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Ecology and evolution of algal–fungal symbioses

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Ecological interactions and symbiosis between algae and fungi are ancient, widespread, and diverse with many independent origins. The heterotrophic constraint on fungal nutrition drives fungal interactions with autotrophic organisms, including algae. While ancestors of modern fungi may have evolved as parasites of algae, there remains a latent ability in algae to detect and respond to fungi through a range of symbioses that are witnessed today in the astounding diversity of lichens, associations with corticoid and polypore fungi, and endophytic associations with macroalgae. Research into algal–fungal interactions and biotechnological innovation have the potential to improve our understanding of their diversity and functions in natural systems, and to harness this knowledge to develop sustainable and novel approaches for producing food, energy, and bioproducts.

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Introduction

Interactions between fungi and algae are ancient and diverse in form and function, ranging from parasitisms to mutualisms [1,2]. Such cross-kingdom interactions are hypothesized to have been essential in the terrestrialization of Earth, and to have led to evolutionary radiations of fungal diversity, as well as the origin and radiation of land plants [3,4]. Lichens are the best-known and most diverse examples of algal–fungal mutualisms [4], yet new forms of symbiosis between fungi and algae continue to be discovered and described [5].

Algal and fungal diversity

Algae constitute a polyphyletic group of eukaryotic photosynthetic organisms that arose through the endosymbiotic acquisition of a cyanobacterial plastid ancestor and account for at least ten major radiations and eukaryotic clades [6]. The majority of algae are unicellular. However, over the past billion years, multicellularity evolved independently in *Chlorophytes*, as well as streptophyte algae enabling the colonization of land and biological radiations [7,8]. While some algal clades are strictly photoautotrophic, many are mixotrophic, switching between heterotrophic and photosynthetic modes [9]. The capacity of mixotrophic nutrition has been shown through modeling to increase the efficiency of energy flow through ocean food webs [10], and may impact how and when fungi and algae interact.

In contrast to algae, fungi comprise a monophyletic kingdom of heterotrophic organisms [11]. The early-branching fungal lineages *Cryptomycota*, *Sanchytriomycota*, and *Chytridiomycota* are aquatic endoparasites of algae and other organisms, although the nutrition of chytrids can span from strict saprotrophs to obligate parasites [12–14]. Fungi have been hypothesized to have had a freshwater origin, to have evolved within microbial crusts colonizing land, or to have originated through the transition from water to terrestrial environments, leading to polar multicellular mycelial growth [15,16]. Even today, *Cryptomycota* can be found in alpine snow packs where they parasitize diverse algae from *Chorophyta* and *Ochrophyta* [17,18].

Fungi are osmotrophic organisms and rely on secretory pathways for interacting with other organisms and for obtaining carbon, nutrients, and water from their environment [19]. Fungal heterotrophic nutrition may be one factor in the landscape of natural selection that may explain why such a significant amount of fungal biodiversity has evolved to be symbiotic and dependent on photosynthetic organisms [2,20]. This allows fungi to directly derive their carbon in a high-quality form that can easily be assimilated. At an ecosystem level, such multikingdom symbioses between photosynthetic algae and plants with heterotrophic fungi are likely to improve the efficiency of energy flowing through terrestrial food webs [21].

