoobenthos on the sediment (Attermeier et al., 2013). Macrozoobenthos represents an excellent food source for higher trophic levels in the pelagic zone, such as fish, and thus increases the efficiency of trophic transfer throughout the aquatic benthic and pelagic food webs. These three concepts take the various lifestyles and interactions (e.g., parasitism and saprotrophy) of aquatic fungi into account and highlight their ecological and biogeochemical importance in freshwaters. In 2.3.1 and 2.3.2 we describe two prime examples for interactions with fungi-like and fungi interactions with organisms and virus which until now have received only a little attention.

Aquatic fungi-like organisms

The fungi-like organisms represent non-fungal organisms from a taxonomical point of view but are often considered as a fungal group (Shearer et al., 2007a,b; Grossart et al., 2019) given that they show ecological traits and functions in water similar to true fungi (Wong et al., 1998; Khallil et al., 2020). Aquatic fungi-like organisms are frequently found in the orders of *Saprolegniales* and (to a much lesser extent) *Peronosporales* within the class of Oomycetes. *Saprolegniales* has nearly 15 genera known as water molds causing destructive endemics in aquatic animals. *Achlya*, *Aphanomyces*, and *Saprolegnia* are the most dangerous threats to fishes and crabs across the world. In addition, *Pythium* and *Phytophthora* represent common parasitic genera in freshwater ecosystems although not all members of *Peronosporales* occur in aquatic environments. It's worth mentioning that zoosporic fungi are another term for describing both aquatic fungi and fungi-like organisms with motile spores (Wong et al., 1998; Dick, 1989; Shearer et al., 2007a,b). Obviously, the word became obsolete when oomycetes and fungi got separated taxonomically.

Within the phylum Oomycota, oomycetes consist of two main assemblages including basal and crown oomycetes. Basal oomycetes as early-diverging ones are usually obligate parasites in marine ecosystems. Crown oomycetes, however, are considered to mainly occur in freshwater ecosystems. This group of fungal-like parasites has six orders with *Saprolegniales* and *Peronosporales* (see “**Diversity and ecology of aquatic fungi and fungi-like organisms**” section) as the biggest and most recent taxa, both including aquatic genera (Beakes and Sekimoto, 2009). *Saprolegniales*, or water molds, are well-known, exclusively aquatic organisms in freshwater ecosystems belonging to the phylum Oomycota. They are phylogenetically and systematically separated from the kingdom fungi and placed within the kingdom Chromista (Thines and Kamoun, 2010). Their positive association with water-related ecosystems is mainly due to their life cycle consisting of motile zoospores. The littoral zone, which is rich in **allochthonous organic matter** from animal and plant debris, seems to be their main niche (Marano et al., 2016). Their parasitic lifestyle on various species of fishes, crayfishes, etc. causes not only billions of dollars of damages to fisheries but also seriously endangers native aquatic animals (Van West, 2006).

Aquatic *Saprolegniales* such as *Achlya*, *Aphanomyces*, and *Saprolegnia* species are considered among the most widespread and dangerous animal pathogens worldwide (Bruno et al., 2010). Consequently, the multiple aspects of *Saprolegniales* pathogenicity in terms of ecology, diversity, as well as taxonomy, have been studied for more than a century. Several species of *Saprolegnia* and, to a lesser extent, *Achlya*, are responsible for drastic annual economic losses in salmonids and massive amphibian and crustacean mortality events, called *Saprolegniosis* (Hussein and Hatai, 2002; Fregeneda-Grandes et al., 2007). Their destructive potential is intensified by predisposing factors such as increases in mean temperatures, extreme drought periods, and aquatic contamination.

The species *Aphanomyces astaci* represents a key example of the destructive potential of parasitic *Saprolegniales*. This species causes the crayfish plague, which has been studied in terms of physiological adaptations and host responses toward parasitism since the early 1960s (Unestam, 1965; Makkonen et al., 2012). The involvement of *A. astaci* in crayfish plague points to its crucial ecological role in freshwaters. Crayfish species significantly affect aquatic food webs and biogeochemical cycling via control of macrophyte biomass and growth, species richness, benthic primary productivity, etc. (Matthews and Reynolds, 1992). *A. astaci* is considered a significant threat to European crayfish populations that were transmitted to mainly Europe and other continents through the commercial exchange of American crayfish species (which are resistant against *A. astaci*, but transmit it) in the 19th century (Schrimpf et al., 2013). Now, *A.*

astaci is listed among the world's 100 worst invasive species owing to the extremely high susceptibility of Non-American crayfish species (Luque et al., 2014).

Aside from parasitism, the ecology of Saprolegniales has been largely ignored with studies often limited to seasonality, occurrence, and correlation to various environmental parameters. Saprolegniales may be as common as their fungal counterparts in aquatic ecosystems since they may also colonize different **allochthonous** animal and plant debris in addition to being parasitic. This notion raises the question of whether Saprolegniales are as enzymatically active as fungi, making them important for **allochthonous organic matter** degradation. Interestingly, it has been shown that several genera in Saprolegniales behave opportunistically, quickly benefitting from the availability of small organic molecules while being ineffective in the degradation of more complex polymers (Masigol et al., 2019, 2020). This inefficiency is unlike fungi that can degrade a plethora of organic molecules by producing laccases and peroxidases. However, studies dealing with enzymatic capacities of Saprolegniales are rare and additional work is much needed to test whether ligninolytic inefficacy in Saprolegniales is universal.

