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FUNGI–CYANOBACTERIA ASSOCIATIONS

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What are fungi–cyanobacteria associations?

Fungi and cyanobacteria are among the oldest, most genetically diverse, and most ubiquitous organisms on Earth. Fungi is a Kingdom containing very diverse life forms, from mushrooms to yeasts and molds, and lifestyles, from saprotrophs degrading organic matter, to pathogens, to symbionts with plants. Such symbioses comprise mycorrhizae associating with roots, endophytes inside plants, and lichen-forming fungi associating with green algae. Cyanobacteria are a Phylum of prokaryotes that appeared at least 3.5 billion years ago. They were the first group of organisms to develop oxygenic photosynthesis, a process that led to the Great Oxidation Event, and they are also among the few groups of bacteria that can fi x nitrogen from the atmosphere. Both groups of organisms are found in a wide range of symbioses with plants. But fungi and cyanobacteria also associate together in mutualistic interactions, the best-known and most conspicuous examples of them being cyanolichens. Although frequently overlooked, fungi–cyanobacteria associations may be just as significant as the better known ones involving plants.

What are cyanolichens?

Lichens are symbioses formed between a fungal partner, called the mycobiont, and one or several photosynthetic partner(s), called the photobiont(s). When cyanobacteria are involved in the association, it is called a cyanolichen, whereas if only green algae are involved, it is referred to as a chlorolichen. Symbionts together form a conspicuous structure called a thallus (**Figure 1A–C**). The degree of complexity can vary greatly, from a few intertwined cells to large, stratified structures. Lichens are often considered obligate symbioses, the fungus at least being unable to grow alone.

What kinds of cyanolichens are there?

Cyanolichens can be bipartite, involving only fungi and cyanobacteria, or tripartite, also containing green algae. The most common tripartite association involves cephalodia, which are specialized, usually spherical structures containing cyanobacteria (**Figure 1C**). The cephalodia can be either internal, as in *Lobaria* species, or external as in *Peltigera*. Because cephalodia can be located under the thallus, it suggests that access to light is of little importance. Indeed it is usually thought that in such associations there is a division of work, with the green algae producing most of the sugar through photosynthesis, while cyanobacteria mostly fi x nitrogen.

In other cases, the same fungus can associate with either a green alga or a cyanobacterium. The two forms, called the photomorphs, can grow together or separately. In some cases, the two types of photomorph look similar (except for the color), whereas in other cases, the cyanobacterial photomorph forms unique arbuscules (**Figure 1B**). The establishment of the symbiosis with either of the two photosynthetic partners seems to be mostly related to fitness and photosynthetic performance under different ecological conditions. Yet, re-creating cyanolichens under laboratory conditions has proven very difficult, highlighting the complexity of the symbioses and the probable role of the associated microbiome in forming the thallus.

How diverse are cyanolichens?

Out of the ~150,000 described fungal species, ~20,000 are lichen-forming, and cyanobacteria are present in ~12% of the lichen symbioses. The vast majority of fungi associated with cyanobacteria are Ascomycota, but a few are Basidiomycota. Within Ascomycota, most lichen-forming fungi belong to class Lecanoromycetes, and most Lecanoromycetes are lichen-forming fungi; however, they can also be found in several other distantly-related groups within Ascomycota. On the cyanobacterial side, most symbionts belong to the Nostocales, usually the genera *Nostoc* and *Rhizonema*. Other lichenized cyanobacteria belong to Chroococcales, such as the genus *Gloeocapsa*.

Within one thallus there is usually a single species of fungi associated with a single strain of cyanobacteria, but at the species level, the degree of specificity is highly variable, with some species being strict specialists towards a partner, and others more generalist. Ongoing studies are attempting to understand the factors driving this specialization. Lichenized *Nostoc* strains are usually closely related to strains associating with plants such as *Gunnera* or *Blasia*, and fungus *Geosiphon*.

As mentioned above, green algae are also involved in lichens: the photobionts can thus belong to different kingdoms of life. Mycobionts and photobionts are therefore polyphyletic assemblages. Hence, a lichen must be seen as a nutrition mode or a lifestyle rather than a taxonomically-relevant category.

Are there other notable symbioses?

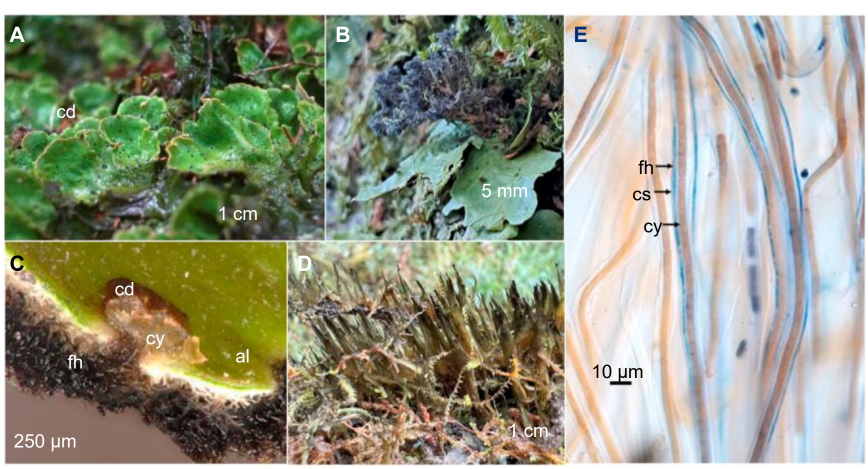
Yes. Another less conspicuous but fascinating example includes cyanobacterial symbionts of the genus *Nostoc* inside the cells of the fungus *Geosiphon pyriformis*. *Geosiphon pyriformis* is the only species of Glomeromycota that is known to form a symbiosis with cyanobacteria (others are involved in arbuscular mycorrhizae, a symbiosis with roots of plants). This rare fungus is only known from a few locations in Central Europe. The *Geosiphon–Nostoc* symbiosis is usually not considered a lichen, because within a lichen the photosynthetic partners are not located inside the cells of the fungus.

