

CHAPTER 19-2

BRYOPHYTE BACTERIA EFFECTS ON COMMUNITIES

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CHAPTER 19-2

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Figure 1. *Fontinalis dalecarlica* showing collection of sediments that harbor many bacteria, including *Methylocystis* that oxidizes CH_4 , releasing CO_2 . Photo by Jean Faubert, with permission.

Community Effects

During and van Tooren (1990) noted that bryophytes occur in microhabitats that are formed by the physical environment and typically modified by the tracheophyte vegetation occurring with them, but the bryophytes are typically treated as if they are isolated from other plants and other organisms in the environment. More realistically, we are now beginning to realize the importance of the interactions between bryophytes and other organisms. These interactions are involved in competitive, parasitic, symbiotic, and mutualistic relationships. During and van Tooren pointed out that information regarding the relationships of bryophytes with other organisms, including bacteria, is essential for understanding mineral nutrition, carbon economy, herbivory, growth, development, and the overall ecological role of the bryophytes.

Reboledo and León (2021) again pointed out the importance of bryophyte-microorganism interactions. They pointed out that these interactions had developed during coevolution of the bryophytes with microorganisms. Some of the interactions took the place of substances the bryophytes would otherwise have needed to produce themselves, thus saving them energy. They also avoided complex pathways that responded to environmental differences and changes such as seasons.

Sun *et al.* (2017) used bryophyte removal experiments to learn that absence of bryophytes caused a change in the soil microbial community in the conifer-dominated forest and an ericaceous shrubland of the alpine Tibetan Plateau. Frahm *et al.* (2012) suggested that bacterial contamination may affect the antibiotic effect of bryophytes on seed germination.

Ma *et al.* (2017a) examined the bacterial communities on four moss species [*Campyliadelphus polygamus* (Figure 2), *Cratoneuron filicinum* (Figure 3), *Grimmia pilifera* (Figure 4), *Pylaisia polyantha* (Figure 5)]. They found a total of 279 genera comprised of 558 OTU's (operational taxonomic units). Of the 16 bacterial phyla found, the **Pseudomonadota** and **Actinomycetota** were the two most abundant phyla. The most common bacterial genera were *Bosea*, *Cellvibrio*, *Friedmanniella*, *Jatrophihabitans*, *Lapillicoccus*, and *Oligoflexus*. The two wet-habitat mosses (*Campyliadelphus polygamus*, *Cratoneuron filicinum*) had similar bacterial communities, differing from those of the two relatively dry habitat species (*Grimmia pilifera*, *Pylaisia polyantha*) that also had similar bacterial communities. The bacterial communities in the summer and autumn were most similar on each moss species. However the season was not the most important factor in causing community differences.



Figure 2. *Campyliadelphus polygamus*, a moss species that hosts mostly *Pseudomonadota* and *Actinomycetota*. Photo by Jean Faubert, with permission.



Figure 3. *Cratoneuron filicinum*, a moss species that hosts mostly *Pseudomonadota* and *Actinomycetota*. Photo by David T. Holyoak, with permission.



Figure 4. *Grimmia pilifera*, a moss species that hosts mostly *Pseudomonadota* and *Actinomycetota*. Photo by Wayne Lampa, through Creative Commons.

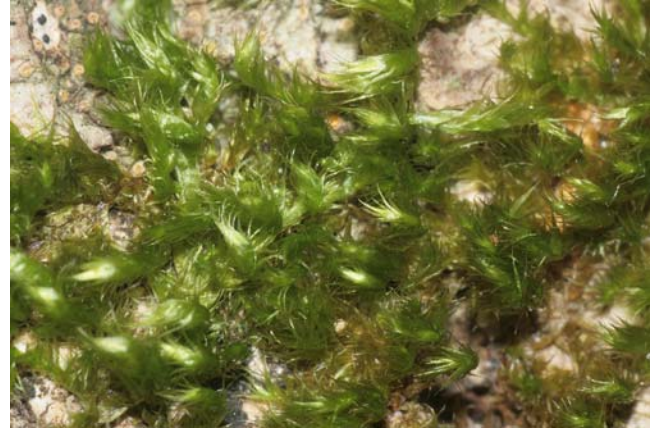


Figure 5. *Pylaisia polyantha*, a moss species that hosts mostly *Pseudomonadota* and *Actinomycetota*. Photo by Hermann Schachner, through Creative Commons.

Tang *et al.* (2016) were curious about the specificity of the bacteria on the bryophytes. They investigated ten liverworts and ten mosses from Tibet, China, using sequencing techniques. Six of the mosses had bacterial communities with a higher community similarity, but the remaining four mosses had communities that were more similar to those of the ten liverworts. Tang and coworkers concluded that the phylogeny of hosts has a strong influence on the associated bacterial community and that niche also plays important roles when the hosts are phylogenetically more similar.

Harris and Tibbles (1997) compared bacterial productivity in four Antarctic habitats. These included soils from four different habitats: beneath moss beds, from nests of snow petrel (*Pagodroma nivea*), exposed unvegetated soil (polygon soil) 5 m away from nests, and exposed polygon soil on nunataks without nests of breeding birds. The moisture levels from nest entrances and beneath mosses were much higher than in those from unvegetated exposed polygons. Mosses also modify temperatures, providing much cooler summer temperatures than exposed polygons on continental Antarctica, which are greater than 20°C at midday, and exhibited less temperature fluctuation. Harris and Tibbles considered these moss beds to be bacterial "hotspots," although based on temperature "coolspots" might be more appropriate. They considered that bacterial productivity in moss soils was typically nutrient limited, whereas in the polygons moisture was a more important factor.

Opelt and Berg (2004) considered the bryophytes to serve as a diverse community reservoir of bacteria that provided antibiotics against plant pathogens. Koua *et al.* (2015), in Japan, found that many of the bacteria associated with bryophytes played critical roles in soil nutrient enrichment, especially in nitrogen fixation. They seem to be especially important as hosts of nitrogen-fixing bacteria, contributing to biogeochemical cycling (Cornelissen *et al.* 2007).