Fungi-virus interactions: An emerging topic

One of the least studied topics in fungal ecology in inland waters is their interactions with viruses. In fact, little is known about the diversity of viruses in aquatic ecosystems, their relationships with fungal hosts such as their possible role(s) in regulating aquatic fungal populations e.g., chytrids after a diatom bloom, modes of dispersal, seasonal dynamics, and geographic distributions (Kotta-Loizou, 2019; Prussin et al., 2020). Yet, studies of viruses that infect economically important fungi (e.g., crop and aquaculture pathogens), reveal that **mycoviruses** are widespread in all major fungal groups and that most of them evolved at a very early stage of their fungal host's evolution and cause little or no apparent symptoms in their hosts (Ghabrial, 1998; Liu et al., 2012; Roossinck, 2015).

Recently, the number of reported **mycoviruses** has increased dramatically due to the use of high-throughput sequencing of fungal genomes and transcriptomes, which also allow the detection of their viromes (Nerva et al., 2016; Neupane et al., 2018; Ponsoero and Hurwitz, 2019; Zoll et al., 2018). There are currently 12 classified and seven unclassified families of **mycoviruses** (Peyambari et al., 2020). The majority of **mycoviruses** are double-stranded RNA (dsRNA) viruses, while single-stranded RNA or DNA viruses are less common (Castón et al., 2020; Jiang, 2020; Li et al., 2020). The fungal viruses with dsRNA genomes, in most cases, encode for only two proteins: a capsid protein and an RNA-dependent RNA polymerase. Some families of dsRNA fungal viruses like Totiviridae can infect protozoa, while members of Partitiviridae can also infect plants (Liu et al., 2010; Yokoi et al., 2007). The broad host range of dsRNA fungal viruses, including hosts from different eukaryotic kingdoms, hints at their ancient origin (Peyambari et al., 2020).

Mycoviruses can be transmitted intracellularly during cell division, sporogenesis, or cell-to-cell fusion, resulting in life cycles generally without an extracellular phase. Each virus strain has a narrow host range, although certain viral families may have a broader spectrum of hosts. Most **mycoviruses** are asymptomatic, but those that reduce pathogenicity in fungal hosts are of great biotechnological interest for developing natural fungicides (Ghabrial et al., 2015; Preisig et al., 2000; Yu et al., 2013).

The effects of **mycoviruses** on aquatic fungal communities remain unknown, such as the virus-induced mortality that can provoke large-scale alterations of the fungal community structure and the subsequent impact on carbon and nutrient cycling, modification of fungal metabolism (e.g., by gene disruption or the introduction of new genes), and alteration of fungal fitness, e.g., by virus-borne toxins (Roux, 2019; Suttle, 2005; Wilhelm and Matteson, 2008). The associations of viruses with fungi should be explored with a higher resolution given the high diversity existing in the fungal kingdom. Of particular interest are the associations with early divergent fungi belonging to groups such as Chytridiomycota and Rozellomycota, which, despite being abundant in aquatic environments, have been relatively little studied.

In summary, the vast majority of **mycoviruses** in freshwaters (both in natural and urban environments) and their ecological roles remain poorly understood. Freshwater **mycoviology**, although accepted as a conventional research area, is less developed compared to human, animal, or plant virology (Kotta, 2019). Due to their potential key role for freshwater fungi, **mycoviruses** deserve considerably more attention from aquatic microbial ecologists.

Aquatic fungi in the Anthropocene

Fungi inhabit a broad range of habitats (Grossart et al., 2019). In the case of those that inhabit natural aquatic ecosystems, there has been a growing interest in studying their diversity and ecology (Bärlocher and Boddy, 2016; Krauss et al., 2011), but much less is known about fungi in the urban aquatic environments (such as houses, hospitals, recreational parks and wastewater treatment plants) that are steadily increasing worldwide. Urban aquatic environments provide a series of conditions that result in a very different composition of fungal species from that found in natural environments. In other words, the human-build environment favors the enrichment of some fungal species, whose effects on environmental and human health are yet unknown. On the other hand, these enriched species may be of great biotechnological interest. Few studies have been conducted to understand the diversity of fungi in different human-made aquatic systems, the effects of pollutants and human waste on fungal community structure, and the abundance of opportunistic pathogens (Assress et al., 2019; Biedunkiewicz and Górska, 2016; Newbound et al., 2010).

Human homes contain numerous habitats for aquatic fungi, particularly in kitchens and bathrooms (Fig. 2). For example, fungal populations are regularly found in sinks, drinking water pipes, showers, and toilets (Flores et al., 2011; Gashgari et al., 2013; Hamada and Abe, 2009; Zhou et al., 2017). Aquatic fungi frequently occur in household appliances such as washing machines and dishwashers,



Fig. 2 Overview of habitats (in red circles) for aquatic fungi within urban environments. Houses contain numerous habitats for aquatic fungi, particularly in the kitchen and bathroom (e.g., sinks, tap water, showers, toilets, washing machines, and dishwashers), which are extensible to more massive constructions such as apartment buildings, hospitals, shopping malls, and industries. Aquatic fungi are also found in open spaces such as fountains, ponds, and swimming pools, as well as in wastewater treatment plants.

where they adapt to extreme conditions of high temperatures, drastic changes in pH, high salinity, presence of detergents, and high shear forces (Babič et al., 2016; Raghupathi et al., 2018; Zupančič et al., 2016). House conditions, and thus habitat for fungi, are extensible to more massive constructions such as apartment buildings, hospitals, shopping malls, and industries (Steinberg et al., 2015).