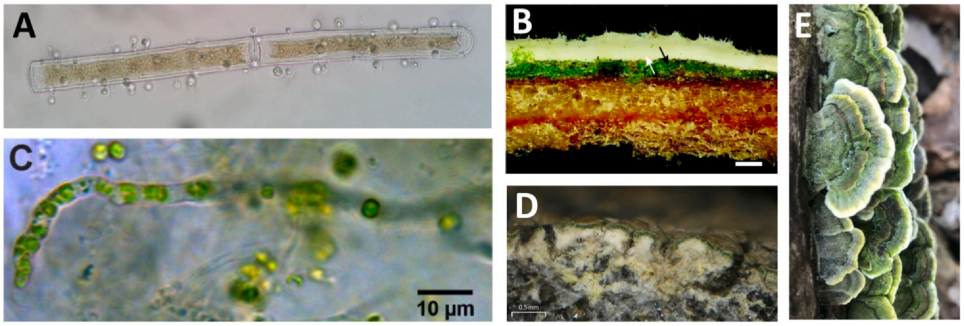
The evolution of symbiotic interactions between algae and fungi necessitates that these organisms coexist spatially and temporally in a habitat during some point of their life cycle. This is the ecological context that gives rise to evolutionary processes. It is relevant that early-branching aquatic fungal lineages evolved to be endoparasites of many diverse groups of algae [1,12,32]. This implies that sophisticated and adaptive genetic networks existed in ancestral fungi for locating, interacting with, and colonizing algae, which may have later been co-opted to facilitate the evolution of lineage-specific symbioses between fungi and algae. For example, it has been shown that green algae and land plants share orthologous proteins for recognition of fungi, homologous to Lysin-motif Receptor-like kinase receptors [22]. These receptors are involved in symbiosis and are known to trigger immune responses. Thus, streptophyte algae were already equipped to detect, and potentially defend themselves, against fungal parasites [23]. A comprehensive phylogenomic analysis of green algal and nonvascular land plant genomes demonstrated that the common symbiotic signaling pathway that underlies arbuscular mycorrhizal symbiosis predated the first land plants, indicating that their algal ancestors may have been preadapted for symbiosis with fungi [22]. Indeed, divergence time estimates indicate that fungi first occupied terrestrial environments in a mycelial form around 790 million years ago, after the loss of the flagellum [4]. At this time in Earth's history, embryophytes might not have yet differentiated from their closest aquatic green algal relatives (*Zygnematophyceae*), thus, fungi would have been living in associations with existing microbial communities, including terrestrial green algae. This scenario has been hypothesized to provide the context to explain the extreme diversity (~20 000 species) of fungi that associate with algae, predominantly those that form lichen symbioses [4].

Lichens: the quintessential algal–fungal symbiosis

Lichens are perhaps the most well-known and ecologically successful form(s) of algal–fungal symbioses (Figure 1d). Lichens are estimated to colonize nearly 8% of Earth's surface where they play important roles in soil formation, stabilization, and functioning, particularly in dryland and tundra ecosystems [24–26]. One particularly intriguing aspect of the lichen symbiosis is the morphological diversity that arises from these complex symbioses, called a holobiont, which distinguishes them from that of the individual and distinct lichen-forming organisms. Such specialized structures and growth forms distinguish lichens from other algal–fungal symbioses. Further, the lichen holobiont is able to occupy niches that neither partner could occupy independently. Although lichens have long been considered to be composed of a single fungal and algal species, it was recently shown that basidiomycete yeasts (i.e. *Cystobasiodiomycetes*) can be part of the lichen holobiont, and can impact lichen metabolism and phenotypes [27,28]. Further, while photosynthetic and N-fixing cyanobacteria are known to be associated with many lichens, such as the *Peltigerales*, a much larger diversity of bacteria have been detected in lichen thalli, although their functional roles are still not clear [29].

Lichenized fungal forms have evolved independently across *Ascomycota* and *Basidiomycota*, however, most lichen diversity is found in *Lecanoromycetes* and *Eurodiomycetes*. In contrast, the algal partners of the majority of lichens belong to *Chlorophyta* and are largely dominated by *Trebouxiales* and *Trentepohliales*, and in some known cases *Ochrophyta* or streptophyte algae [30]. Still, even new lineages of green algae, including within *Trebouxia*, are being found associated with lichenized fungi [2,31]. For further details on lichen diversity,

Figure 1



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Examples of algal–fungal interactions. **(a)** Chytrid PSC-L40 on *Mougeotia* sp. Image by Kensuke Seto, used with permission [32]. **(b)** Vertical section of the *Lyomyces* crust with a distinct algal layer described as alcobiosis [5], used with permission. **(c)** Intracellular *Nannochloropsis* microalgae within *Linnemannia elongata* hyphae [47]; image by Zhi-Yan Du, used with permission. **(d)** Section of lichen thallus of *Lecidea uniformis*; image by Jason Hollinger. E. Image of *Trametes versicolor* showing bands of green algae growing on the pileus.

ecology, symbiosis, and evolution, a recent review on the evolutionary biology of lichen symbioses covers these topics in depth [2].

Noncanonical algal–fungal symbiosis

Aside from lichens, there are a number of other examples of algal–fungal interactions. As already mentioned, chytrid fungi and *Cryptomycota* are known to be endoparasites of microalgae (Figure 1a) [12–14]. However, their diversity is still undercharacterized and consequently characterized as 'dark-fungal matter' [32]. Recently, in a workflow that included baiting, culturing, photographing, and single-cell sequencing, 71 phylogenetic lineages belonging to seven phylum-level clades of fungi were documented, with most of the species being novel [32]. Given that microalgae are increasingly being cultivated in bioreactors and open-pond systems at industrial-scale for biomass, oil, and bioproducts, outbreaks caused by fungi, including chytrids and *Aphelidiales*, in particular, can be economically impactful [33,34].