Vollár *et al.* (2018) found that among the 42 bryophyte species in their study, the families **Brachytheciaceae** and **Amblystegiaceae** produced the greatest numbers of antiproliferative extracts – extracts that worked against the proliferation of cancer cells. *Plagiomnium cuspidatum* (Figure 6) seemed to be the most active, affecting 8 bacterial strains. As in several other bryophyte studies (*e.g.*

Bodade *et al.* 2008; Liu & Wang 2010; Liyanage *et al.* 2015; Sabovljević *et al.* 2010), *Staphylococcus aureus* (Figure 7) was the most susceptible to the antiproliferation activity. *Paraleucobryum longifolium* (Figure 8) exhibited the highest activity.



Figure 6. *Plagiommium cuspidatum*, most active among 42 species of bryophytes, affecting 8 bacterial strains. Photo by Hermann Schachner, through Creative Commons.

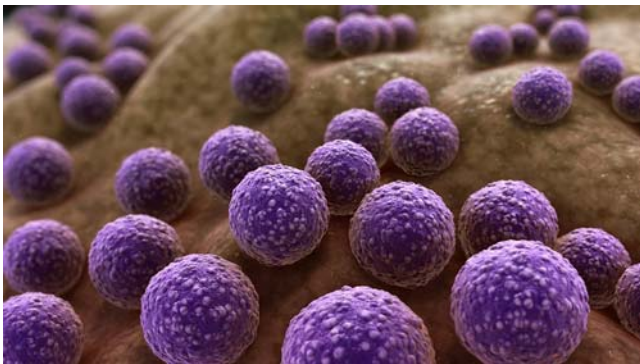


Figure 7. *Staphylococcus aureus*, a species that among the most susceptible to inhibition by bryophyte extracts. Photo from <www.scientificanimations.com>, through Creative Commons.



Figure 8. *Paraleucobryum longifolium*, the species with the greatest antibacterial activity among 42 species of bryophytes tested. Photo by Hermann Schachner, through Creative Commons.

Koua *et al.* (2015) reiterated that little is known about the bryophyte-associated microbial diversity or their role in

soil enrichment and nitrogen fixation. As community members, the bacteria associated with bryophytes have the potential to infect other members of the community. This is especially true for plant pathogens, but the bryophytes can also serve as a refuge for bacteria that affect animals and fungi.

Zhu *et al.* (2006) assayed 60 bryophyte species for their antibacterial activity and found that 93.3% of the species demonstrated antibacterial activity against at least two of the seven tested bacterial species [*Priestia megaterium* (Figure 9) – syn. = *Bacillus megaterium*, *Bacillus subtilis* (Figure 10), *Bacillus thuringiensis* (Figure 11), *Escherichia coli* (Figure 12), *Pseudomonas aeruginosa* (Figure 13), *Pseudomonas putida* (see Figure 13), and *Staphylococcus aureus* (Figure 7)]. This activity was particularly strong in the liverwort genera *Conocephalum* (Figure 14), *Frullania* (Figure 15), *Herbertus* (Figure 16), *Marchantia* (Figure 17), *Mastigophora* (Figure 18), and *Porella* (Figure 19). But what does this activity against human tracheophyte pathogens mean for the communities where these bryophytes live?

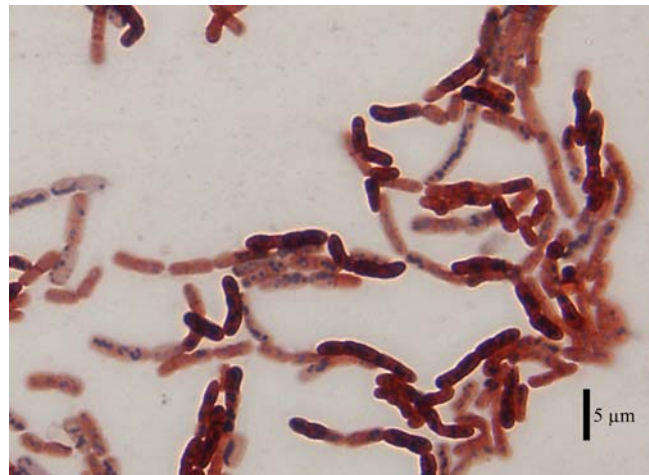


Figure 9. *Priestia megaterium* DSM-90 cells colored with Sudan black and safranin, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Osmoregulator at English Wikipedia, through Creative Commons.

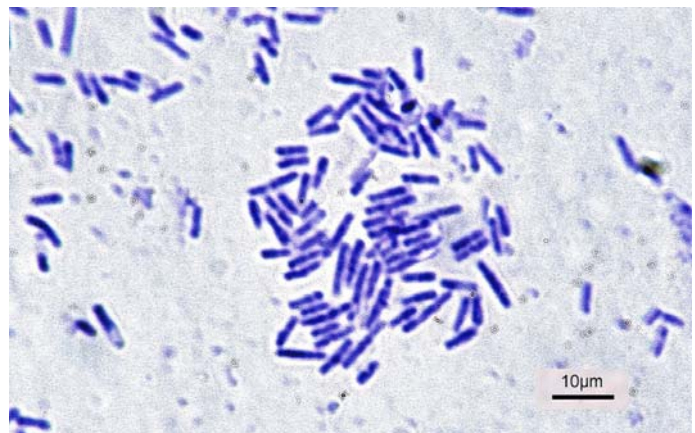


Figure 10. *Bacillus subtilis*, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Graham Beards, through Creative Commons.



Figure 11. *Bacillus thuringiensis*, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Dr. Sahay, through Creative Commons.

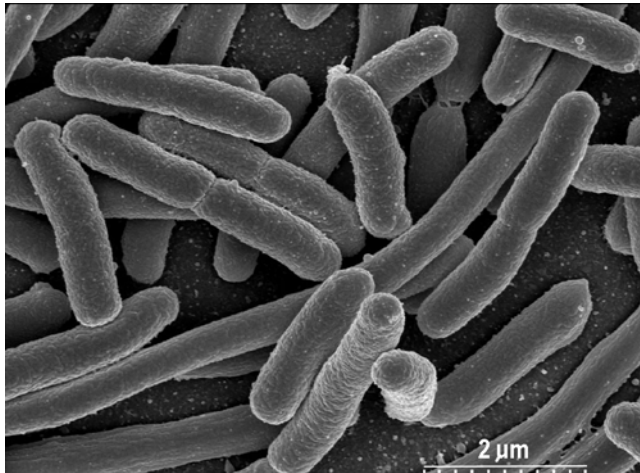


Figure 12. *Escherichia coli*, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Rocky Mountain Laboratories, NIAID, NIH - NIAID, through public domain.