Aquatic fungal communities have also been identified in habitats that are in close contact with humans such as fountains, artificial lakes, and swimming pools of public parks and recreational areas (Brandt et al., 2007; Jankowski et al., 2017). Fungi are found in the municipal systems designed for collecting and transporting wastewaters, including street gutters and sewers (Hervé et al., 2017; Yuan et al., 2020). Wastewater treatment plants (WWTPs), the endpoint for most of the waters from cities, provide aquatic fungi with a habitat that is better characterized than most urban aquatic environments, possibly for their sanitary and biotechnological interest (Assres et al., 2019; Espinosa-Ortiz et al., 2016; Matsubayashi et al., 2017; Wei et al., 2018).

Studies to date indicate that the majority of urban aquatic environments are dominated by a relatively small number of fungal taxa, i.e., opportunistic yeasts (*Candida*, *Cryptococcus* and *Rhodotorula*), black yeasts (*Aureobasidium* and *Exophiala*), filamentous fungi (*Fusarium*, *Aspergillus*, *Cladosporium*, *Trichoderma*, and *Acremonium*) and some members of Cryptomycota. Interestingly, a common feature among many of these genera is their ability to form biofilms (Babič et al., 2017; Raghupathi et al., 2018; Zupančič et al., 2016). Although fungal diversity in urban aquatic ecosystems is likely lower than in natural ecosystems (Newbound et al., 2010; Wei et al., 2018), we propose that studying the diversity and ecology of fungal communities in human-disturbed environments is deserving of greater

importance since approximately half of the world's population lives in cities and people spend about 90% of their lifetime in indoor ecosystems (Adams et al., 2013; Bello et al., 2018; Flores et al., 2011; Humphries, 2012).

Fungal metabolism and anthropogenic pollutants

Generally, fungi are characterized by a broad spectrum of extracellular enzymes (Harms et al., 2011) that allow them to break down highly polymeric substances consisting of very large molecules or macromolecules, composed of many repeating subunits. This metabolic feature renders fungi ideal candidates to break down natural polymeric substrates (Rojas-Jimenez et al., 2017) and anthropogenic pollutants that contain a large variety of macromolecules. Thereby, the high resistance against anthropogenic pollutants makes them ideal bioindicators of anthropogenic stressors in the environment. Aquatic fungi are ubiquitous and promising candidates for polymeric organic matter decomposition and humification of plant litter, which provides energy for microbes in various aquatic habitats (Webster et al., 1999). Aquatic **hyphomycetes** are considered one of the most prevalent microbial communities associated with emergent plant materials and submerged terrestrial plant residues in aquatic ecosystems, comprising 63–100% of total microbial biomass (Gulis and Suberkropp, 2003). These fungi exhibit a high degradation potential for lignocellulosic compounds due to their constant activity in a wide range of climatic conditions (Graça and Ferreira, 1995) and production of a wide array of extracellular ligninolytic enzymes such as cellulases, xylanases, pectinase, laccases and peroxidases (Harms et al., 2011; Rojas-Jimenez et al., 2017).

This degradation potential enables fungal colonization and growth and results in subsequent plant litter mass loss, skeletonization, and maceration (Bärlocher, 1998). The formed fungal biomass provides a significant feedstock for other aquatic heterotrophic microbes and higher trophic levels, leading to accelerated mineralization and transformation of plant biomass into humic substances (e.g., humic acids, fulvic acids, and humin) (Bärlocher, 1985). Furthermore, the quantity and quality of additional labile materials, such as algal exudates, determine the dominance of fungal groups within aquatic ecosystems and, consequently, terrigenous C turnover (Fabian et al., 2017). Moreover, environmental conditions and the fungi's enzymatic repertoire ultimately affect the rate of litter decomposition in streams (Benstead and Huryn, 2011). This relationship remains little studied for lacustrine environments (Grossart et al., 2019). Other polymeric compounds such as pollen grains and non-plant material, e.g., chitin and keratin, are mainly decomposed by chytrids and non-fungal oomycetes via the production of specific exoenzymes (Wurzbacher et al., 2014), resulting in fungal biomass and spore formation serving as a food source for higher trophic levels such as invertebrates.

Fungal processing of pollutants

One of the most evident traces of human activity on the planet is increasing pollution, which negatively impacts the biosphere. Today, the discharge of toxic liquids from urban and industrial activities carrying a large amount and variety of pollutants has reached dangerous levels in both freshwater and marine ecosystems. There are at least six pathways by which humans pollute freshwater ecosystems: (a) sewage, (b) nutrients and terrigenous materials, (c) crude oil, (d) synthetic dyes, (e) heavy metals, and (f) plastics (Häder et al., 2020). Fungi, as one of the most important and conspicuous components of aquatic microbial communities, are detrimentally affected by these pollutants. For example, species diversity and richness, functions, and physiology of aquatic fungi can be severely impacted by the ever-increasing discharge of pollutants into freshwaters (Krauss et al., 2003; Lecerf and Chauvet, 2008; Zeng et al., 2012; Op De Beek et al., 2015). Yet, some aquatic fungi have developed a high capacity to deal with numerous environmental pollutants and are being used as part of environmental remediation strategies.

Many traditional pollutants are degraded by aquatic fungi, including surfactants (Mallerman et al., 2019; Nakamiya et al., 2005), 2,4,6-Trinitrotoluene (TNT) (Hoehamer et al., 2006), pesticides (Purnomo et al., 2011; Rodríguez-Castillo et al., 2019; Ulčnik et al., 2013; Wang et al., 2015) and other toxic persistent organic chemicals (Aranda, 2016; Marco-Urrea et al., 2009; Sun et al., 2016; Xu et al., 2014). However, the number of fungi that have been studied for their degradation capabilities is relatively small. Therefore, the likelihood to find new species with the potential for bioremediation of aquatic pollutants is high.

