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Abstract
Fungi are phylogenetically and functionally diverse ubiquitous components of almost all ecosystems on Earth, including aquatic environments stretching from high montane lakes down to the deep ocean. Aquatic ecosystems, however, remain frequently overlooked as fungal habitats, although fungi potentially hold important roles for organic matter cycling and food web dynamics. Recent methodological improvements have facilitated a greater appreciation of the importance of fungi in many aquatic systems, yet a conceptual framework is still missing. In this Review, we conceptualize the spatio-temporal dimensions, diversity, functions and organismic interactions of fungi in structuring aquatic foodwebs. We focus on currently unexplored fungal diversity, highlighting poorly understood ecosystems, including emerging artificial aquatic habitats.

Introduction:

Recent advances in DNA sequencing technology have revealed that fungi are abundant in many, if not all, aquatic ecosystems. However their diversity, quantitative abundance, ecological function and, in particular, their interactions with other microorganisms, remain mainly speculative, unexplored and missing from current general concepts in aquatic ecology and biogeochemistry[1-4]. This is surprising as terrestrial-focused research has understood the outstanding ecological role of fungi for > 100 years, and therefore fungi constitute a major component of general concepts in terrestrial science[5,6]. In aquatic ecosystems, the systematic analysis of fungal diversity and their ecological roles had several setbacks due to methodological limitations and a too small scientific community, in particular in the marine environment[7-11].

Aquatic fungi form a morphologically, phylogenetically and ecologically diverse group[7]. We broadly define 'aquatic fungi' as fungi that rely for the whole or part of their life cycle on aquatic habitats (**FIG. 1**). Three groups have been previously defined based on their degree of adaptation, activity and dependence on aquatic habitats [12], namely indwellers **[G]**, periodic immigrants **[G]** and versatile immigrants **[G]**.

In aquatic systems, fungal sequences constitute a substantial proportion of eukaryotic sequences[13-15]. However, there is almost no information available on their quantitative abundance; that is comparing the proportion of fungal biomass with total eukaryotic biomass. The only reliable information on fungal biomass comes from studies on litter degradation, mainly leaf litter in running waters[16], where higher fungi dominate over bacteria in terms of biomass, production and enzymatic substrate degradation. Direct counts suggested that fungal biomass typically contributed 90%–95% to the total microbial biomass during early stages of leaf decay, confirming earlier conclusions on the ecological importance of aquatic fungi[16]. More recently, measurements of ^{13}C isotope enrichments in all identified phospholipid-derived fatty acids (PLFAs) revealed that the fungal biomass was up to 10-fold higher than for bacteria[17].By contrast, in the pelagic zone of numerous lakes and kettle holes in northeast Germany, bacteria generally dominated microbial communities, and fungi in average accounted for solely $9.2 + 5.2$ % of all PLFAs in seston biomass[18].

To our knowledge, there is no study available which has precisely quantified the fungal contribution to microbial respiration, mainly because current respiration methods measure total microbial respiration and cannot distinguish between the proportion of different microorganisms such as algae, fungi and bacteria. Currently, there is a great need to determine more precisely fungal activities to explore the role of fungi in aquatic food webs. Generally, there is little information on fungal activities, predominantly from leaf litter studies in flowing water systems. Comparing numerous studies simultaneously measuring ^{14}C-acetate incorporation into ergosterol (fungal hyphomycetes biomass production) and ^{14}C-leucine or ^3H-thymidine into bacterial proteins or DNA, respectively (bacterial biomass production), revealed that on leaf litter fungal production rates often greatly exceed those of bacteria[16]. Repeated measurements of fungal biomass production and their standing stock on leaf litter estimated an annual fungal production of 16 to 193 g m^{-2} from which up to ≥ 50% can be channelled into biomass of microscopically identifiable conidia of aquatic hyphomycetes (reviewed in REF. [16]).

However, molecular studies revealed that fungal taxa in aquatic systems often comprise taxa other than aquatic hyphomycetes[19]. These aquatic fungi have emerged

as an important source of 'microbial dark matter' - the composition and ecology of which are largely unknown[20]. It has been suggested that fungi can hold the potential to largely affect aquatic food web structures, stability and functionality through syntrophic to parasitic interactions with other organisms and organic matter[21-23]. However, for most aquatic ecosystems, little is known about how fungal interactions will affect vital ecosystem functions such as the efficiency of the oceanic carbon pump [G] and ecosystem health[24]. Consequently, it is urgent to extend our knowledge on the diversity and ecology of aquatic fungi, to better understand ecosystem feedback mechanisms to climate and anthropogenic change[10]. This knowledge is crucial to reliably project future developments and sustainably manage almost any aquatic ecosystems on Earth.

Currently, aquatic organisms and ecosystems face a 'post-stability-era' with increasing intensity of short-term disturbances [G] and long-term anthropogenic disturbances [G]. Many novel and hidden interactions between aquatic fungi and other components of the food web await the discovery and recognition in a holistic ecosystem and landscape context. In this Review we aim to integrate, in a broad framework, knowledge and knowledge gaps about aquatic fungal diversity, habitats, interactions and functions, and provide a conceptual framework for aquatic fungi in natural and artificial aquatic environments by integrating fungal processes and their consequences for the functioning of various aquatic ecosystems. Of note, we do not explore the many existing gaps in the fungal phylogenetic tree.

[H1] Underexplored diversity of aquatic fungi.

Microbiologists have uncovered a high diversity of uncultivated microbial taxa, termed microbial dark matter[25]. So far, unexplored taxa have been only detected by molecular tools, mainly for prokaryotes[25-27], but also increasingly for eukaryotic microorganisms[28], including fungi[20] (fungal dark matter). For example, most fungi in a large number of lakes and ponds in northeast Germany and Scandinavia are uncharacterized[29, 30]. Although not yet isolated into culture, these organisms may be highly abundant and dominate natural ecosystems[31]. Targeted isolation approaches have started to reveal that some of those novel lineages within the early diverging fungi such as Rozellomycota, Aphelidiomycota and Chytridiomycota represent parasitic fungi of phytoplankton[32,33]. In comparison with terrestrial and wetland fungi, the exploration and knowledge of most aquatic fungi and their ecological function remain limited[8,34] and often focussed on specific habitats predominantly in flowing water (that is, lotic) ecosystems.

In contrast to soil ecosystems[35,36], studies on aquatic fungi are still insufficient or lack the adequate spatial and temporal resolution considering, for example, different latitudinal zones, ecosystems (water column and sediments), marine snow and extreme environments such as deep-sea vents. Moreover, studies on aquatic fungi have with a few exceptions addressed distribution patterns at the regional scales (for example, river basin[37], Scandinavian lakes[30], or ocean basin[38]). However, the availability of large-scale public datasets such as the International Census of Marine Microbes, the Tara Oceans Expeditions or the Earth Microbiome Project has enabled the global analysis of microbial communities, including marine fungi[39,40]. Also, a first, literature compiled study on the global distribution of aquatic hyphomycetes emerged[41].