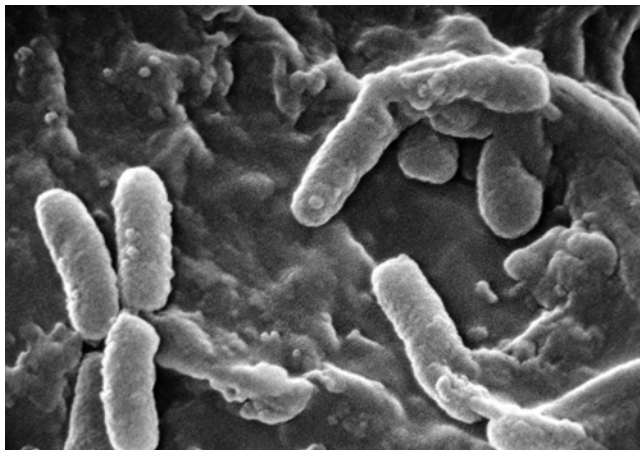


Figure 13. *Pseudomonas aeruginosa* SEM, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Janice Haney Carr, CDC, through public domain.



Figure 14. *Conocephalum*, a genus in China with particularly strong antibacterial activity. Photo by Don Loarie, through Creative Commons.



Figure 15. *Frullania dilatata*, in a genus in China with particularly strong antibacterial activity. Photo by Bernd Haynold, through Creative Commons.



Figure 16. *Herbertus aduncus*, in a genus in China with particularly strong antibacterial activity. Photo from Botany Website, UBC, with permission.



Figure 17. *Marchantia polymorpha*, in a genus in China with particularly strong antibacterial activity. Photo by Denis Barthel, through Creative Commons.



Figure 18. *Mastigophora woodsii*, in a genus in China with particularly strong antibacterial activity. Photo by Jo Denyer, with permission.



Figure 19. *Porella platyphylla*, in a genus in China with particularly strong antibacterial activity. Photo by Hermann Schachner, through Creative Commons.

In one study *Pseudomonas putida* (see Figure 13) is most sensitive to the extracts of mosses, and *Bacillus subtilis* (Figure 10) is most sensitive to the extracts of liverworts (Zhu *et al.* 2006). *Staphylococcus aureus* (Figure 7) is the most resistant of the seven tested bacteria to the extracts of both liverworts and mosses, contrasting

with its widespread susceptibility to bryophyte extracts in a number of other studies (*e.g.* Bodade *et al.* 2008; Liu & Wang 2010; Liyanage *et al.* 2015; Sabovljević *et al.* 2010). This suggests that some bryophytes could serve as a refuge for the *Staphylococcus aureus*, but there is evidence that suggests that the antibiotics against *S. aureus* from some of the bryophytes are only produced when the bacteria are present (Sabovljević *et al.* 2010).

The importance of this inducible response to the community has not been investigated. If the antibiotics manufactured by bryophytes are effective against these bacteria that are not known to be pathogenic to bryophytes, how might these antibiotics affect other bacteria in the ecosystem? What selection pressures kept these antibiotic properties in the library of secondary compounds produced by bryophytes that weren't harmed by them? How can we explain that *Bacillus subtilis* is the most sensitive of the seven tested bacteria to liverwort extracts and that *Pseudomonas putida* is the most sensitive to moss extracts (Zhu *et al.* 2006)? And why do 99% of the bacteria found with mosses produce antifungal compounds (Opelt and Berg 2004)? Why are there no compounds produced by any liverwort as protection against fungi (Banerjee & Sen 1979)? Why should bryophytes produce so many compounds that protect other organisms, but at the same time depend on bacteria to produce some compounds that protect the bryophytes?

Many of the bacteria associated with bryophytes appear to be unknown because they do not grow on standard media (see Vesty *et al.* 2020).

Are some of these undetected bacteria the sources of any of the antibiotic compounds that we attribute to the bryophytes? Are we missing some antibiotic compounds when we culture the bryophytes axenically before testing them, thus failing to elicit any inducible responses (see Sabovljević *et al.* 2010)? Among these bacteria, how important are they to soil nutrient cycling? Are they nucleators that affect our weather? Are the bryophytes a reservoir for ice-nucleators that may be beneficial or detrimental to other kinds of plants? What sorts of selection pressures exist for these less known or unknown bacteria?

Using DNA and RNA techniques we are able to assess such differences without the need to name the bacteria involved. In China, Wang *et al.* (2018) found abundant bacteria associated with all the mosses they sampled and identified in this manner. These were mostly in the phyla **Pseudomonadota** and **Actinomycetota**. Their OTU level hierarchy separated the bacteria into two main branches of aquatic vs terrestrial. The aquatic habitat showed larger differences in the bacterial community composition than did the terrestrial habitat. Thus, the habitat of the host bryophyte is an important factor in determining the community.

Streams and Rivers

Bryophytes in streams typically are covered with bacteria, making it difficult to assess productivity of the bryophytes alone (Arscott *et al.* 1998). These are difficult to remove, and the role of the bacteria in producing CO₂ that bryophytes can use in photosynthesis needs to be assessed. Furthermore, the bryophytes trap silt and organic

matter (Figure 20) that flows in the stream or river, making them an important habitat for some kinds of bacteria.



Figure 20. *Fontinalis antipyretica* with detritus that can serve as food for bacteria and macroinvertebrate scrapers. Photo by J. C. Schou, with permission.

In their study of carbon sources used by primary consumers in two oligotrophic rivers, McWilliams-Hughes *et al.* (2009) found that tracheophyte macrophytes and **Cyanobacteria** were unimportant as food sources for insect scrapers. Rather, 98% of the scrapers exhibited $\delta^{13}\text{C}$ values that were enriched with bryophyte $\delta^{13}\text{C}$ values, especially when slow-flowing habitats were excluded from the analysis. *Fontinalis* sp. (Figure 21) was abundant in headwater (low order) streams, where it exhibited more dependence by scrapers than the dependence by scrapers associated with the *Drepanocladus* (Figure 22) sp. of the high-order streams (with higher order streams having more combining tributaries). This is consistent with the greater cover by bryophytes in the headwater streams. They suggested that scrapers might switch to marginal food sources such as bryophytes in the headwaters where productivity and nutrients are low. But what is really providing their food? Might it be the bacteria and other periphyton that are always associated with the mosses? I have seen a Dipteran larva eat "dirty" mosses (Figure 20) and watched the feces come out as clean moss fragments.