Aquatic fungi can use at least four mechanisms for processing and transforming a wide variety of pollutants in inland waters (Fig. 3). They are highly unspecific and can act independently or synergistically. The first mechanism involves the production of two main types of extracellular enzymes: peroxidases and phenoxidases (Grinhut et al., 2011b; Majeau et al., 2010; Rodríguez-Rodríguez et al., 2019). The second consists of the production of low-molecular-weight redox mediators such as reactive oxygen species (e.g., singlet oxygen, peroxide and the hydroxyl radical) that also act extracellularly and with low specificity on the substrates (Grinhut et al., 2011a; Grossart and Rojas-Jimenez, 2016; Jensen et al., 2001). The third involves intracellular degradation by enzymes such as the cytochrome P450 complex (Haroune et al., 2017; Marco-Urrea et al., 2009). The fourth is related to the biosorption of compounds (Ulčnik et al., 2013; Xu et al., 2020) (Fig. 3).

Fungi possess enormous metabolic diversity, which makes them critical organisms for processing **pollutants** in aquatic systems (Grossart and Rojas-Jimenez, 2016; Harms et al., 2011; Krauss et al., 2011). Some of the most concerning are the so-called “**emerging pollutants**” that include synthetic or naturally occurring chemicals that are generally not controlled but could have adverse effects on human and ecosystem health (Llorca et al., 2016; Rodríguez-Rodríguez et al., 2019). Members of Basidiomycota and Ascomycota are capable of degrading pharmaceuticals, which are considered among the most diverse group of aquatic pollutants, including antibiotics, antidepressants, anti-cancer, antiepileptics, steroid hormones, and anti-inflammatory substances (Asif et al., 2017; Ferrando-Climent et al., 2015; Haroune et al., 2017; Kovalakova et al., 2020; Liu et al., 2016; Rusch et al., 2019; Silva et al., 2012). Moreover, aquatic

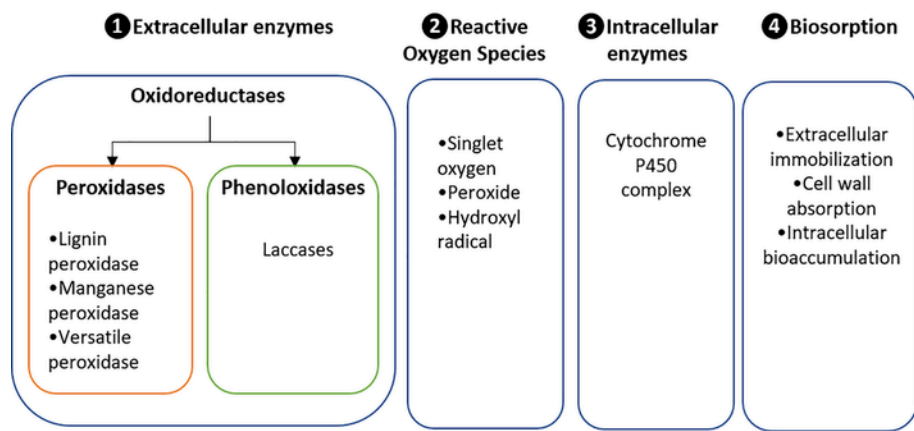


Fig. 3 Four mechanisms via which aquatic fungi process a wide variety of pollutants in inland waters. In general, these mechanisms are not specific for the type of molecules to degrade and can operate independently or synergistically. The first mechanism involves the production of two main types of extracellular enzymes: peroxidases and phenoloxidases. The second consists of the production of low-molecular-weight redox mediators such as reactive oxygen species that also act extracellularly and with low specificity on the substrates. The third involves intracellular degradation by enzymes such as the cytochrome P450 complex. The fourth is related to the biosorption (adsorption and absorption) of compounds.

fungi are capable of degrading various types of plastics (Ali et al., 2014; Deguchi et al., 1997; Jeyakumar et al., 2013; Krueger et al., 2015; da Luz et al., 2013; Wang et al., 2016) as well as accompanying contaminants such as plasticizing substances that can have endocrine-disrupting effects or carcinogenic effects on environmental and human health (Ahuactzin-Pérez et al., 2018; Ferrer-Parra et al., 2018; Loffredo et al., 2012; Skinner et al., 2009; Zhao et al., 2018).

In recent years, aquatic fungi have been studied and established as one of the most active groups of microorganisms for degrading synthetic dyes (Wesenberg et al., 2003). In fact, aquatic fungi degrade/adsorb dyes and intermediates such as aromatic compounds and mineralization of azo dyes (Papanikolaou et al., 2008). The high capacity of fungi, especially of white-rot basidiomycetes, to produce extracellular ligninolytic enzymes including laccase, manganese peroxidase, and lignin peroxidase (Gomi et al., 2011) renders them important for bioremediation measures.

In general, fungal dye decolorization is achieved in two ways: (a) biosorption and (b) biodegradation. In biosorption approaches, fungal biomass in wastewater is a byproduct of industrial fermentations. It contains amino, carboxyl, thiol, and phosphate groups in the cell wall, which can be applied for dye removal (Crini and Badot, 2008). In biodegradation approaches, fungi are used to degrade a wide variety of recalcitrant dyes via non-specific attachment of ligninolytic enzymes to the target substrate. Although results of biodegradation from lab-scale studies have been promising, their performance in the purification of various industrial effluents is little studied (Kaushik and Malik, 2009). The application of a broad spectrum of fungi resisting the toxicity of dyes allows for optimizing the overall biosorption and biodegradation ability at changing environmental conditions.