Advances in sequencing technologies have stimulated a new wave in research of aquatic fungi. In particular, molecular-based detection of marker genes revealed novel fungal biodiversity in the aquatic realm[9,42] and revealed knowledge gaps in our

understanding of fungal phylogeny[20]. As the fungal dark matter is slowly becoming more visible, there is a large potential to discover new fungal lineages, particularly associated with early diverging lineages at the base of the fungal tree, for example, Chytridiomycota and Rozellomycota[13,43-45], the latter being hyperdiverse and underexplored. New approaches such as single-cell genome sequencing[47] will help to gain a better understanding of the evolution of the fungal kingdom.

DNA databases are increasingly populated with sequences for which little or no morphological and functional information is available, leading to an increasing gap between well annotated reference data and dark matter DNA sequences. This 'annotation gap' does not only affect functional genes, but is also evident in curated fungal barcode reference data. Attempts have been made towards unifying all ribosomal regions into one single ribosomal fungal marker that covers all of the eukaryotic ribosomal regions[29,47], which greatly improves taxonomic resolution of non-cultured and unknown fungi. However, there is a great need for increased cultivation of fungal strains both for phylogenetic and physiological characterization, which enables linking phylogenetic, morphological as well as physiological features in a reliable manner.

[H1] Fungal habitats.
[H2] Natural habitats.

It was previously thought that the diversity and abundance of fungi in aquatic ecosystems was relatively low to that in soil[7,48]. However, recently a large number of studies in different habitats of freshwater and marine environments indicated that aquatic fungi can be abundant eukaryotes in aquatic ecosystems. Particularly in freshwater, fungi can reach relative abundances of > 50% of all eukaryotic sequences. In other habitats, such as some saline habitats, abundances are low (> 1%)[42,49-51]. Thus, the fungal proportion of all aquatic eukaryotes can be extremely variable and depends on the respective ecosystem and its environmental settings.

The first morphological characterizations of aquatic fungi in the mid-19th century were carried out in ponds, lakes, rivers and streams using rudimentary microscopes[52]. In spite of the methodological limitations of the time, first detailed descriptions of zoosporic freshwater fungi were made, for example of the genus *Chytridium*, one of the first parasitic phytoplankton fungi known[52]. Subsequent technological advances in microscopy enabled better morphological characterizations and hence descriptions of multiple species of Phycomycetes and Hyphomycetes colonizing the mulch of streams, estuaries and coastal areas, including genera such as *Tetracladium*, *Cercospora* and *Ophioceras*[53-56]. A large number of aquatic habitats have been identified in which fungi grow and thrive (Fig. 2; Table 1).

Through the use of cultivation-dependent techniques, several species of filamentous fungi and yeasts (aerobic and fermentative forms) have been isolated from numerous natural habitats. Some of the predominant genera in aquatic ecosystems include *Aspergillus, Penicillium, Cladosporium, Aureobasidium, Cryptococcus, Malassezia, Candida* and *Rhodotorula*, which have been isolated from various ecosystems such as the deep-sea[57-61], subsea floor[62-64], hydrothermal vents[65-67], marine coastal waters[68,69], lakes[70-71], ice and snow[72-74] as well as other freshwater and brackish ecosystems[7,48,75].

The use of cultivation-independent methods confirmed, in some cases, the predominant groups determined via cultivation techniques, particularly in habitats such as marine sediments[61,69,76,77], aquifers[78,80], and polluted aquatic environments[81-

[83]. However, high-throughput sequencing has enabled the scientific community to unravel an enormous diversity and abundance of aquatic fungi in most natural habitats previously hidden[20]. Many of these unknown fungi belong to early divergent lineages of Rozellomycota and Chytridiomycota, with LKM11, *Rhizophydium* and *Lobulomyces* representing some of those abundant lineages with references in current databases. These uncharacterized fungi have been shown to dominate fungal communities in large parts of aquatic ecosystems on Earth, including temperate freshwater lakes[9,42,49,84-88], coastal and marine environments[11,89-92], snow[93], and polar aquatic systems[50,5194,95].

[H2] Artificial habitats.

Humans continue to increase the generation of novel aquatic habitats such as street gutters, water pipes, sewage systems, wastewater treatment plants, reservoirs for cooling power plants and storing waste, which are readily colonized by microorganisms, including a broad variety of fungi (**FIG. 3, TABLE 1**). Understanding the microbiome of the built environment is still in its infancies; however, will rapidly gain importance in a more urbanized world[96]. Cultivation-independent fungal studies on tap water, bathroom or shower pipes are still rare[97] and thus only a few data on fungal biodiversity in these semi-closed systems are available, besides typical indoor fungi that are associated with moisture[96]. Aquatic fungal communities of infrastructures are until now little investigated and next to the most obvious lentic-like habitats of garden and irrigation ponds, reservoirs, pools, puddles, rice fields, tree holes, fountains or aquaria, new interesting habitats emerge. For instance, currently uncharacterized fungi reside in intermittent aquatic autotrophic street gutter biofilms[98], but knowledge gaps exist on a large spatial scale, including many hidden urban habitats, such as street runoff systems and complete sewer networks.

The probably best described urban fungal habitats are wastewater treatment plants[99]. Several recent studies confirmed that in addition to fermentative yeasts so far uncharacterized fungi (mainly Rozellomycota) are dominant, often in the anaerobic biofilms[100-104]. Their function in wastewater processing is unclear, and it will be interesting to investigate whether those unknown fungi have the same potential for biotechnological applications as yeasts and filamentous fungi[105-107]. Moreover, microalgae reactors and open ponds for algal compound production (for example, biofuels) are economically important new habitats were parasitic fungi can have detrimental effects on the productivity[108,109]. Algal mass cultures provide habitats for parasitic fungi, including chytrids and aphelids[110-112]. By contrast, animal aquacultures are more dominated by fungal-like parasites (oomycetes), and yet it is unclear if uncharacterized fungal groups other than microsporidian parasites have a substantial functional role[113,114]. Hydroponic systems for plant and animal cultivation represent other economically important habitats in which fungal mycorrhiza [G] and fungal pathogens are the focus of current research, while very little is known on emerging aquaponic systems[115] that represent simplified pond-like aquatic foodwebs.

There are numerous man-made extreme aquatic habitats such as biogas reactors[116] or even nuclear reactors[117] for which little is known about fungal diversity and function. Consequently, most of engineered or constructed aquatic systems and urban ecosystems comprise largely unexplored fungal habitats. For the coming years, we foresee a growing interest in studying diversity, function and ecological role of aquatic fungi in urban and man-shaped environments. Furthermore, humans

continuously introduce terrestrial matter and waste products such as microplastics and other anthropogenic debris into natural aquatic ecosystems in an unprecedented scale. These pollutants can represent new artificial surfaces for colonization of fungal communities[118], whose diversity and structure are different from the natural assemblages[119]. These novel habitats are provoking the development of complex interactions between autotrophic and heterotrophic organisms, with profound consequences for functionality and evolution of aquatic ecosystems[120], for example, through gene exchange of functional genes. Thus, the rapid increase in a multitude of artificial fungal habitats implies extensive, yet unknown human interferences with the natural environment and the potential to change key components and functions of aquatic ecosystems worldwide.