Figure 21. *Fontinalis antipyretica*, home for macroinvertebrate scrapers in streams. Photo by Claire Halpin, with permission.



Figure 22. *Drepanocladus aduncus*, in a genus in slower water in streams than that of *Fontinalis* and where scrapers are less dependent on it for food. Photo by Hermann Schachner, through Creative Commons.

Špoljar *et al.* (2012) found that when the bryophyte coverage was scattered the diversity of algae, protozoa, and meiofauna was governed by the amount of suspended organic matter and epiphytes. They concluded that this was the result of enrichment by seston travelling downstream. One can assume that bacteria are associated with this seston (Bowden *et al.* 2017), but what is their role? Are the bacteria food themselves, or are they only important in releasing nutrients from the seston?

Heino *et al.* (2015) examined the metacommunity structure by surveying the diatoms, bacteria, bryophytes, and invertebrates in three drainage basins in Finland. The species were mostly distributed independently of one another in the southernmost drainage basin, but in the northernmost drainage basin there were discrete community types. These relationships seem only to be related to geography and not to environmental heterogeneity. They suggested that environmental variables may vary between organismal groups.

Stream conditions would seem to be ideal for many kinds of bacteria. The constant supply of sediments that get carried during times of rapid flow are trapped by the bryophytes, where these sediments can accumulate. But what protections do the stream bryophytes have against this potential associated bacterial onslaught? Basile *et al.* (1998) used an acetone extract to assess the bacterial activity of the stream moss *Platyhypnidium riparioides* (Figure 23) against 11 strains of bacteria. They found that this extract was active against some Gram-negative strains. Are these antibacterial properties effective against the bacteria that normally inhabit this moss? Most of the testing has been with human pathogens, but early assessments did not determine the natural bacterial flora of the mosses.

What quickly becomes evident by these studies is that we know little about the bryophyte bacteria and their role in the stream ecosystems. Meyer *et al.* (2007) commented that whereas we have an understanding of stream fungal diversity and know that fungi are critical to the organic matter dynamics and food webs in headwater streams, we know little about bacterial diversity.



Figure 23. *Platyhypnidium riparioides*, a stream moss with antibacterial activity against 11 strains. Photo by J. C. Schou, with permission.

Demars *et al.* (2020) showed that addition of carbon caused a rapid increase in both photosynthesis and heterotrophic respiration in a stream. In the control stream, with no added carbon, the carbon exchange between the autotrophs and bacteria accounted for ~49% of the bacterial production and 37% of the net primary production during periods of stable flow. The researchers considered the bryophyte contribution to primary productivity to be negligible, so they did not include them in their food flow calculations. Furthermore, the added sucrose (carbon) in the experiment did not end up in the bryophytes. It is likely that such carbon exchange between the bacteria and bryophytes in an important occurrence when the predominant autotrophs are bryophytes.

Yakubik *et al.* (2000) noted that some bacteria in bryophyte mats contribute to denitrification. This can be accentuated in lower reaches of a stream where the water is slower. This lower flow rate results in less mixing and permits the bacteria to colonize the mosses more easily, and provides a longer residence time for the denitrification to occur.

On the other hand, Leppänen (2013) demonstrated that N_2 fixation can occur in association with *Fontinalis dalecarlica* (Figure 1), although the rates are low. The highest activity was in the upper, green portion, compared to the lower, brown portion of the plants. In boreal forest streams in Finland, it oxidized CH_4 at the highest rate among the boreal mosses investigated, which included peatland and feather mosses. It seems certain that the N_2 fixation is dependent on an external energy source and is closely connected with the oxidation of CH_4 . But N fixation must take place in an oxygen-free environment. As much as 74% of this fixation is tied to the *nifH* sequences best identified as the bacterium *Methylocystis* (Figure 24). This evidence, coupled with the high CH_4 rates, suggests that *Fontinalis dalecarlica* is important in the CH_4 of boreal rivers. The bacteria are located on the leaf, in the cavity between the leaf and stem, but can also occur inside the outer stem cells. There is a mucous-like substance in the cells of the moss that may be important in the relationship. Solheim *et al.* (2004) suggested that the mucous might result from or contribute to a symbiotic relationship between the bacteria and moss. On the other hand, Postgate (1998) suggested that it could be a protective strategy to create an anaerobic environment for the nitrogenase to work.

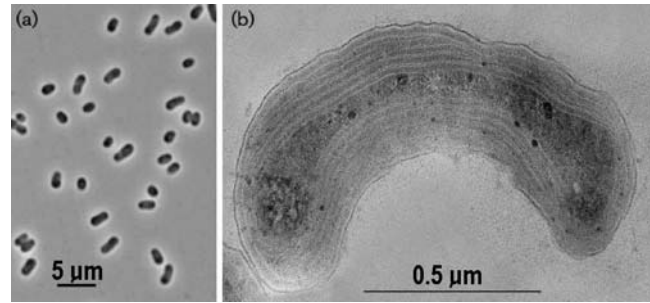


Figure 24. *Methylocystis bryophila* extracted from peat. **a.** Phase-contrast micrograph of cells. **b.** Electron micrograph of an ultrathin section of a cell. From Belova *et al.* 2013, with permission from Svetlana Dedys.

Martinez-Abaigar *et al.* (1993) evaluated the effects of organic pollution on the mosses *Fontinalis antipyretica* (Figure 20, Figure 21) and *Brachythecium rivulare* (Figure 25) and the leafy liverwort *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 26) in rivers in Spain. They suggested that the morphology of the bryophytes influenced the sensitivity to the pollution, resulting from differences in their ability to capture suspended organic materials (Figure 20). This organic matter promotes the growth of bacteria and their ability to degrade and cause senescence in the bryophytes.



Figure 25. *Brachythecium rivulare*, a species that captures organic materials that promote the growth of bacteria. Photo by Hugues Tinguy, with permission.



Figure 26. *Jungermannia exsertifolia* subsp. *cordifolia*, a species that captures organic materials that promote the growth of bacteria. Photo by Claire Halpin, with permission.

