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Aquatic fungi: targeting the forgotten in microbial ecology

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Fungi constitute important and conspicuous components of aquatic microbial communities, but their diversity and functional roles remain poorly characterized. New methods and conceptual frameworks are required to accurately describe their ecological roles, involvement in global cycling processes, and utility for human activities, considering both cultivation-independent techniques as well as experiments in laboratory and in natural ecosystems. Here we highlight recent developments and extant knowledge gaps in aquatic mycology, and provide a conceptual model to expose the importance of fungi in aquatic food webs and related biogeochemical processes.

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Introduction

The limited knowledge about fungi constitutes one of the last frontiers of Earth's microbial biodiversity, despite the fact that no other group of organisms is known to be capable of degrading such a wide variety of structurally complex organic matter. In particular, the diversity and metabolic potential of aquatic fungi is poorly characterized, even when a number of recent reviews highlight the increasing awareness of their unknown biodiversity, their participation in nutrient and organic matter fluxes, and their potential role in the global carbon budget.

New discoveries in organic matter processing by aquatic fungi, call for a better understanding of their diversity, and ecological functions as well as its relation to prediction and mitigation of global change effects. For example, the observed increase in thawing permafrost soils in large parts of the northern hemisphere, in combination with extreme weather events, is leading to a dramatic increase in the runoff of terrestrial organic matter into surface waters. Furthermore, in flowing-water systems, changes to hydrological regimes promote accumulation of terrestrial organic matter during dry periods, which results in large pulses of organic matter input during flood events. Therefore, aquatic fungi and their interactions with bacteria should be regarded as important elements in the carbon cycle, whose influence is significant and far-reaching for atmospheric processes and climate.

Unexplored diversity of aquatic fungi

Most aquatic fungi belong to Ascomycetes and Chytridiomycetes, while comparatively less Basidiomycetes are reported in this ecosystem [1]. The internal transcribed spacer of the nuclear ribosomal DNA constitutes the standard barcode for the molecular identification of fungi [2], but also the large subunit and the small subunit of the nuclear ribosomal cistron are also frequently used to address phylogenetic relationships [3•]. Within these, the small subunit has been particularly useful for phylogenetic placing of Chytridiomycota and Cryptomycota and other aquatic fungi [4]. There is some evidence, however, suggesting that ribosomal markers underestimate diversity in comparison to more variable markers [5].

Currently, only a rather small number of fungal species (3000–4000) have been classified as aquatic fungi, despite the fact that estimations indicate that the global fungal diversity ranges from 0.5 to 10 million species [6•,7]. Furthermore, the 1112 species described as marine fungi to date seems sparse considering that approximately 71% of the planet is covered by saline and brackish water [8]. A single investigation detected >600 species on the common reed *Phragmites australis* [9] and more recent studies also showed high diversity and significant differences among fungal communities in different aquatic habitats [4,10]. Thus, it is very likely that estimation of the global fungal diversity for aquatic systems is greatly underestimated.

Aquatic fungi contribute to ecosystem functions and services

Over the past two decades, aquatic mycology has become a promising emerging discipline for various reasons. Firstly, fungi play key roles in aquatic ecosystems. Secondly, aquatic fungi hold a wide variety of metabolic capabilities that are valuable for humans and the natural environment, for example, discovery of novel secondary metabolites of medical, industrial, or agricultural interest, bioremediation of various types of pollutants in wastewaters, and humic matter remineralization.

Today fungal species have been recovered from a wider range of aquatic habitats including the deep sea, hydrothermal vents, the pelagic open ocean, sea ice, and numerous freshwater ecosystems [11,12]. They also display a multitude of lifestyles such as organic matter decomposers, parasites, predators, endophytes, symbionts, and pathogens. Although aquatic and parasitic fungi are well known for >100 years [13], they have been little studied, except for their role in degradation of leaf litter and other coarse particulate organic matter in stream ecosystems [14•].

The enormous metabolic diversity of aquatic fungi renders them key organisms for organic matter remineralization and energy cycling in aquatic food webs with important consequences for ecosystem health not only on a local but also global scale. In this regard, it is imperative to determine the fungal contribution to aquatic ecosystems and the provision of environmental services, taking into account their widespread distribution in aquatic environments, and their potential sensitivity to global change and anthropogenic pressures.