[H1] Fungal interactions.
[H2] Biotic interactions with aquatic fungi.

The outcome of ecosystem processes is governed by a complex network of direct and indirect interactions between organisms (**FIG. 4**). Within this interaction network, the genetic, morphological and functional diverse aquatic fungi play multiple roles, engaging in both antagonistic as well as synergistic interactions with all members of the aquatic community.

Mycoviruses have been well studied in endophytic and phytopathogenic fungi, where they play both mutualistic and antagonistic roles in complex interactions between fungi and host plants[121]. Recently, mycoviruses and plasmid symbionts were detected in a collection of marine fungi isolated from the seagrass *Posidonia oceanica*[122]. Yet, the ecological effects of aquatic mycoviruses are almost entirely unknown and remain to be elucidated.

Antagonistic interactions between fungi and bacteria are widespread and several studies have shown inhibition of bacterial growth by aquatic hyphomycetes[123]. Moreover, antifungal compounds producing bacteria associated with the skin of amphibian hosts have been found to inhibit the growth of the pathogenic amphibian chytrid fungus *Batrachochytrium dendrobatidis*[124]. Antagonism between bacteria and fungi has been shown to be often connected to direct resource competition[125]. Recently, direct trophic interactions between the largest freshwater bacterium *Achromatium* and chytrid fungi have been observed[126] (**FIG. 4**). Antagonism between fungi and bacteria seem to be more prevalent, although synergistic effects have also been demonstrated[127,128]. A recent review[129] highlights the ecological importance of fungi-prokaryotes interactions as important drivers of many ecosystem functions and organismic health (metaorganism concept). Much is known about the complex mechanisms of these interactions in terrestrial ecosystems, but for aquatic ecosystems these interactions are not yet fully understood and fungal-like organism may occupy certain antagonistic niches in aquatic ecosystems[40].

Moreover, fungi can be both predators and/or parasites and prey of heterotrophic protists. For example, amoebophagous fungi have been described from all major fungal groups: Basidiomycota, Ascomycota, Zygomycota, Chytridiomycota and Cryptomycota[130]. Zoosporic fungi have been found to be parasitic as well as being a food source for Heliozoa[131]. Although fungi-protist interactions have gained great interest in research on rumen fluids[132], rice fields[133] or soil ecosystems[134], yet, these interactions have gained little attention in aquatic systems.

Zoosporic true fungi (for example, Chytridiomycota) and fungi-like protists that belong to the kingdom Chromista (for example, Oomycota, Hyphochytriomycota, Labyrinthulomycota) have similar ecological life styles and can occupy similar

ecological niches[135,136]. As parasites they often share the same phytoplankton host species[137,138] and as saprotrophs they can utilize similar organic matter, for example, pollen or zooplankton carcasses[139]. In terrestrial ecosystems interactions between pathogenic fungi and oomycetes and their consequences for the development of plant disease has been recognized[140]. In aquatic ecosystems our knowledge remains restricted to descriptive studies on their co-occurrence on similar hosts and substrates, whereas studies investigating direct ecological interactions between true fungi and fungi-like protists and their consequences for organic matter transformation are lacking.

Zoosporic fungi are well known as parasites of freshwater and marine phytoplankton[23] and mutualistic symbiosis are rare exceptions[141]. Other antagonistic interactions such as allelopathic interactions between diatoms and aquatic hyphomycetes fungi have been demonstrated to negatively affect primary production in biofilms[142]. By contrast, mutualism is the predominant life form of aquatic lichens in freshwater and marine ecosystems[143], yet rather little is known about their ecological role. 'Engineered' mutualism has been established between *C. reinhardtii,* the yeast *Saccharomyces cerevisiae* and filamentous Ascomycota[144], which increases biomass productivity. In the water tanks of bromeliads, diverse yeast communities are present and display a wide variety of extracellular enzymatic activities which can promote plant growth by increasing nutrient availability and absorption[145]. However, for natural aquatic systems there are only very few reports on syntrophic interactions between fungi and higher organisms. This is also true for studies on fungal interactions with aquatic macrophytes, which are severely limited by comprehending the scope and functionality of the association of arbuscular mycorrhizae and endophytes with this group of plants[146,147].

Mycoparasitism [G] has been frequently described[148]. Rozellomycota can be parasites or hyperparasites [G] of chytrid fungi[149]. The hyphomycete *Crucella subtilis* forms hyphal branches around the hyphae of several species of aquatic hyphomycetes and thus negatively affects early colonization and sporulation of the hyphomycete *Anguillospora filiformis*[150]. Although several examples have been found in aquatic ecosystems, their consequences for aquatic foodweb structure and dynamics remain largely unknown.

The pathogenic chytrid *Batrachochytrium dendrobatidis* is an important factor for the worldwide decline in amphibian populations[151]. Invertebrates (for example, zooplankton) also constitute common hosts and occasionally prey for a variety of fungal parasites, such as microsporidia, yeast and chytrids, with varying virulence [152,153]. Evidence for detrimental and beneficial interactions between fungi and the holobiont of marine sessile invertebrates such as corals, sponges and ascidians has been reviewed[154]. *Coelomomyces psorophorae* constitutes an example of a fungal parasite that uses differently sized invertebrate hosts, such as the malaria mosquito and a Copepod host, to complete its life cycle[155]. By contrast, fungi can be prey for aquatic invertebrates; for example, fungal mycelia contribute substantially to the diet and growth of aquatic shredders, whereas fungal zoosporic propagules rather serve as a food supplement of zooplankton[156,157]. An alternative form of interactions is represented by Trichomycetes, which display a diverse ecological group of obligate endosymbionts, including Zygomycota fungi, in the gut of many aquatic insect. Relationships between these gut fungi and their hosts range from mutualistic to parasitic, largely depending on environmental conditions[158], although these fungi are more generally regarded as commensals[159]. Consequently, fungi-animals interactions can range from parasitism to symbiosis, and fungi can provide food for various

aquatic animals. Yet, most of these interactions and their ecological consequences remain to be explored.

[H2] Studying interactions in aquatic ecosystems.

Symbiotic relationships are greatly unknown and difficult to study because of their microscopic scale, community complexity and intricate nature. Early diverging fungi[160] have been frequently found to establish parasitic and symbiotic interactions with other aquatic organisms. However, the phenotypic distinction between early diverging fungi and fungi-like protists is often impossible hampering detection, and making studies of their specific interactions only possible using molecular-based methods or co-occurrence based statistics.

The largely unknown fungal interactions indicate that inferring the nature of fungal interactions *in situ* is not always trivial. Phytoplankton associated chytrids present an example where mutualistic, saprophytic or parasitic relationships can be hard to distinguish[161]. Moreover, fungal life styles and interactions are not static but often present a highly dynamic continuum that is context dependent[162]. Spatial and temporal variations in local selection and gene flow create complex geographic mosaics of coevolutionary hot and cold spots, which can lead to highly divergent species interactions across geographic scales[163]. Spatial connectivity and dispersal have central roles in the coevolutionary dynamics of species interactions by connecting populations and communities in a landscape context (metacommunity concept). Currently, little is known about the dispersal potential and population structure of aquatic fungi[164] and how this potentially reshapes interactions across different spatial and temporal scales.