The leafy liverwort *Solenostoma vulcanicola* (Figure 27) exhibits rod-shaped bacteria associated with numerous holes in its cell walls, suggesting that bacteria play a role in its decomposition (Satake & Miyasaka 1984).



Figure 27. *Solenostoma vulcanicola* in Japan, a species with colonies of rod-shaped bacteria that create numerous holes in its cell walls. Photo by Masaki Shimamura, with permission.

Faunal Connections

Bryophytes can play a key role in food for stream nematodes (Dražina *et al.* 2014). Dražina *et al.* (2013) found that it is the suction-feeding nematodes that dominate among the stream bryophytes, the same group that is common among terrestrial mosses in Europe (Barbuto & Zullini 2006). The nematodes use their stylets to pierce the bryophyte cells and suck out the contents (Traunspurger 2002; Dražina *et al.* 2013). Other nematodes feed on the epiphyton and deposits associated with the bryophytes (Suren 1992; Majdi *et al.* 2011). Thus, not only do some stylet-feeding nematodes eat bryophytes, but bryophytes provide the substrate for detrital pathways for nematode food. Furthermore, uptake of bacterial-respired CO₂ by the bryophytes (and algae) finds its way into these photosynthetic bryophytes, thus increasing the food available to both stylet bryophyte-feeding nematodes and other invertebrates (Demars *et al.* 2021).

In contrast to many earlier studies, Demars *et al.* (2021) suggested that the aquatic bryophytes covered by periphyton might contribute to the macroinvertebrate diet, a suggestion already supported by some earlier researchers (Jones 1949; Dangles 2002; Parker & Huryn 2006; Carroll *et al.* 2016). This also contrasts with their earlier conclusion (Demars *et al.* 2020) that this bryophyte-periphyton association does not contribute much to primary productivity. Stream ecologists are beginning to rethink the role of bryophytes in streams.

Antarctic

Christie (1987) contrasted the nitrogen in a wet carpet and dry peat in the Antarctic. The numbers of sulphate-reducing bacteria [*Desulfovibrio* (Figure 28) and *Desulfotomaculum* (Figure 29) and of *Clostridium* (Figure 30) were very low, even in the wet carpet. The low acetylene reduction activity of these bacteria and absence of *Azotobacter* (Figure 31) suggest that nitrogen fixation was not an important contributor to nitrogen present. There

furthermore were no nitrifying bacteria. However, there were substantial numbers of proteolytic and nitrate-respiring bacteria as well as a small number of denitrifying bacteria. The heterotrophic groups were more abundant in the wet carpet than in the dry turf.

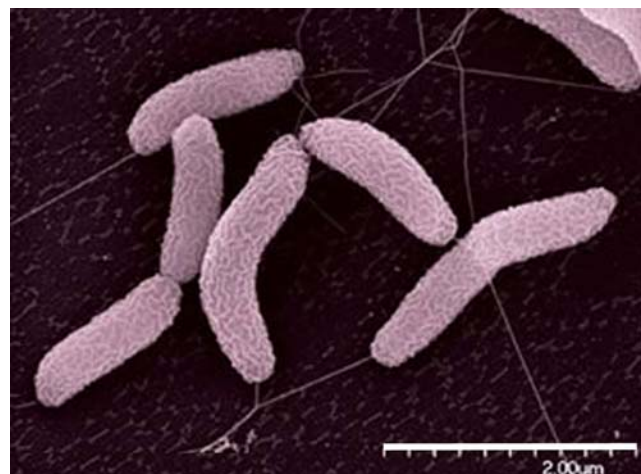


Figure 28. *Desulfovibrio desulfuricans*, a sulfate-reducing bacterium in a genus with low numbers in the Antarctic peat. Photo through public domain.



Figure 29. *Desulfotomaculum*, a sulfate-reducing bacterium with low numbers in the Antarctic peat. Photo by Manfred Rohde, through Creative Commons.

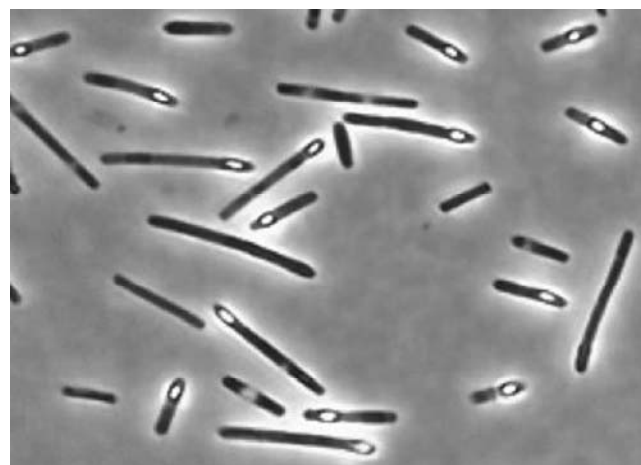


Figure 30. *Clostridium perfringens* sporulating, in a bacterial genus with low numbers in the Antarctic peat. Photo by Oregon State University, through Creative Commons.

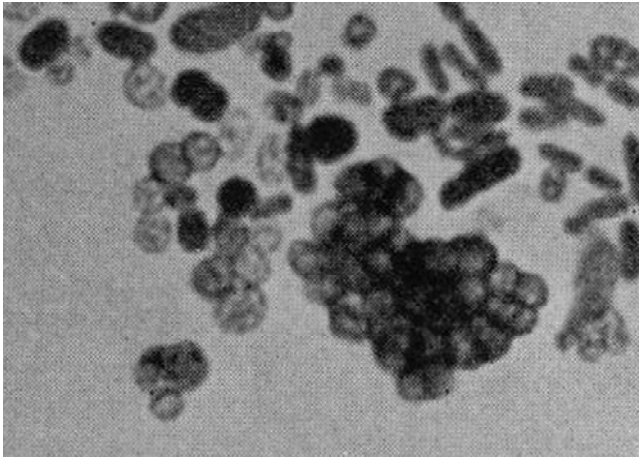


Figure 31. *Azotobacter*, a nitrogen-fixing bacterium that is absent in the Antarctic peat. Photo by Dan H. Jones, through public domain.