Increasing concentrations of heavy metals lead to deleterious impacts on fungal biodiversity, communities, and biological activities in aquatic ecosystems (Solé et al., 2008), including respiration, sporulation, and growth/biomass formation and fungal leaf-degradation rates (Krauss et al., 2001; Lecrerf and Chauvet, 2008; Sridhar et al., 2000).

However, some aquatic fungi possess tolerance and resistant mechanisms for metal-induced toxicity through the production of extracellular and intracellular biomolecules (protein chelating agents, enzymes, slimes, and other metabolites) (Krauss et al., 2011). Furthermore, the structure of fungal cell walls possesses unique characteristics for heavy metal removal through adsorption mechanisms including: hydroxyl (OH), amino (NH), carbonyl (C=O), phosphate (P=O) groups in the fungal biomass, in addition to the porous nature with the high surface area cell wall (Braha et al., 2007; Hassan et al., 2018). Consequently, due to their high biosorption or bioaccumulation capabilities, aquatic fungi may play a critical role in the sequestration of heavy metal ions than bacteria (Massaccesi et al., 2002).

Case study: Fungal communities in the Plastisphere

The **Plastisphere** is a term used to describe the newly emerging habitat created by the massive introduction of microplastics to all environmental areas (Eckert et al., 2018). Microbiologists frequently study bacteria on plastics, but much less information exists for fungi (Amaral-Zettler et al., 2020). We suggest that fungi on plastic debris are an important emerging area of research (Fig. 4).

Fungi are paramount to carbon and nitrogen degradation and transfer within aquatic food webs (Soares et al., 2017) and it has been shown that plastics have an impact on the heterotrophic activities of fungi (Arias-Andres et al., 2018). Furthermore, fungal parasites can control algae and cyanobacteria (Frenken et al., 2017), which are also present in plastic biofilms. Thus, it is important to know the implications of plastics on various ecological interactions and biogeochemical cycles.

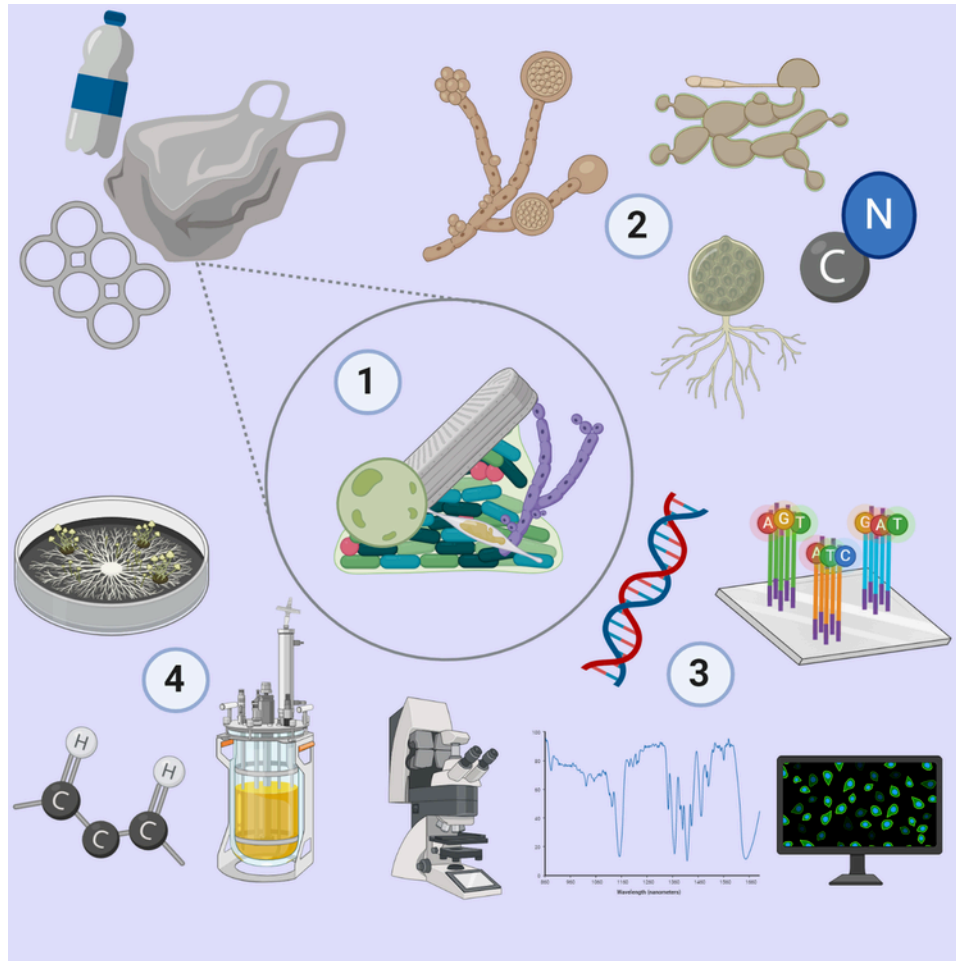


Fig. 4 There are many reasons and methods for studying fungi on plastic debris. (1) Plastic debris results in biofilm structures that include fungi, together with bacteria, green algae, diatoms, and other heterotrophs, termed the **Plastisphere**. (2) Fungi in the **Plastisphere** can include yeasts, filamentous, and parasitic fungi (e.g., some Chytridia). These groups contribute significantly to freshwater carbon and nitrogen cycling. (3) DNA-based sequencing technologies are well suited to decipher the fungal diversity within these biofilms. Other methods that combine fluorochrome-tagged genetic probes and spectral imaging techniques can help to observe and study different species of fungi within the biofilm structure and thus to determine their ecological role. (4) Isolation of fungi from the **Plastisphere** can lead to the discovery of new metabolic pathways of plastic polymer degradation.