Algal symbionts growing in association of polypore wood-degrading fungi have been previously reported and characterized [30,35,36]. These are commonly observed in nature as green bands or patches growing across the pileus of basidiocarps of *Cerrena*, *Fomes*, *Lenzites*, *Stereum*, *Trichaptum*, and *Trametes* spp. (Figure 1e). These algal–-fungal associations do not appear to be particularly selective, and consist of diverse green algal partners composed of one to few species of *Chlamydomonas*, *Desmococcus*, *Elliptochloris*, *Interfilum*, *Klebsormidium*, *Pseudococcomyxa*, *Scotiellopsis*, *Sporotetras*, *Stichococcus*, and *Trebouxia*, as sometime photosynthetic *Cyanobacteria* [37]. Efforts to label and trace carbon flow between the symbionts with $^{14}CO_2$ have demonstrated the capacity of *Trametes* to utilize photosynthesized carbon from algal symbionts, however, the transfer amounts and rates were low [35]. More recent $^{14}CO_2$ labeling experiments show that fixed $^{14}CO_2$ by the algae could be traced to fungal basidiocarps as well as the decomposing wood that the fungal mycelial network had colonized [37].

Recently, a noncanonical but pervasive algal–fungal symbiosis referred to as alcobiosis, was described between algal members of *Trebouxiales* and a diversity of corticoid fungal symbionts belonging to *Agaricomycetes*. These included *Exidiopsis calcea*, *Tubulicrinis subulatus*, *Lyomyces sambuci*, *Resinicium bicolor*, *Skvortzovia furfuracea*, *Kneiffiella abieticola*, *Botryobasidium botryosum*, *Exidiopsis calcea*, and *Xylodon* spp. — fungal species generally considered to be saprotrophs [5]. In this apparent mutualism that is found on bark and decomposing wood, green algae form a stratified layer beneath the crustose fungal basidiomata, sometimes growing within the substrate, and in the case of *Lyomyces sambuci*— *Desmococcus* form goniocyst-like bundles characterized as algae surrounded by fungal hyphae (Figure 1b) [5]. Alcobiosis appears to be facultative, whereby the algae and the fungal symbionts can live independent of each other, yet when growing together, the algae thrive and in the case of *Lyomyces sambuci* — *Desmococcus* carbon transfer from the algal to the fungal partner was verified through isotope ratio mass spectrometry [5]. Interestingly, it appears that snails may help in the stimulation and co-dispersal of these symbionts [5].

Macroalgal mycobiomes and environmental sequencing

Some fungi are known to be algicolous endophytes of macroalgae, where they colonize their algal hosts without causing symptoms [38,39]. Macroalgae, including those of *Chorophyta*, *Rhodophyta*, and *Ochrophyta*, are primarily colonized by filamentous ascomycetes, including but not limited to *Penicillium*, *Aspergillus*, *Cladosporium*, and *Pseudogymnoascus*, yeasts, including *Metschnikowia*, *Rhodotorula*, and *Cryptococcus*, and in some cases early- branching fungal lineages such as *Mortierellaceae* [38]. In culture-based studies on macroalgae, individual macroalgal hosts were shown to be colonized by a few dominant species of saprotrophic fungi, and these algicolous fungal taxa were capable of producing enzymes for degrading algal biomass as a means for utilizing algal-derived carbon [40,41]. Research into algicolous fungal endophytes of brown algae has also demonstrated that fungal pyrenocine metabolites were protective against oomycete and protist pathogens of algae, indicating the mycobiome may provide a defensive function to the benefit of their algal host [42].