Production of secondary metabolites

Fungi are known for their capacity to produce a wide diversity of bioactive secondary metabolites. The first compound of medical and economic importance derived from an aquatic fungus, is the Cephalosporin C, a broad-spectrum antibiotic isolated from *Acremonium chrysogenum* [15]. The evident commercial interest has led to numerous investigations performed by pharmaceutical companies and academic institutions during the last three decades. This has resulted in the discovery of >1000 compounds derived from aquatic fungi, with possible applications for treating cardiovascular diseases, diabetes, cancer, immune-suppressants, antibiotics, antioxidants, antivirals, among others [16•,17,18]. Fungi producing those compounds were isolated from both marine and freshwaters, considering environments such as the deep sea, coral reefs, mangroves, or the associations with sponges, macroalgae, and other organisms [17,19,20•]. Aquatic fungi turned into an important reservoir of new chemical structures and bioactive natural products [20•,21,22]. Furthermore, recent genomic studies indicate that the fungal capacity to produce metabolites has been largely underestimated [23]. It is important to highlight that there is still an overwhelming knowledge gap of bioactive compounds isolated from aquatic fungi as compared to their terrestrial counterparts.

Fungal bioremediation

Industrial effluents often contain metals such as cadmium, chromium, copper, lead, mercury, palladium and zinc, posing a serious threat to public health and natural ecosystems. The use of fungi as biosorbents represents a promising technique for heavy metal removal. Because of the excellent fungal performance, for example, rapid growth, high biomass production, and hence cost effectiveness [24•]. Some of the fungal genera used for this purpose include *Aspergillus*, *Mucor*, *Rhizopus* and *Penicillium*, which can produce weak organic acids that form water-soluble complexes with the metals [25,26]. Effluents from several agro-industrial activities contain high levels of broad-spectrum organochloride pesticides, which are persistent and highly toxic to aquatic organisms. Experimental tests revealed *Fomitopsis*, *Daedalea* and *Penicillium* species to degrade DDT [27], whereas *Trametes*, *Pleurotus*, *Phanerochaete*, and *Aspergillus* species decompose endosulfan, imazalil, thiophanate methyl, *ortho*-phenylphenol, diphenylamine, and chlorpyrifos. The degradation of these compounds was concomitant with increases in laccase and manganese peroxidase activities but only in some cases, suggesting that other processes, most likely oxidative, may also be involved in degradation [28].

Globally, the discharge of liquids from urban and hospital wastes that contain pollutants of pharmaceutical origin have reached dangerous levels in both freshwater and marine ecosystems [29]. Furthermore, removal of these compounds in wastewater treatment facilities is often incomplete. Therefore, the high effectiveness of several fungal species to degrade numerous recalcitrant pharmaceuticals is very promising. Basidiomycetes and Ascomycetes have shown to degrade compounds such as the endocrine disruptor Bisphenol A [29], steroid hormones [30], xenoestrogen nonylphenol [31], iopromide and ofloxacin [32], anticancer drugs [33], and pharmaceutical active compounds [34,35], mainly via oxidation and hydroxylation by enzymes of non-specific nature like oxidases or hydrogen peroxide oxidoreductases [32].

Among all anthropogenic pollutants, plastics are possibly the most widespread ones in marine and freshwater environments. In experiments, the fungal genera *Aspergillus*, *Pleurotus*, *Panerochaete* and *Trametes* were capable of degrading polyester polyurethane [36], nylon [37], polypropylene [38], polyvinyl chloride [39], and oxo-biodegradable plastics [40] via enzymatic hydrolysis and oxidation [41]. Fungi have also shown the capacity to bioremediate several aromatic contaminants from aquatic systems, including synthetic azo and anthraquinone dyes by filamentous ascomycetes and yeasts [42•]; petroleum and polycyclic aromatic hydrocarbons by *Fusarium*, *Scopulariopsis* and *Aspergillus* species [43,44•]; polychlorinated biphenyls by autochthonous species of Ascomycota and Zygomycota [45]; chlorobenzenes by *Trametes versicolor* [46], and halophenols by brown-rot fungus *Gloeophyllum striatum* [47]. In most cases, the proposed mechanisms involved classical enzymatic degradation by lacasses, cytochrome P450