Park *et al.* (2013) investigated the neglected bacterial relationships among Antarctic bryophytes, using the moss *Sanionia uncinata* (Figure 32). They found that the *Pseudomonadota* was the dominant phylum, comprising 65.5% of the associated bacteria. The *Bacteroidota* (29.1%) and *Actinomycetota* (11.7%) were also important. The bacteria on the mosses exhibited zonation, with the *Alphaproteobacteria* comprising only 2% of the bacterial flora in the upper green parts, but were in significantly greater proportion at 22.2% in the lower brown portions. Park and coworkers considered it likely that there were specific relationships between these endophytes and the host moss.



Figure 32. *Sanionia uncinata*, a species with *Proteobacteria* comprising 65.5% of the associated bacteria in an Antarctic study. Photo by Hermann Schachner, through Creative Commons.

Raymond (2016) answered a question I raised earlier, before reading this – Is it the bryophyte or the bacterium that produces the external ice-binding proteins? A strong ice-pitting activity was known in the Antarctic moss *Bryum argenteum* (Figure 33). Raymond realized that this was a sign of ice-binding proteins that protect against freezing damage. He found that this ice-binding activity is the result of ice-binding proteins produced by bacteria living on the moss leaves. These were mostly

Actinomycetota and *Bacteroidota*. He found 42 bacterial ice-binding proteins. These operate in a symbiotic relationship with the moss, with the latter providing the sustaining energy source and the bacteria protecting the moss from freezing damage.



Figure 33. *Bryum argenteum*, an Antarctic moss with a strong ice-pitting activity. Photo by Claire Halpin, with permission.

Arctic Alpine

Löffler *et al.* (2008) found that an increase in the occurrence of bryophytes and shrubs along an arctic-alpine gradient in Scandinavia would also increase the microbial activity. They also found that higher temperatures promoted greater soil microbial activity in the summer. Whereas these temperatures are expected to promote shrub growth as the climate warms, the higher moisture expected with climate change is expected to promote bryophyte growth. Both temperature and moisture increases should increase the microbial activity in the soil in heathlands in Scandinavia. Spruce forests (Figure 34) had the highest bacterial α -diversity, whereas the aspen forests (Figure 35) exhibited greater turnover (β -diversity) and higher γ -diversity.



Figure 34. *Picea mariana* in Alaskan taiga, a forest type that had the highest bacterial α -diversity in Scandinavia. Photo from NOAA, through public domain.



Figure 35. *Populus tremuloides* (aspen), a forest type that had the highest turnover (β -diversity) and higher γ -diversity of microbes in Scandinavia. Photo by Famartin, through Creative Commons.

Boreal Forest

The boreal forest bryophyte bacterial communities have thus far been widely neglected. Only the **Cyanobacteria** (Figure 36) have attracted the attention of researchers. They will be covered in a separate chapter, but their relative role needs to be clarified here.



Figure 36. *Chroococcus*, one of the common **Cyanobacteria** associated with *Sphagnum*. Photo by M. Lorenz, through Creative Commons.

In boreal forests in Finland and elsewhere, the feather mosses *Hylocomium splendens* (Figure 37) and *Pleurozium schreberi* (Figure 38) predominate (Leppänen 2013). The N fixation activity associated with these mosses is well known (Meeks 1998; DeLuca *et al.* 2002; Gundale *et al.* 2012). As in *Fontinalis dalecarlica* (Figure 1), Gavazov *et al.* (2010) found higher nitrogen fixation in the upper portions of *Hylocomium splendens*. This suggests that light has an important role in the fixation (Meeks 1998; Gundale *et al.* 2012), implicating **Cyanobacteria**. But in the boreal forests of Finland, there was no significant amount of methane (CH_4) oxidation activity, a phenomenon that Leppänen (2013) attributed to

the low concentrations of CH_4 in the forest habitats and moisture conditions that are unsuitable for methanotrophs (Larmola *et al.* 2010). Since methane oxidation is often accompanied by nitrogen fixation, this leaves us wondering which organisms are contributing to these higher levels of nitrogen fixation in younger portions of the mosses.



Figure 37. *Hylocomium splendens*, a boreal forest feather moss that is important in hosting bacteria that fix nitrogen. Photo by Clare Halpin, with permission.



Figure 38. *Pleurozium schreberi*, a moss shown to be less important in driving bacterial communities in the boreal forest than the forest type. Photo by Hugues Tinguay, with permission.

DeLuca *et al.* (2002) reported that the **Cyanobacteria** (Figure 36) association with *Pleurozium schreberi* (Figure 38) alone fixes $1.5\text{--}2.0 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in the mid to late successional forests of northern Scandinavia and Finland. Gavazov *et al.* (2010) found that liverworts did not fix detectable amounts of N_2 in the boreal/sub-Arctic forests. Lichens had the highest rates of fixation, but because of their greater biomass, the mosses served as the nitrogen sink through their nitrogen fixation associations.

Rodríguez-Rodríguez *et al.* (2022) hypothesized that moss species would be the driver in the composition of the ecologically important bacterial communities associated with them. They quantified changes in bacterial communities as a function of host species [mosses *Pleurozium schreberi* (Figure 38) and *Ptilium crista-castrensis* (Figure 39)] and forest type [coniferous black spruce (Figure 34) versus deciduous broadleaf trembling

aspen (Figure 35)] in eastern Canada. But in fact, it was forest type, not moss host species, that was the main factor affecting bacterial community composition on the mosses.



Figure 39. *Ptilium crista-castrensis*, a moss shown to be less important in driving bacterial communities in the boreal forest than the forest type. Photo by M. Porcius Cato, through Creative Commons.

Among these boreal bryophytes, at least some of the nitrogen fixation seems to occur without the activity of **Cyanobacteria** (Figure 36), as for example associations with members of *Dicranum* (Gundale *et al.* 2011). *Pleurozium schreberi* (Figure 38) and *Sanionia uncinata* (Figure 32) exhibited relatively similar mean rates of N_2 -fixation ($46.1 \mu\text{g N g}^{-1} \text{ day}^{-1}$ and $52.4 \mu\text{g N g}^{-1} \text{ day}^{-1}$ respectively), despite a dominance of **Alphaproteobacteria** N_2 -fixers 21.4% vs 6.8% **Cyanobacteria**) on *Pleurozium schreberi* and a dominance of **Cyanobacteria** (79%) on *Sanionia uncinata*, with only 7.2% **Alphaproteobacteria** as N_2 -fixers (Holland-Moritz *et al.* 2018).