While most fungal diversity within macroalgae may be culturable, the ability of culture-independent methods for accessing fungal diversity has improved our resolution and ability to detect fungal diversity and complexity associated with various focal host species and environments. For instance, a recent study used ITS amplicon sequencing to access fungal diversity within the brown macroalgae *Turbinaria* and *Sargassum* (as well as sponges), and found that the brown algae mycobiome was dominated by *Botryosphaeriales*, *Chaetothyriales*, *Eurotiales*, and *Hypocreales* [43]. In particular, *Trichoderma* was identified as a core member of these macroalgae mycobiomes [43]. In another study that combined culture-based and culture-independent approaches to characterize fungal diversity within brown and red algae, culture-independent methods based on ITS2 amplicon sequencing detected a much higher diversity of fungi than did culturing, and found the mycobiomes were largely composed of *Ascomycetes*, including many putative novel taxa [44]. Further, algal mycobiomes differed between host species and host tissue types [44].

Synthetic algal–fungal interactions

In addition to algal–fungal interactions that have been discovered in nature, there are intriguing examples of mutualistic interactions that can be induced between various algal and fungal partners in the lab that are not known to interact in nature, considered here as synthetic symbioses. This latent capacity for mutualism and co-dependence was elegantly shown through spontaneous mutualistic interactions between *Chlamydomonas* and *Saccharomyces* under conditions of atmospheric CO_2 limitation, whereby glucose is metabolized by the yeast into CO_2 that the algae can fix through photosynthesis, and nitrate is reduced by the algae to ammonium, making it available to the yeast [45]. Such synthetic and obligate mutualisms spontaneously formed between other diverse yeast and *Chlamydomonas* species, only so long as the partners were metabolically dependent upon each other for usable forms of carbon and nitrogen, indicating a nutrient basis for the interaction. The obligate nature of these interactions breaks down if supplemented forms of usable carbon or nitrogen are supplied to the cocultures. Further, *Chlamydomonas* was shown to interact with the filamentous fungus *Aspergillus nidulans* forming a tight fungal–algal contact interface. However, obligate associations were only formed between mutant isolates unable to reduce nitrite. In a more recent study that combined these two organisms with a toxigenic bacterium, *Aspergillus nidulans* was found to protect *Chlamydomonas reinhardtii* from azalomycin F, an algicidal compound secreted by *Streptomyces iranensis* [46]. *Chlamydomonas reinhardtii* cells exhibited chemotaxis toward *Aspergillus nidulans* mycelium and increased algal survival, which appeared to be a consequence of polar lipids in *Aspergillus nidulans* that bind and neutralize the toxin.

In another example of spontaneous mutualisms occurring in a lab setting, the fungal species *Linnemannia elongata* (=*Mortierella elongata*) was shown to attract and flocculate the microalgae *Nannochloropsis oceanica* [47]. This interaction phenotype was conserved among only certain *Mortierellaceae* species among the diverse panel of fungal taxa assessed, and was accompanied by the loss of the smooth outer component of the *Nannochloropsis* cell wall revealing pseudopodia-like structures that appeared to fuse with the fungal cell wall. Through isotope tracer experiments using independently ^{14}C- and ^{15}N-labeled fungal and algal cells, a net carbon transfer to the fungal colony from living algal cells in physical contact with the mycelium was observed. However, this was not observed in treatments with heat-killed algal cells or those separated from the fungus by a membrane, demonstrating a biotrophic nature underlying this interaction. In contrast, a net transfer of nitrogen to the algae from the fungus was found, yet, no contact between the cells was needed for this transfer. Perhaps most remarkable, through longer-term (30-day) interaction studies, and under carbon-limited conditions, the *Nannochloropsis* cells were found to internalize with living fungal cells, where they were able to mitotically divide and colonize the fungal tissue. While fungal endophytes are common in macroalgae, this is perhaps the only example of algae colonizing and becoming internalized within fungal cells (Figure 1c).

Biotechnology and applications related to algal–fungal interactions

Given the propensity of microalgae for producing neutral lipids and polyunsaturated fatty acids, along with other industrially important metabolites that can be produced natively or through engineering, there has been a concerted effort to cultivate microalgae at large scales to sustainably produce algal biomass for food, energy, and industry [48,49]. Yet, while microalgae can be grown sustainably using wastewater and materials, harvesting microalgae still poses many challenges as centrifugation is energy-intensive, and chemical flocculants can compromise downstream processing [50]. Further, there continue to be challenges in controlling fungal pathogens of algae in cultivation systems [51]. Interestingly, metabolites produced by fungal endophytes of macroalgae may have utility in managing diseases in aquacultural systems, including those of microalgae [52].