In particular, fungi are well known for their xenobiotic degrading capacity, and more testing is needed to quantify fungal degradation of different plastic polymers (Brunner et al., 2018). Fungal metabarcoding and metagenomics will allow for great advances in the exploration of fungal biodiversity and functionality (Matsuoka et al., 2019) in the **Plastisphere**. Given the 3D structure of biofilms on plastic debris and the importance of interactions between fungi, algae, and bacteria, tools allowing for spatial and taxonomic analyzes should be included. For this purpose, methods that combine both high taxonomic and spatial resolution must be considered and adapted to studying fungi in the **Plastisphere** (Arias-Andres, 2020; Schlundt et al., 2019).

Fungi as bioindicators of ecosystem's health: A conceptual proposal

Structural bioindicators describe the composition or biodiversity of a given organismic group whereas functional bioindicators assess a specific function (e.g., the degradation of lignocellulose) or an ecosystem service (e.g., carbon or nitrogen cycling). Complex ecological indicators address the interconnection between structure and function through the food web (Parmar et al., 2016). Aquatic fungi are relevant bioindicators of freshwater ecosystem's health because of their role in the degradation of **allochthonous organic matter** (e.g., leaves falling from a nearby tree into a stream) in aquatic food webs (Baudy et al., 2019).

Fungal enzymatic tools for degrading lignocellulose (the main component of plant matter) are very well known (see "Fungal metabolism and anthropogenic pollutants" section) and explain their role from a biological point of view (Krauss et al., 2011; Rossi et

al., 2017). For freshwater fungi, the most studied functional indicators are leaf litter degradation rate, biomass (ergosterol found in fungal cell membranes), and the capacity to produce spores for reproduction or sporulation (Bruder et al., 2016; Gomes et al., 2018; Krauss et al., 2011; Soares et al., 2017). Meanwhile, the most common group described in the literature are different spore (or conidia)-producing fungi, commonly referred to as “Ingoldian” or aquatic **hyphomycetes** (see above; Bärlocher, 2016; Baudy et al., 2019; Chauvet et al., 2016). The OMICS era is identifying more potential indicator groups (Ceci et al., 2019; Kettner et al., 2017).

Ecological indicators often involve changes in fungal community composition which, e.g., indicate high invertebrate feeding pressure (Baudy et al., 2019; Canhoto et al., 2017; Mora-Gómez et al., 2016). Consequently, specific fungal communities are well suited to serving as bioindicators of anthropogenic stressors and environmental change in aquatic systems. Differences among types of aquatic ecosystems (e.g., streams vs. wetlands), habitats (e.g., pelagic zone vs. sediment), and multiple stressors, however, need to be taken into account since they may affect the role of fungi as environmental indicators (Graça et al., 2016; Gulis et al., 2019; Ortiz-Vera et al., 2018; Röhl et al., 2017).

Two major and relevant anthropogenic stressors in aquatic systems, i.e., pollution and eutrophication due to nutrient input (N and P) (Reid et al., 2019) can be well detected by changes in fungal communities. Accordingly, the fungal community response to pollution and eutrophication is relatively well documented. Overall, eutrophication selects for specific tolerant groups (Bai et al., 2018; Samson et al., 2020), increases the abundance and diversity of fungal taxa, and lowers fungal sporulation rates and biomass (Pereira et al., 2016; Pietryczuk et al., 2018).

In contrast to eutrophication, the usage of fungal indicators to detect other factors is much less studied. For example, higher flow velocity increases fungal diversity (Fiuza et al., 2019) in running waters. In low-flow areas downstream of dams, there is a lower fungal richness and biomass production (Colas et al., 2016), probably due to sedimentation and lower concentrations of dissolved oxygen (Bruder et al., 2016). Salt concentration is well known to affect fungal community composition (Gonçalves et al., 2019). Thus increasing salinization due to climate change (Pesce et al., 2016) and run-off from salted roads in winter can be deduced from specific changes in fungal communities in parallel to a significant reduction in fungal sporulation and biomass (Canhoto et al., 2017; Gonçalves et al., 2019). So far, metal and chemical pollution effects on aquatic fungal communities are least analyzed (Barros et al., 2020; Pimentão et al., 2020), but indicate a high bioindication potential. Most of this information stems from rivers and streams, and the role of fungal bioindicators for anthropogenic stress in standing waters has been less explored.

Emergent metal pollution selects for specific species of tolerant fungi and affects fungal leaf litter degradation (Duarte et al., 2019), protein expression, and enzymatic activities (Barros et al., 2020). For synthetic chemicals, the scarcity of fungal models for ecological risk assessment of fungicides is noteworthy (Ittner et al., 2018; Ortiz-Cañavate et al., 2019). Other emergent contaminants have been evaluated for their effect on fungal communities and include antibiotics (Bundschuh et al., 2009), nanomaterials (Du et al., 2020), and microplastics (Kettner et al., 2017). In these cases, enzymatic activities have been identified as potential fungal bioindicators for chemical stress, in particular those related to lignin degradation (Rossi et al., 2017).