Fungal parasite-phytoplankton interactions, for example, have been mainly studied at the population and community level, considering aquatic habitats as spatially isolated and closed systems, thus studies that include spatial connectivity and metacommunity interactions on an ecosystem level are urgently required. Additionally, studies and modelling exercises are extremely challenging as there are multiple fungal parasites competing for the same host[86], cryptic diversity of hosts and fungal parasites[33], and even hyper-parasites of fungal parasites[165,166]. Moreover, very little is known about the interactions of these parasitic fungi with bacteria, or heterotrophic protists acting as potential grazers[1] (see below).

The interpretation of the nature of fungal interactions is not always straightforward, particularly when considering different temporal, spatial and environmental contexts and current climate and anthropogenic changes. Despite this, recent metabarcoding and metagenomic studies of pelagic habitats of lakes[88,167] and oceans[14,49,50] found a rich diversity of parasitic, (or facultative parasitic) zoosporic fungi associated with phytoplankton and zooplankton[23,168,169]. In this regard, several studies[2,8,170,171] confirmed that fungal parasites on planktonic organisms constitute the rule rather than the exception. Thus, the role of fungal parasites in structuring aquatic foodwebs can be equally important as shown for other planktonic parasites[8,172].

[H1] Foodweb and landscale context.

The current methodological advancements both of cultivation-independent and cultivation-dependent tools (see below) enable the study of aquatic fungal communities in a more holistic and overarching manner. We propose to consider the 'aquatic mycobiome' in an entire landscape context, following the global water cycle; that is water flowing via streams and rivers from the mountains through lakes and wetlands into the ocean (**FIG. 2**). Moving through the landscape, water carries

inorganic matter and organic matter in a temporally dynamic manner from the adjacent land constantly reshaping microbial communities and the corresponding metabolic demands. Due to their unique enzymatic capabilities and metabolic versatility[173] aquatic fungi form important components of the global aquatic carbon and nutrient cycle[10] and may provide feedbacks to changes in global climate and anthropogenic activities.

[H2] Fungi in open lakes and oceans.

As described above, there is a high degree of unknown fungal interactions among almost all components of the aquatic systems, with often unspecified ecological consequences for foodweb dynamics and functions (**FIG. 5**). In freshwater ecosystems, hyphomycetes fragment litter, thus generating fine particulate organic matter[174], but little is known about the role of aquatic fungi in the transformation of other organic matter aggregates in rivers, lakes and oceans[175]. Parasitic fungi, for example, may lead to disintegration of planktonic species with negative consequences for sinking fluxes[176], while there is limited knowledge about the role of saprophytic aquatic fungi in processes such as transformation of carbon in lake or marine snow[177]. In marine systems, saprotrophic mycoplankton can utilize algal polysaccharides, indicating that aquatic fungi can affect the flow of organic matter in multiple yet poorly understood ways[178].

Furthermore, parasitic fungi such as chytrids efficiently utilize living phytoplankton organic matter and have the ability to change quality and quantity of phytoplankton-derived organic matter, which not only feeds back to higher trophic levels such as zooplankton (mycoloop, **FIG. 5**), but also to the microbial loop[128]. As saprotrophic fungi also utilize phytoplankton-derived organic matter[11], questions arise whether and how they compete with parasitic fungi and heterotrophic bacteria for dissolved organic matter (DOM) or particulate organic matter, and whether this affects microbial foodweb dynamics and thus organic matter fluxes. This knowledge gap comprises several pelagic organic matter transformation pathways mediated by aquatic fungi such as phytoplankton lysis, organic matter aggregation and disintegration. Therefore, we use the term 'mycoflux' (**FIG. 5**), which refers to currently unknown fungal interactions, their ecology and effects on the aquatic carbon pump.

[H2] Benthic recycling.

Aquatic fungi have been early recognized as major recyclers of coarse plant materials in streams, sustaining a detritus-based foodweb[174,175]. Also, associations between fungi and phytoplankton, especially diatoms, have been reported in benthic habitats such as tidal flats[179] and under the Arctic ice[94]. In the benthic environments of lakes, it has been demonstrated that leaf-colonizing fungi have the potential to improve the palatability of litter for macrozoobenthos grazers[175,180]. Furthermore, it has been shown for leaf litter that fungi, in particular hyphomycetes, upgrade the nutritional value of leaf litter, for example by lowering C:N:P ratio (reviewed in REF.[16]). Fungi-mediated changes in organic matter stoichiometry have also been described in other systems, for example in bromeliad ecosystems[145,181]. In benthic systems, this specific pathway, termed 'benthic shunt', efficiently channels refractory organic matter up to higher trophic levels, for example to fish[180], in which the fungal participation depends largely on the quality and type of organic matter[17] (**FIG. 5**). The benthic shunt has not been explicitly described for marine ecosystems, although a similar mechanism can be expected, as marine fungi can colonize and degrade organic

litter, such as sea grass and kelp[182]. These recent discoveries, together with discovery of dark matter fungi in open waters[49,50], suggest that fungi have an important, but largely neglected, role in aquatic biogeochemical cycles.

[H2] Spatial patterns.

All freshwater and marine habitats (for example, rivers, lakes, coastal and open oceans, sea ice, hydrothermal vents and deep-sea sediments) are to a various degree linked to each other (**TABLE 2**) and differ greatly in specific habitat characteristics and availability of organic matter. Consequently, we can expect morphologically and functionally highly diverse fungal communities, differing mainly by the degree of connectivity and the specific characteristics of the habitat[183].

In analogy to the river-continuum concept[184], we propose that fungal community structure, functions and the ecological role change with the flow of water through the landscape and the degree of the aquatic-terrestrial coupling (**FIG. 2**). The flow of water follows numerous gradients such as altitude, water depth and/or pressure, water residence time, carbon sources (DOM, fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM) and age (generally older from terrestrial and younger from aquatic sources) as well as salinity (**FIG. 2**). These gradients connect and shape the respective fungal habitats along its path greatly controlling the availability of fungal substrates (DOM, CPOM and FPOM). Thus, we consider the aquatic mycobiome as a function of the intrinsic features and connectivity of the respective aquatic ecosystems[185]. In this scenario, the fungal species turnover is structured accordingly, influencing the presence and abundance of size-dependent saprophytes (for example, aquatic hyphomycetes as consumers of CPOM, chytrids as consumers of FPOM), yeasts (as consumers of DOM) and parasites (as consumers of saprophytes and primary producers).