A number of studies have now shown interactions between fungi and microalgae that can be harnessed technologically for bioflocculation of microalgae, thus improving the harvesting efficiency of these systems [48,50,53]. Although the mechanisms of bioflocculation are not understood in all cases, one mechanism for this interaction has to do with cell-wall surface charge of the organisms whereby positively charged fungi attract negatively charged microalgae [53]. In the case of *Aspergillus niger* and *Chlorella vulgaris*, this attraction has been optimized with extracellular polymeric substances to improve harvesting efficiency while reducing energy and harvesting time [53]. Cell-wall attachment and extracellular polymeric substances were suggested to be responsible for flocculation efficiency of *Chlamydomonas reinhardtii* by the fungus *Mortierella alpina* [54]. In another example, the oleaginous fungus *Linnemannia elongata* was used to bioflocculate *Nannochloropsis oceanica* and not only improved the recovery of the algae, but also improved the oil yield and composition of the bioflocculants [55].

In addition to the use of fungi for the bioflocculation of algae, numerous value-added compounds can be obtained from the coculture biomass, including fatty acids, polysaccharides, triglycerides, pigments, surfactants, and vitamins that have industrial relevance [56].

Table 1

Types of algal–fungal interactions.

Common name	Fungi	Algae	Habitat	Citations
Endoparasites	*Cryptomycota* *Chytridiomycota*	Green algae Yellow-green algae Diatoms Glaucophytes	Aquatic	[1,13,32,51]
Lichens	*Lecanoromycetes* *Eurodiomycetes* *Agaricomycetes*	*Trebuxiales*	Terrestrial	[2,31]
Alcobiosis	*Agaricomycetes*	*Trebuxiales*	Terrestrial	[5]
Polypore epiphytes	*Polyporales*	Green algae	Terrestrial	[30,35–37]
Algicolous endophytes	*Eurotiales* Yeasts *Mortierellales* *Chaetothyriales* *Botryosphaeria*	*Chlorophyta* *Rhodophyta* *Ochrophyta*	Aquatic	[38–41,43,44]
Synthetic symbioses	*Aspergillus* spp, *Saccharomyces* spp. *Ganoderma lucidum* *Mortierellales*	*Chlamydomonas* spp. *Chlorella vulgaris* *Nannochloropsis oceanica*	Aquatic	[45–49,54–57]

New tools and techniques continue to be developed to study algal–fungal interactions, and may have biotechnological potential. For example, a recent approach involves the use of 3D-printed living architecture embedded with fungal–algal cocultures with nanocellulose hydrogel. Another study used the white-rot fungus *Ganoderma lucidum* and microalgae *Chlorella vulgaris* to form algal–fungal pellets and demonstrated their efficiency at removing antibiotics and nutrients from wastewater [57]. Such emerging approaches could help in developing experimentally tractable synthetic systems for studying the evolution and ecology of algal–fungal symbioses, while generating new approaches and sustainable technologies for developing bioproducts and industrial biomaterials.

Conclusions

Heterotrophic fungi and autotrophic algae have a long history of ecological and evolutionary interactions that include parasitism and different types of nutritional symbioses (Table 1). It is clear that much of the living fungal dark matter, known only from environmental sequencing, includes early-branching aquatic fungal diversity whose ecology is still not well- understood or described [32,58]. Environmental amplicon sequencing has helped to demonstrate the diversity of fungi associated with algae in nature, but new approaches, including bait-assisted culturing coupled with microscopy and single-cell sequencing, are poised to improve our understanding of the poorly understood fungal diversity and function in aquatic ecosystems and soils [32,59]. Ancestral fungi were parasites of microalgae and other organisms, thus, fungi and algae have each evolved genetic mechanisms and receptors for detecting and responding to each other, from ancient gene circuits that originated before terrestrialization. This may in part explain how algae and fungi appear to be preadapted to forming symbioses with each other, including the multiple origins of lichen symbiosis, alcobiosis, and other algal–fungal interaction types. The basis, limits, and contingencies to forming nutritional symbioses are still not well-resolved. Fungal endophytes associated with macroalgae are derived from halotolerant terrestrial lineages, but have acquired the enzymatic capacity for accessing algal-derived carbon. New techniques, including machine learning and 3D printing, provide new opportunities to test and utilize biotic interactions for the good of humanity. Through further research and biotechnological innovation, we have the opportunity to harness algal–fungal interactions to improve our understanding of natural systems and to use this knowledge to develop sustainable technology approaches for producing food, energy, and bioproducts while decarbonizing the economy.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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