Very recently a new type of symbiosis, Phyllosymbia, was discovered in Taiwanese mountain cloud forests (**Figure 1D,E**). Unlike typical lichens where fungi construct the main outer and interior thallus structure, this unique association consists of a structural matrix built by cyanobacteria that hosts Basidiomycota fungi (**Figure 1D,E**). It involves orders of fungi (Sebacinales) and cyanobacteria (Coleofasciculales) that were not known to form symbioses together before. The discovery of this novel symbiotic complex highlights how far we are from an exhaustive have been found interacting with each other at both ends of the temperature and humidity spectrum: from the arctic tundra and mountain tops, where biocrusts and cyanolichens often dominate, to warm and moist tropical forests that host a high diversity of cyanolichens, and where the new Phyllosymbia symbiosis was found; from marine cyanolichens, living on rocks battered by the waves, to deserts where they are often interacting together in biocrusts.

Figure 1. *Diversity of associations between cyanobacteria and fungi. (A) Macroscopic picture of thalli of tripartite Peltigera aphthosa with cyanobacteria-containing cephalodia (cd). (B) Macroscopic picture of a Dendriscocaulon-like cyanobacterial photomorph growing closely to a green algal lichen on a trunk in a Taiwainese mountain cloud forest. (C) Microscopic picture of tripartite Peltigera aphthosa where the fungal hyphae (fh) are engulfi ng the Nostoc sp. cyanobacteria cells (cy) in the unique nitrogen-fi xing cephalodia structure (cd) (the green layer is made of Coccomyxa sp. (al) algal cells). (D) Macroscopic view of a thallus of Phyllosymbia and (E) microscopic view of Phyllosymbia with fungal hyphae (fh, stained with Trypan Blue) engulfed in cyanobacterial sheath (cs) (photo credits: Che-Chih Chen, Ko-Hsuan Chen, Romain Darnajoux, and Nicolas Magain).*

What can explain the success of their association?

One key element is their dual ability to survive extreme conditions that most organisms cannot withstand, and to accumulate organic matter literally out of thin air, with only a few sprinkles of mineral dust for inorganic nutrition (providing for example phosphorus, electrolytes and micronutrients). Most of the cyanobacteria in these associations are diazotrophic organisms that can fi x (chemically reduce) nitrogen from the large atmospheric reservoir, with evidence of nitrogen transfer to surrounding organisms, even in their less conspicuous associations such as biocrust or bryophytes.



Cyanobacteria also possess carboxysomes, specialized structures that can act as a carbon concentration mechanism to reduce the cost of photosynthesis. In cyanolichens, the fungal partner is thought to contribute to inorganic nutrition, including phosphorus or essential trace metals for nitrogen fixation. The details of the underlying mechanisms are not understood but previous work on chlorolichens indicates it could involve specific secondary metabolites. All these metabolic features help alleviate key limitations for acquiring micro- and macronutrients. It gives them several edges to compete for large, nitrogen-limited, ecological niches.

How important are these associations within ecosystems?

They are important nitrogen fixers at different stages of ecological succession. Cyanolichens' average contribution to the total nitrogen fixation in a model temperate chronosequence ranges from none to over two kilograms of nitrogen per hectare per year, with highs in mid-successional stages. In drylands, nitrogen input is dominated by biocrusts. Cyanolichens can contribute over 80% of the total biological nitrogen fixation in selected arctic habitats, and their contribution to tropical forests remains understudied. The new Phyllosymbia symbiosis shows evidence of nitrogen fixation, but its ecological importance remains unknown. The new Phyllosymbia symbiosis shows evidence of nitrogen fixation, either due to the cyanobacterial partner itself or to its associated microbiome, but its global ecological importance remains unknown.

Biocrusts and cyanolichens are important ecosystem starters, referred to as pioneer species. The drought protection, sunlight tolerance, and their ability to fi x nitrogen allow them to establish on bedrocks and other newly exposed surfaces, such as lava fl ow, retreating glaciers, or mountain tops. There, a mix of physical and chemical weathering action and their decomposed organic matter will create the initial soil where less tolerant photosynthetic species such as bryophytes and vascular plants will settle and start accumulating organic matter faster. As both fungi and cyanobacteria were already present in the Precambrian, the earliest biocrust analogs that have contributed to the colonization of continental land might have relied on similar mechanisms.

How are environmental changes going to affect them?

Cyanolichens can modulate the nature of their association to adapt their nutrient acquisition strategies to environmental conditions. Tripartite associations that include a green alga have higher water stress tolerance than bipartite ones, as green algae can use water vapor for photosynthesis, whereas cyanobacteria need it in liquid form. In tripartite cyanolichens, increased nitrogen deposition has been shown to reduce the frequency of the cyanobacterial partners. Nitrogen is such an important part of their life contracts that the cyanobacterial partners often possess two genetically distinct nitrogenases, which use either molybdenum or vanadium as the metallic co-factor. It allows the symbioses to adapt to areas with varying metal availability.

All this indicates that the biogeography of cyanolichens and other fungi–cyanobacteria symbioses has changed and will likely continue to change according to their metabolic constraints, with dryer conditions and increased nitrogen pollution probably reducing their range. As important, their involvement in ecosystem succession and the nitrogen cycle will also be pivotal in shaping the future of high-altitude and high-latitude ecosystems with global environmental change.

Where can I find out more?

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DECLARATION OF INTERESTS

The authors declare no competing interests.