Holland-Moritz *et al.* (2018) indicated that the moss microbiome in the boreal forest is highly diverse, includes many undescribed taxa (including an undescribed phylum), and is a major contributor to nitrogen fixation beyond that from the **Cyanobacteria**. The average richness is 924 phylotypes per sample, dominated by 8 bacterial phyla: **Pseudomonadota** (44.8% of reads across all samples), **Acidomycetota** (10.8%), **Verrucomicrobiota** (9.8%), **Bacteroidota** (9.3%), **Cyanobacteria** (6.5%), **Candidate phyla WPS-2** (5.7%), **Planctomycetota** (5.2%), and **Actinomycetota** (4.2%). Cutler *et al.* (2017) found similar relative abundances on *Pleurozium schreberi* (Figure 38). Many of these bacteria are novel and undescribed lineages within the **Alphaproteobacteria** sub-phylum and the **Verrucomicrobiota** phylum (Bragina *et al.* 2015).

But many of the boreal forest phylotypes could not be classified beyond phylum or class (Holland-Moritz *et al.* 2018), emphasizing how little we know about these communities. Contrasting with the study of Rodríguez-Rodríguez *et al.* (2022) in eastern Canada, the identity of the moss species was more important than the site in

determining the composition of the bacterial communities associated with the mosses near Fairbanks, Alaska, USA, with moss species accounting for 63% of the variation in bacterial community composition. The pleurocarpous moss *Sanionia uncinata* (Figure 32) had communities quite distinct from those of the other 6 moss species [*Pleurozium schreberi* (Figure 38), *Tomentypnum nitens* (Figure 40), *Aulacomnium palustre* (Figure 41), *A. turgidum* (Figure 42), *Dicranum elongatum* (Figure 43), and *Sphagnum capillifolium* (Figure 44)]. Of the bacteria on *Sanionia uncinata*, 59% were unique to that moss species. Only 77% of the 30 most abundant phylotypes present on the other mosses were present on *S. uncinata*, whereas 90% of the 30 most abundant phylotypes were found on all the other moss species.



Figure 40. *Tomentypnum nitens*, a species of fen mosses with bacteria that are similar to most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Hermann Schachner, through Creative Commons.



Figure 41. *Aulacomnium palustre*, a species of fen mosses with bacteria associates that are similar to those of most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Kristian Peters, through Creative Commons.



Figure 42. *Aulacomnium turgidum*, a species of fen mosses with bacteria that are similar to those of most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Mark Hill, with permission.



Figure 43. *Dicranum elongatum*, a species of fen mosses with bacteria that are similar to those of most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Hermann Schachner, through Creative Commons.



Figure 44. *Sphagnum capillifolium*, a species of fen mosses with bacteria that are similar to those of most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Blanka Aguero, with permission.

The moss-associated bacteria are likely to be anoxygenic phototrophs capable of carbon fixation via Rubisco, with an ability to utilize by-products of photorespiration from hosts via a glyoxylate shunt (Holland-Moritz *et al.* 2018). Furthermore, whereas most of the mosses were dominated by **Acetobacteraceae** (**Alphaproteobacteria**), **Acidobacteriaceae** (**Acidobacteriota**), and **Methylophilales** (**Verrucomicrobiota**), *Sanionia uncinata* (Figure 32) had either a low abundance or total absence of these bacterial taxa. It was dominated instead by **Comamonadaceae** (**Betaproteobacteria**), **Nostocaceae** (**Cyanobacteria**), and **Chitinophagaceae** (**Bacteroidota**). But why are these communities on *Sanionia uncinata* so different? Is it differences in microhabitat, or are the chemical defenders of these mosses different?

In an attempt to predict the effect of climate change on nitrogen fixation in the boreal forest, Gundale *et al.* (2012) assessed the effects of elevated temperatures on the relationship between bacteria and the feather moss substrate. They surmised that *Pleurozium schreberi* (Figure 38) may become a larger source of N in boreal forests relative to *Hylocomium splendens* (Figure 37) as climate warming progresses. Although the feather mosses have been considered to be cyanobacterial hosts, it is quite possible that these are also accompanied by Methanobacteria or other forms of non-cyanobacterial bacteria that are able to fix atmospheric nitrogen.

De Long *et al.* (2016) found that global warming altered the microbial communities in the soil, favoring communities based on bacteria. These, however, were mediated by mosses and shrubs, varying with successional stage. Mosses can serve as a buffer, like a heavy quilt, in modifying the soil temperature, as well as slowing the loss of moisture from the soil.

Peatland Bacterial Flora

Peatlands (Figure 45), often dominated by *Sphagnum* (Figure 46) as the keystone species, contain dead plant material accumulated over thousands of years (Kamal & Varma 2008). This habitat covers ~5-8% of the world's surface and contains ~3-3.5 times the amount of carbon stored by tropical rainforests. Weston *et al.* (2015) noted the importance of *Sphagnum* as a keystone species in a habitat that holds more than one-third of the terrestrial carbon on the planet Earth.



Figure 45. Peatland in Estonia. Photo by Martin Küttim, through Creative Commons.



Figure 46. *Sphagnum* spp. in Estonia. Photo by Martin Küttim, through Creative Commons.

In this role, *Sphagnum* (Figure 46) plays an important role, along with its associated microbiome, in carbon and nitrogen cycling (Kamal & Varma 2008). The combination of high acidity, low temperatures, and extremely low concentrations of nutrients in many *Sphagnum* habitats suggests that we should find unique communities of bacteria associated with these bryophytes.

Kostka *et al.* (2016) noted that *Sphagnum* (Figure 46) displays a diverse community of microorganisms on its surface and within the tissues. The prokaryotes and fungi can act as mutualists, symbionts, or antagonists. In these roles, methanotrophic and nitrogen-fixing bacteria may provide up to 20-30% of *Sphagnum* carbon and nitrogen.

Methane Oxidation

The production of methane (CH₄) in peatlands has become a hot topic recently because of its potential role in global warming. Wetlands, including peatlands, are the largest natural sources of atmospheric methane (Raghoebarsing *et al.* 2005). Nevertheless, most of the methane formed in wetlands stays in wetlands, where it is recycled. *Sphagnum* (Figure 46) species in peatlands use this methane through symbiosis with partly endophytic methanotrophic bacteria. These bacteria occur both on the stem leaves and in the hyaline cells of the *Sphagnum*. The methane is rapidly oxidized by the bacteria to form CO₂ that is then fixed by the *Sphagnum* in photosynthesis and ultimately into plant sterols. The methane, through this pathway, provides 10-15% of the carbon source for *Sphagnum*.