For example, in high altitude, alpine flowing water systems, organic matter is to a large extent supplied by snow and ice melt runoff from the surrounding terrestrial ecosystem of a well-defined and relatively small catchment basin. In these high flow velocities systems, most of the microbial activity takes place in microbial biofilms[186] and thus we can expect that fungi are mainly situated in biofilms, able to degrade the terrestrial and algal organic matter. Intriguingly, high-altitude alpine lakes also comprise an unexpected richness in Chytridiomycota and thus presumably a large proportion of parasites of phytoplankton[187]. These examples suggest a close coupling between autotrophs and fungi and an important role of fungal parasites for foodweb structure in these oligotrophic and cold lentic systems.

Further downstream, rivers exhibit lower flow velocities and receive a greater extent of fresh terrestrial DOM and CPOM such as leaves and an increasing fraction of autochthonous, labile organic matter. As a consequence, in the pelagic zone, pools of organic matter greatly diversify and a more diverse and functionally versatile fungal community is formed, which is able to utilize refractory and allochthonous organic matter (specialists) as well as more labile, autochthonous organic matter (generalists). Light availability will also change the relative importance of allochthonous versus autochthonous organic matter in flowing water ecosystems and thus affect fungal community structure and function. For example, light facilitates the growth of sessile algae and change the epilithic fungal community with profound consequences for riverine organic matter cycling[188,189].

The more that flow velocity decreases and water residence time of an aquatic system increases, the more FPOM and less CPOM will be available as a fungal substrate[8], facilitating a shift from a detrivore-based towards an herbivore-based food

chain. In these ecosystems, particularly in isolated lakes, less terrestrial fungi will be introduced and a native fungal community may develop. By contrast, rivers downstream receive diverse fungal communities from their tributaries and, therefore, the respective diversity of fungi should be higher. However, freshwater fungi might become inactive in estuaries and oceans as increasing salinity may constrain their growth[190]. In a landscape context (**FIG. 2**), the relative proportion of fungi able to produce and degrade organic matter originating from terrestrial and aquatic ecosystems, the intensity of related mechanisms used (for example, secretion of reactive oxygen species and specific enzymes), the concentration of generated by-products and the rate of fungal organic matter mineralization may substantially change from freshwater ecosystems to the open sea. This will also affect their interactions with prokaryotic microorganisms as bacteria have an increasing advantage over fungi the smaller the organic matter gets and the more it is available in the dissolved form[189].

[H2] Temporal dynamics.

       Aside from spatial patterns, there are also temporal constraints linking fungal interactions with seasonal events of organic matter availability, for example, pollen and litter fall, algal blooms (prevalent in temperate to polar regions) and rainy seasons (prevalent in equatorial latitudes). Other more short-term events such as storms and tropical rain showers may increase the availability of organic matter in a more pulsed manner (see also the flood pulse concept[191]). Consequently, the timing and quantity of organic matter inputs, both allochthonous and autochthonous, greatly affect the dynamics of aquatic foodwebs and their functioning in a highly dynamic temporal manner[11,192]. For example, pollen rain, when pine trees flower in temperate regions, represents a considerable input of organic matter and phosphorus into lakes[193]. Chytrid fungi are amongst the few organisms that are able to penetrate through the extracellular wall (exine) of pollen grains[22], and they produce zoospores constituting an effective resource for zooplankton in terms of size, shape and nutritional quality[2].

       For lakes, the plankton ecology group model[194], which describes the seasonal succession of phytoplankton related to physical and biological variables, has been extended by fungal parasitism[3,23]. Fungal parasitism is often caused by chytrids, which can be highly host-specific and lethal, driving the temporal succession of phytoplankton species towards unsusceptible ones. Global warming has the potential to change seasonality of host-parasite interactions, that is an accelerated termination of spring diatom blooms and zooplankton peaks[23].

       Fungi can render inedible or indigestible organic matter accessible to zooplankton forming the mycoloop[1,2], which can seasonally shape planktonic foodwebs, especially when inedible allochthonous organic matter (such as pollen) or autochthonous organic matter (such as large algae or toxic cyanobacteria) dominate[2,4]. To better understand the temporal dynamics of fungal foodweb interactions and their ecological consequences in dependence on specific environmental settings, it will be crucial to explore in detail the underlying mechanisms (for example, the fungal secretome or cycling of organic matter[178]).

[H1] Emerging methods and concepts.

       First-generation and second-generation sequencing methods (that is, Sanger and high-throughput sequencing) have played a central part in expanding our understanding of the dimensions of aquatic fungal diversity by accessing DNA sequences from environmental samples. However, as the early diverging fungal

lineages do not share a consistent barcode and suffer from severe reference database gaps, a unifying ribosomal barcode is currently being established and refined[29,47] for third generation long-read sequencers (for example, PacBio, Oxford Nanopore Technologies). Currently, there is a great need to enhance global isolation efforts as the number of unknown sequences is disproportionally increasing in comparison to the number of described species[195]. Fungal isolates, in particular of currently uncultured fungal groups or those with a few cultured strains, will greatly improve current reference databases[32,33]. Furthermore, when coupled to single cell microscope inspections, third-generation long-read sequencing may help to close the huge reference data gaps for aquatic fungi[47,86]. The increased read length enables the sequencing of whole genes (for example, the complete ribosomal operon) or gene clusters, which facilitate a potential subspecies level of taxonomic resolution.

Targeted sequencing enables the phylogenetic placement and identification of formerly unknown internal transcribed spacer barcodes[36]. Additional spiking of reference DNA may enable a more accurate estimate of the relative abundances that are generated in amplicon sequencing projects[196]. Recently, the use of the precursor rRNA [G], provided the first insights into the living aquatic fungi[80]. Coupled to the new generation of RNA sequencers (Oxford Nanopore), this may be a powerful approach to primarily focus on active fungi. Moreover, it is possible to extract fungal genomes from metagenomes[197] and single cells[46], and to apply new high-throughput culturing techniques for potentially co-culturing aquatic fungi and bacteria[198].

It has been shown that high-quality annotated fungal genomes are an important fungal research resource, for example, for broad-scale comparative gene assessments[199] and large-scale phylogenomics[200]. These resources can have vital roles in studying aquatic fungi as they enable a deeper understanding of genome-encoded pathways and enzymatic evolution in uncultivated lineages, such as basal fungi[10,201]. Insights gained will help disentangle the multitude of fungal interactions, particularly as early diverging fungal lineages are poorly represented in annotated genome repositories. Finally, ecosystem relevant research on aquatic fungi requires quantifying the fungal contribution, either by model systems[202], fatty acids[17], stable isotopes or labelled fluorescence in situ hybridization[177,203-206]. Further, to better understand their physiology, metabolic processes and other behavioural aspects of their life cycle, it is necessary to intensify the isolation and co-cultivation of novel models from both marine and freshwater environments, including host-parasite systems[33]. We also call for increased efforts to better quantify fungal biomass and activity in the aquatic realm, which requires application of new analytical biochemical methods including new approaches based on stable isotopes and fluorescent markers.