Conclusions and perspectives

In this article, we have highlighted the immense diversity and metabolic versatility of fungi and fungi-like organisms in natural and human-made aquatic ecosystems (Fig. 5).

Aquatic fungi are key organisms for organic matter cycling and the transformation and detoxification of anthropogenic pollutants, including synthetic dyes, aromatic hydrocarbons, and other polymeric and potentially toxic substances. Urbanization leads to increased inland water pollution affecting environmental and human health. We highlight the role of aquatic fungi in breaking down natural polymers such as cellulose, lignin, and chitin as well as more complex substances of anthropogenic origin such as antibiotics, anti-depressants, dyes, surfactants, hormones, and plasticizers, known as **emerging pollutants**. Thus, we demonstrate how aquatic fungi play an important ecological role in the cycling of nutrients and carbon and in mitigating the increasing effects of humans on the environment. However, there are still large knowledge gaps in the field of inland water **mycology**. It will be of paramount importance to further study the effects of **emerging pollutants** on the structure of aquatic fungal communities and their interactions with other organisms such as bacteria, viruses, and other eukaryotes. Finally, we need to better understand pollutant-fungi relationships, including those on microplastics, given the abundance, low degradability, and wide distribution of anthropogenic pollutants on the planet.

New technologies will continue to expand our knowledge and appreciation for aquatic fungi in natural and urban ecosystems. For example, the combination of molecular and advanced microscopy tools and new physiological and cultivation approaches will result in better characterization of fungal metabolic processes. This biotechnological research could also lead to discovering new pathways for the degradation of pollutants such as plastic polymers. Further, a deeper understanding of the ecological role of fungi and fungi-like organisms is required to identify new fungal bioindicators of anthropogenic stress. Filling these knowledge gaps is key to tackle the many challenges facing future environmental and human health due to urban development and anthropogenic pollution, including biodiversity loss and alteration of aquatic ecosystem functions.

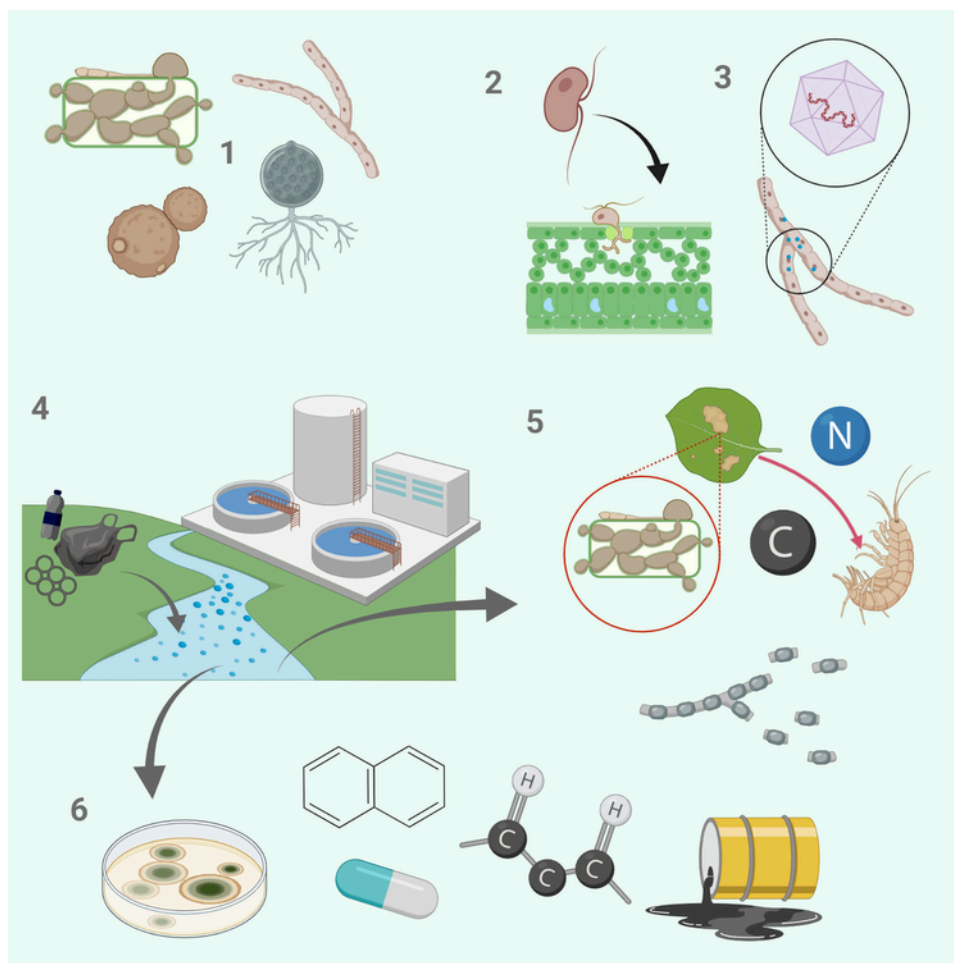


Fig. 5 We provide a summary of important and unexplored aspects of aquatic fungi in the **Anthropocene**. (1) Fungi in freshwaters display multiple lifestyles, e.g., saprophytic and parasitic, spore, and hyphae-forming species. All of them respond in an as yet largely unknown manner to anthropogenic stressors. Thus, further research is needed to better understand the fungal ecology and effects of inland water pollution in an urbanized world. For example, (2) fungi-like organisms such as aquatic oomycetes (some of which are prevalent plant and fish pathogens); (3) fungi-virus infections in aquatic systems; (4) increasing anthropogenic pollution via the release of nutrients, industrial chemicals, and urban waste into aquatic ecosystems effects; (5) fungal transfer of carbon and nitrogen from allochthonous organic matter to the aquatic food web, whereby sporulation (reproduction) rates act as common bioindicators of ecosystem health. Finally, (6) new fungal pathways for the biodegradation of emergent contaminants such as pharmaceuticals, persistent organic pollutants, and petroleum-based plastic polymers should be explored in new fungal isolates obtained from urban water ecosystems.