The importance of fundamental biology to mechanistically underpin ecological understanding of aquatic fungi remains paramount. Likewise, ecological perspectives can prioritise biological studies. However, beyond medical and applied and industrial mycology, there are limited model fungi available relevant for aquatic ecosystems. Community-wide efforts must be made to develop new and meaningful model aquatic fungi, including associated experimental capabilities, such as freely accessible annotated genome sequences, live cell imaging and gene editing protocols.

[H1] Conclusions

Aside of a rapid development of molecular approaches, there is an obvious lack of suitable methods to measure fungal activities, biomass and their ecological relevance for overall biogeochemical cycles. Furthermore, our broad conceptual understanding of aquatic fungi has so far been constrained by studies focusing

principally on individual ecosystems in a rather isolated manner (such as lakes, rivers, estuaries, coastal seas and open oceans). However, aquatic ecosystems are interlinked throughout catchments via the hydrological cycle and are intimately connected to a variety of terrestrial ecosystems through runoff and subsurface water movement. Studies on aquatic fungi have already shown that there is clearly exchange of taxa between ecosystems[11,86], yet, we have a very limited understanding of the global aquatic mycobiome and its role in global biogeochemical cycles. Future work should consider aquatic fungi with catchment-wide perspectives and within a spatio-temporal context, alongside understanding their roles within individual ecosystems.

Looking ahead, the future and potential of aquatic mycology is bright. What we know already about the biology and ecology of aquatic fungi is evidently less than the 'known unknowns', such as the impact of parasitic fungi in controlling freshwater and marine phytoplankton dynamics and the connections that aquatic fungi make between ecosystems. Perhaps, even more exciting, through the application of the assorted range of developing techniques now available to microbial ecologists, we can address and answer the numerous open questions about aquatic fungi and make many novel discoveries that are yet to be conceived.

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Author contributions

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Figure 1: Phylogeny of aquatic fungi. Shown is the fungal tree of life, including all fungal phyla (based on data from REFs.[45,160]), illustrating the morphological, phylogenetical and ecological diversity of aquatic fungi. Phyla, subphyla and Pezizomycotina classes, which contain typical aquatic fungi are depicted in blue. The early diverging lineages at the base of the fungal tree have an aquatic origin, displaying morphological adaptations in form of zoospores or amoeboid spores that are adapted to dispersal in aquatic habitats. Many of them can be classified within the ecological group of Phycomycetes, associated as saprophytes or parasites with pollen, macrophytes, algae and phytoplankton. Zoopagomycota and Kickxellomycota include amoebophagous and predatory fungi and Trichomycetes, a diverse ecological group of obligate endosymbionts in the gut of many aquatic insect. The polyphyletic aquatic hyphomycetes, associated with leaf litter, decaying macrophytes and driftwood in freshwater and marine habitats, are mainly found within Ascomycota and occasionally within Basidiomycota. Aquatic hyphomycetes most probably have evolved from terrestrial fungi and morphological adaptations (for example, drifting, branched conidiospores, ascospores with sticky sheaths) to colonize aquatic habitats and attach to submerged substrates. This group contains also species that can alternate their life cycle between aquatic and terrestrial habitats (aero-aquatic fungi). Various single-celled yeast and yeast-like fungi within Ascomycota and Basidiomycota have been found in freshwater and marine environments, ranging from biotechnological fermenters to extremophilic yeast from Antarctic sea ice. Most of the Basidiomycota species are yeast-like species with the wondrous exception of the wood degrading basidiomycete *Psathyrella aquatica*, which is the first discovered underwater species with true gills. Note that the dashed lines indicate the subphylum level of the phylogenetic tree, whereas the solid lines mark the core of the fungal tree. The green boxes mark phyla, which are suspected to contain aquatic lineages while grey boxes display terrestrial lineages.

Figure 2: Natural environments for aquatic fungi. A) This conceptual graph shows diverse habitats, stretching from high montane lentic habitats down to the deep open ocean. The spatio-temporal gradients in relation to factors such as altitude, depth, input of terrestrial organic matter, fungal abundance, evolutionary age and residence time of the water flow are highlighted. More details about the most common fungi in each of the habitats are provided in Table 1. B) The panel presents, for each habitat, the current status of knowledge on aquatic fungi in relation to their diversity, function, interactions and ecological role. This knowledge status is presented in a semi-quantitative scale. POM, particulate organic matter.

Figure 3: Artificial habitats for aquatic fungi. This conceptual graph shows diverse artificial habitats for aquatic fungi resulting from human intervention in landscapes. Humans have transformed natural landscapes by creating new artificial niches, which have been colonized by fungi. Distinctive communities of aquatic fungi can be found in human-transformed habitats such as cities, houses, industries, farming (terrestrial and aquatic), mines and several other aquatic microhabitats within them. However, the effects of these human interventions on aquatic fungal communities remain largely unknown. More details about the most common fungi in some of the habitats are provided in Table 1.

Figure 4: **Images of saprophytic and symbiotic fungal interactions with different components of the aquatic foodweb of lakes.** Fungi are visualized by fluorescent staining with calcofluor white (blue) and/or wheat germ agglutinin Alexa Fluor® 488 conjugate (green). Images in the top row display saprophytic fungi on different organic matter substrates: yeast-like fungal spores associated to lake snow aggregates (**a**), chytrid fungi colonizing and degrading the cellulosic theca of a dinoflagellate (**b**) and chitinous carapace of zooplankton (**c**). Images in the middle row display parasitic fungi on bacteria: chytrid fungi parasitizing the largest freshwater heterotrophic bacterium *Achromatium oxaliferum* (**d**) and the phototrophic cyanobacterium *Dolichospermum* sp. (**e**), unknown 'dark matter fungi' parasitizing cyanobacterial filaments (**f**). The parasitic nature of the interaction can be inferred by the cell death and/or loss of autofluorescence of the host cells. Images in the bottom row display dark matter fungi and interactions: unidentified fungi attached to the cyanobacterium *Dolichospermum sp.* (**g**), unidentified fungal spores that presumably have parasitized a diatom (loss of autofluorescence) (**h**), a potential hyperparasitic interaction between unidentified fungi (green) and a chytrid fungi (blue) that parasitizes the diatom *Fragilaria crotonensis* (**i**).
Note that in image (**b**) the blue color represents the dinoflagellate theca which has been stained by the cellulose binding calcofluor white stain, whereas the green color represents fungi which have been stained by the more specific chitin binding Wheat germ agglutinin stain.
Images provided by S. Van den Wyngaert, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Germany.

Figure 5: Ecological role of aquatic fungi. This conceptual model shows different processes by which aquatic fungi transform and incorporate allochthonous and autochtonous organic matter into the foodweb. Three major processes are highlighted: **mycoloop**, **mycoflux** and **benthic shunt**. The Mycoloop has been well described and refers to parasitic fungi rendering inedible phytoplankton edible to zooplankton grazers either by fragmentation of the phytoplankton or by producing zoospores. The mycoflux has not been specifically named before and describes any fungal interaction leading to aggregation or disintegration of organic matter. The consequences are still largely unknown, but it is likely that they greatly affect the aquatic carbon pump efficiency. The benthic shunt has only been described for lakes and it refers to fungal colonization of organic litter rendering it palatable for macrozoobenthos on the sediment. The macrozoobenthos provides an excellent food source for higher trophic levels such as fish and thus increases the trophic transfer efficiency of the aquatic foodweb. DOM, dissolved organic matter (DOM); POM, particulate organic matter.

Table 1. Predominant fungi in natural and artificial aquatic habitats determined by cultivation and cultivation-independent methods*.

Aquatic habitats for fungi	Dominant groups	Common genera
Rivers, streams and ponds	Hyphomycetes	*Tetracladium, Cercospora, Mycocentrospora, Ophioceras*
Deep-sea	Filamentous fungi and yeasts	*Aspergillus, Penicillium, Cladosporium, Cadophora, Fusarium, Mycosphaerella, Alternaria, Aureobasidium, Cryptococcus, Rhodotorula,*

		Rhodosporidium, Candida, Pichia, Malassezia, Pleurotus, Ganoderma
Subsea floor	Yeasts and filamentous fungi	*Cryptococcus, Trichosporon, Malassezia, Candida, Rhodotorula, Rhodosporidium, Exophiala*
Hydrothermal vents	Yeasts, Chytridiomycota	*Aureobasidium, Malassezia, Rhodotorula, Exophiala*
Coastal and oceanic environments	Ascomycota, Chytridiomycota, Basidiomycota, Rozellomycota	*Candida, Cryptococcus, Debaryomyces and Rhodotorula, Rhodosporidium, Malassezia, Trichosporon, Phaeosphaeria, Aspergillus, Cladosporium, Rhyzophydium, Chytridium, Lobulomyces, Spizellomyces*
Lakes	Chytridiomycota, Ascomycota, Basidiomycota, Rozellomycota	*Rhizophydium, Lobulomyces, Zygorhizidium, Chytriomyces, Kappamyces, Chytridium, Rhizophyctis, Rhodotorula, Rhodosporidium, Sporobolomyces, Cryptococcus, Geotrichum, Debaryomyces, Saccharomyces, Candida, Pichia, Cordyceps, Simplicillium, Trichispora, Agaricus, LKM11, LKM15, Rozella*
Ice and snow	Ascomycota, Basidiomycota, Chytridiomycota	*Cladosporium, Aureobasidium, Penicillium, Coccomyces, Xylaria, Coprinus, Typhula, Mycena, Rhizophydiales*
Aquifers	Ascomycota, Basidiomycota, Zygomycota	*Nectria, Fusarium, Penicillium, Sporobolomyces, Rhodotorula, Cryptococcus, Malassezia, Mortierella*
Polar systems	Chytridiomycota, Rozellomycota, Dikarya	*Rhizophydium, Podochytrium, Rhizoclosmatium, Chytriomyces, Cladochytrium, Cyclopsomyces, Lobulomyces, Mesochytrium, Polychytrium, LKM11, Glaciozyma, Mrakia, Cadophora, Penicillium, Rhodotorula, Epicoccum, Cladosporium, Sporobolomyces, Kluyveromyces, Aureobasidium, Candida, Basidiobolus*
Waste water treatment plants and sludge digesters	Rozellomycota, Ascomycota, Basidiomycota	*LKM11, Claviceps, Aureobasidium, Candida, Geotrichum, Penicillium*
Street gutters and street pipes	Chytridiomycota, yeasts	*Chaetothyriales, Cryptococcus*
Tap water and ice cubes	Yeasts, filamentous fungi	*Aureobasidium, Exophiala, Candida, Cryptococcus, Penicillium, Rhodotorula, Aspergillus*
Swimming pools	Ascomycota	*Candida, Pichia, Saccharomyces, Rhodosporidium, Rhodotorula, Aspergillus, Trichophyton*
Nuclear reactors	Ascomycota, Zygomycota	*Cladosporium, Penicillium, Alternaria, Aureobasidium, Aspergillus, Acremonium, Phialophora, Mucor, Chaetomium*
International space station	Ascomycota	*Penicillium, Aspergillus, Cladosporium, Pezicula, Malassezia, Inonotus*

*The referenced version of table 1 can be found in supplemental (TABLE S1).

Table 2. Fungal occurrence in a landscape concept

Environmental drivers	Global scale	Regional scale	Local scale	Microscale	Molecular scale
Spatial connectivity*	Climatic zones, rivers to oceans (for example, water currents, winds)	River continuum concept, (for example, water currents, winds)	Aquatic-terrestrial coupling, (for example, deep-sea vents, eddies)	Organismic interactions, metabolome exchange	Gene exchange, DOM and/or POM degradation and production
Vectors*	Migrating animals (fish, whales, birds), drifting animals, Air and water currents (particles, wood, resting stages)	Fish, mammals, insects, drifting animals, Organic and/or inorganic particles	Fish, zooplankton, insects, organic and/or inorganic particles	Phytoplankton, zooplankton, organic and/or inorganic particles	Viruses, genes, metabolites
Temporal dynamics*	Climate, seasonality (for example, summer-winter, wet-dry season)	Flood pulse concept, permanent versus temporary	Algal blooms, river plumes, litter input, terrestrial runoff, ocean upwelling, permanent versus temporary, disturbances	Organismic processes and behaviour, blooms, exudation, diurnal cycles	Organismic activity, growth rates

* Human interferences include extreme weather, air-water pollution, artificial waters, channels, pipes, among others.
** Human-interferences include waste water, trash including micro- and macroplastics, boats, among others.
*** Human interferences water pollution, water substraction, damming, among others.

Glossary:

Indwellers: Fungi which are well adapted and constantly active in aquatic habitats (see REF.[12]).

Periodic immigrants: Fungi which are less adapted to and only periodically active in aquatic habitats (see REF.[12]).

Versatile immigrants: Fungi which are little adapted to and only sporadically active in aquatic habitats (see REF.[12]).

Carbon pump: A mechanism whereby atmospheric carbon is sequestered by vertical transfer to deep waters and sediments.

Short term disturbances: Pulsed event based disturbances referring to strong single events such as storms and droughts.

Long term anthropogenic disturbances: Comprise gradually increasing press disturbances such as global climate change or urbanization both leading to species loss and shifts in community composition.

Mycorrhiza: depicts the symbiosis of a fungus and a vascular plant via the root tips in the rhizosphere.

Mycoparasitism: Fungi parasitizing on other fungi.

Hyperparasites: A parasite whose host is also a parasite.

Precursor rRNA: The precursor rRNA is a pre-spliced full length transcribed ribosomal operon including all functional and spacer regions.

Author notes

Please check these figures carefully and return any comments/amendments that you might have to me as soon as possible. In particular, we would like you to check the following:

- Do the figures convey the intended message?
- Are all the labels accurate and in the right place?
- Are all the arrows in the right place?
- Are any chemical structures correct?
- Have shapes and colours been used consistently and accurately throughout the figures?
- Have any of the figures been previously published, or have they been supplied by a colleague(s) who is not a named author on the article?