Knowledge gaps about fungi in the face of urbanization

- Anthropogenic effects of combined environmental factors and hydrologic conditions on fungal growth and organic matter transformation
- Changes in functional diversity of aquatic fungi in the presence of anthropogenic stressors such as eutrophication, warming, salinization, and emerging pollutants
- Loss of fungal diversity following habitat modification due to urbanization as a part of the global freshwater biodiversity crisis
- The ecological role of fungi-like organisms such as oomycetes in agricultural landscapes
- Fungi-virus interactions and their ecological consequences at increasing anthropogenic stress
- Specific fungal degradation processes of polymeric organic matter in urban environments
- Anthropogenic impact on biodiversity, ecology, and function of mycorrhizal fungi and endophytes in urban aquatic habitats

- Specific fungal degradation mechanisms of synthetic dyes and other anthropogenic pollutants
- Role of the emerging anthropogenic pollutant (micro)plastics as fungal habitat and substrate
- Role of fungi as bioindicators of anthropogenic stress and degradation of ecosystem state

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Relevant Websites

- <http://www.indexfungorum.org/>.
- <https://unite.ut.ee/>.
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- <http://fungi.life.illinois.edu/>.
- <http://www.mycobank.org/>.
- <https://www.ncbi.nlm.nih.gov/genomes/GenomesGroup.cgi?taxid=10239&host=fungi>.

Glossary

Aero-aquatic fungi Fungi that need air exposure for sporulation to complete their life cycle. Consequently, they spend one stage of their life cycle underwater and another stage dispersed in the air-water boundaries.

Allochthonous organic matter Organic matter that is introduced into aquatic ecosystems from the terrestrial surrounding, e.g., plant debris, pollen, and leaves.

Anamorphic Asexual state of a fungus, which refers to the asexual morphotype of a fungus, also mitosporic state, i.e., a morphotype that forms spores only by mitosis.

Anthropocene The geological period during which humans have had a significant impact on the planet's climate and ecosystems. Most researchers state that it began at the start of the Industrial Revolution of the 1800s, when—for the first time—human activity had a significant large scale impact on carbon dioxide and methane in Earth's atmosphere.

Autochthonous organic matter Organic matter produced inside aquatic ecosystems, e.g., by algal photosynthesis and organismic biomass production.

Benthic shunt Fungal pathway in which (mainly terrestrial) organic matter is channeled by aquatic fungi in benthic biofilms to higher trophic levels of the aquatic food web.

Conidia Asexual reproductive units that formed from special cell (conidiogenous cells) developed from conidiophore.

Dark matter fungi Group of fungi that has been mainly characterized by sequence-based methods, related mostly to the early branches of the fungal tree, i.e., Aphelida, Rozellomycota, and Chytridiomycota (**Grossart et al., 2016**).

Emerging pollutants Synthetic or naturally occurring chemicals that are generally not controlled but could have adverse effects on human and ecosystem health.

Fungi-like organisms Represents all microorganisms in Oomycota phylum. They are morphologically very similar to fungi. However, molecular studies has revealed their vast evolutionary distance to fungi. While fungi are more related to animals, they are plant's close relative.

Hyphomycetes Fungi with long, branching filamentous structures called hyphae and that represent the main mode of vegetative growth in the form of mycelia.

Ingoldian fungi A fungal group honored for **Ingold (1942)** that is characterized by their ability for sporulation on plant materials underwater.

Microplastics Generally defined as plastic particles equal or smaller than 5 mm in length that result from both commercial product development (primary) and the breakdown of larger plastics (secondary microplastics). As a pollutant, microplastics can exert harmful effects on the environment, animal, and human health.

Mycoflux Fungal pathway in the pelagic zone of water bodies in which fungi lead to changes in organic matter aggregation or disintegration and thus affect organic matter cycling and sequestration.

Mycology Scientific field studying all aspects of fungi and fungi-like organisms.

Mycoloop A fungal pathway in the pelagic zone of water bodies in which parasitic fungi transfer inedible phytoplankton or pollen to higher trophic levels either via edible fungal zoospores of cell fragmentation and/or lysis.

Mycovirology Scientific discipline studying virus infecting fungi, i.e., mycovirus.

Mycovirus A virus that infects fungi.

OMICS era Phrase that relates to the current time period when the use of new molecular and biochemical tools such as metagenomics, metatranscriptomics, metaproteomics and metabolomics, arose to study organisms in the lab and field.

Plastisphere Term to describe a newly emerging microbial habitat created by the massive, anthropogenic introduction of microplastics to practically all environments.

Teleomorphic Sexual state of a fungus, in which two fungal nuclei unite and undergo meiosis, forming offspring with new genetic information.

Transient fungi Group of fungi that is passively introduced into water via high loads of fungal propagules from inflowing streams, rainwater runoff, and wind. These fungi exhibit no activity in the water, presumably due to unfavorable aquatic conditions or interactions with organisms.

Zoosporic fungi Synonym for chytrids and other basal fungi that possess a zoosporic stage during their life cycle.

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