To mark up any corrections, please use the commenting tools in the PDF, or print and draw by hand, rather than directly editing the PDFs.
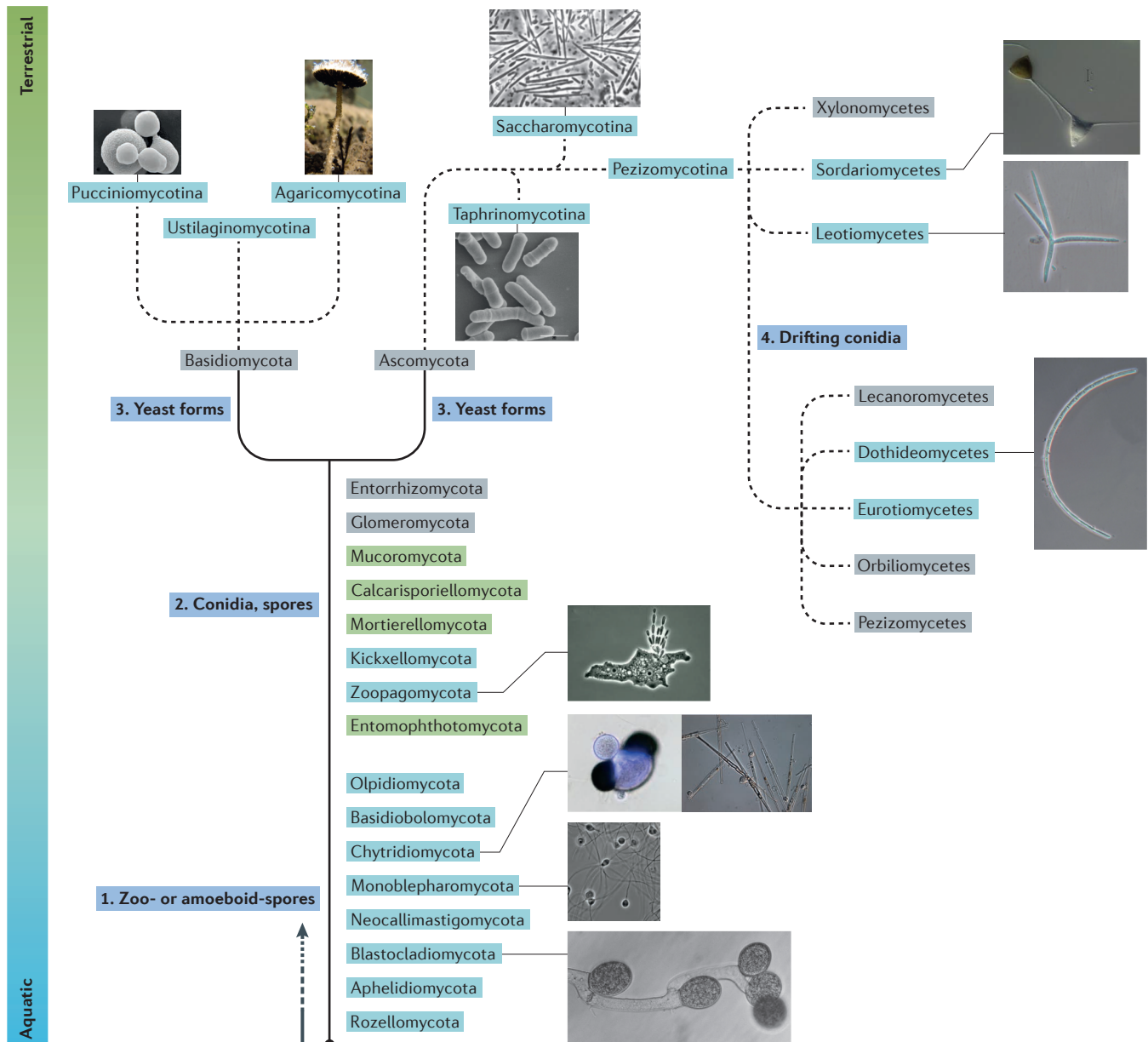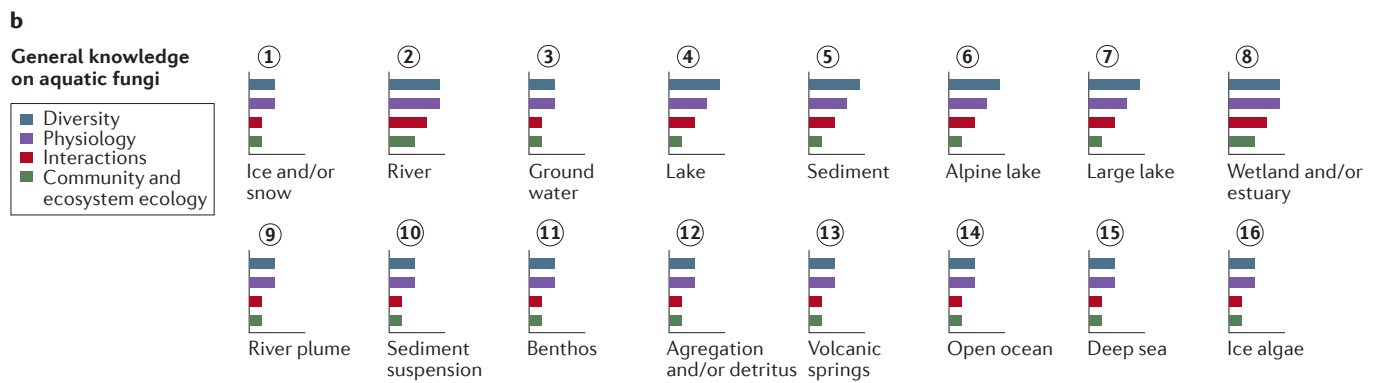
Figure 1

Figure 2

a

b

General knowledge on aquatic fungi

- Diversity
- Physiology
- Interactions
- Community and ecosystem ecology

① Ice and/or snow
② River
③ Ground water
④ Lake
⑤ Sediment
⑥ Alpine lake
⑦ Large lake
⑧ Wetland and/or estuary
⑨ River plume
⑩ Sediment suspension
⑪ Benthos
⑫ Agregation and/or detritus
⑬ Volcanic springs
⑭ Open ocean
⑮ Deep sea
⑯ Ice algae

Figure 3

Waste and landfills

Plastic devices

Roads and waste
Sewers
Wastewater treatment plants
Draining systems
Small water bodies
Plastic, rubber
Bottles
Street gutters

Other artificial habitats
Medical devices
Swimming pools
Air conditioning
Nuclear reactors
Sludge digesters
Microplastics

Industry
Cooling towers
Pipes
Tanks
Waste ponds
Sewers
Storage places

Houses

Shower
Sink
Toilet
Pipes
Aquaria
Wet cellars

Air-transported contaminants

Industry

Reservoirs

Cities

Villages

Waste outlet

Waste input

Aquaculture and algae farms

Water tanks and ponds

River plume and/or waste

Aquaculture

Ocean

Water wells

Manure

Farms

Fields

Roads

Irrigation systems

Stables

Cattle

Mines

Figure 4

Figure 5