Nevertheless, peatlands are a major source of methane (Larmola *et al.* 2010). But *Sphagnum*-dominated peatlands (Figure 45) have lower methane emissions than those known for other mire types. These researchers found that all 23 species of *Sphagnum* (e.g. Figure 46) in a boreal mire supported methanotrophic bacteria. Furthermore, transplanted *Sphagnum* with no indication of these methanotrophic bacteria exhibited the bacteria in their new

location, showing rapid movement and/or activation of the bacteria among the *Sphagnum*, and the importance of habitat. Water level is important in regulating the methane oxidation. The methanotroph *Methylocystis* (Figure 24) was present with *Sphagnum* plants that exhibited both active and inactive in methane oxidation, suggesting that its activity depended on water availability. Larmola and coworkers concluded that there is a loose symbiosis between the *Sphagnum* species and methanotrophic bacteria that contributes to 10-30% of the *Sphagnum* carbon.

In 2013, Belova *et al.* discovered a new species of *Methylocystis*, *M. bryophila* (Figure 24), that could convert methane to CO₂ and could also fix nitrogen. This species was isolated from an acidic *Sphagnum* (Figure 46) peat-bog lake in Germany and from a peat bog in northern Russia. They attributed the nitrogen-fixing capability to an aerotolerant nitrogenase.

The most abundant methanotrophs in peatlands typically are **Alphaproteobacteria** and **Gammaproteobacteria** (Kip *et al.* 2010). Within the hyaline cells, *Sphagnum* hosts other bacteria that decrease the O₂ concentration and increase the CO₂ concentration in these cells (Granhall & Hofsten 1976), thus favoring photosynthesis in the nearby photosynthetic cells and benefitting the **Cyanobacteria** living in the hyaline cells. These **Cyanobacteria** fix N₂ that could be used by both the moss and the other bacteria (Leppänen 2013). But *Sphagnum* (Figure 46) can also house methanotrophic bacteria in these same cells, and these bacteria are capable of N₂ fixation as well. These methanotrophic bacteria can provide up to 30% of the carbon in the moss (Raghoebarsing *et al.* 2005) because they can fix nitrogen and oxidize CH₄ at the same time (Leppänen 2013). Most of the N₂ is fixed in the dark in aerobic conditions in the peat, indicating activity of heterotrophic bacteria (Kravchenko & Doroshenko 2003).

Nitrogen Sources

Aldous (2002) demonstrated that atmospheric nitrogen deposited among *Sphagnum* (Figure 46) plants was translocated to the capitula, with 11% to >80% in the lower and higher influx sites, respectively. Gerdol *et al.* (2006) noted that *Sphagnum papillosum* (Figure 47-Figure 48) was able to grow more when it had higher capitulum N concentrations. Both research groups noted that high water level favored the movement. Gerdol *et al.* (2006) found that the microbial nitrogen fixers were able to increase the nitrogen in the *Sphagnum* peatland. As with atmospheric nitrogen sources, these bacteria (no **Cyanobacteria** found) that occurred in senescing plant tissues, followed by upward transport of the fixed nitrogen, positively affected the growth of *Sphagnum papillosum*. In dry growing seasons, enhancement of fixed nitrogen in the rhizosphere promoted growth of tracheophytes that subsequently increased their competition against the *Sphagnum*. Experimental additions of nitrogen benefitted the *Sphagnum* only when the growing conditions inhibited the bacterial colonies.



Figure 47. *Sphagnum papillosum* in a peatland; microbial nitrogen fixers in senescing cells of this species are able to increase the nitrogen and benefit growth. Photo from Botany Website, UBC, with permission.



Figure 48. *Sphagnum papillosum*, a species positively affected by increased nitrogen that is often contributed by bacteria. Photo by David T. Holyoak, with permission.

Bragina *et al.* (2013) found that genes for nitrogenase were both high in abundance and diverse among the *Sphagnum* (Figure 46). These were usually specific for each *Sphagnum*. The methanotrophs, on the other hand, exhibited highly similar patterns among species. The sporophyte of the *Sphagnum* had a high proportion of specific **diazotrophs** (organisms able to grow without external sources of fixed nitrogen) (4%) but lacked methanotrophs. The nitrogen-fixing bacteria were highly specific and were transferred with the sporophyte.

Waughman and Bellamy (1980) found that nitrogen fixation rates were lower at the nutrient extremes, with that in bogs being especially low. The highest activity measured was $>100 \text{ nmol C}_2\text{H}_4 \text{ mL peat}^{-1} \text{ d}^{-1}$. Nitrogenase activity had a positive correlation with pH and K and a negative correlation with Ca. Lower latitudes have a greater nitrogenase activity in peat than do higher latitudes, even when temperatures are factored in. In the south German mires the nitrogen fixed annually by the heterotrophic bacteria were 2100 mg N m^{-2} in fens, 530 in poor fens, and 70 in bogs.

Comparisons of *Sphagnum* Species

Bragina *et al.* (2012) compared the communities of bacteria on *Sphagnum fallax* (Figure 49) and *S. angustifolium* (Figure 50), two closely related species with distinct habitat nutrient preferences in weakly acid, mesotrophic situations influenced by minerotrophic groundwater. The two species also produce similar secondary metabolites. The two species exhibited high similarity (minimum of 95.5%) of bacterial colonization patterns. The interior of hyaline cells of the leaves were colonized primarily by **Alphaproteobacteria** (in **Pseudomonadota**). This group of bacteria was represented by a high degree of diversity, including *Acidocella*, *Acidisphaera*, *Phenylobacterium*, and *Rhodopila* as the major bacterial taxa on both species of *Sphagnum*, with no statistically significant differences between the microbial communities of the two *Sphagnum* species. The composition of the subdominant **Caulobacteraceae** did, however, vary between mosses, being more abundant with *S. fallax*. In this group *Phenylobacterium* was detected all over, whereas *Caulobacter* (Figure 51), *Gluconacetobacter* (Figure 52), *Methylocystis* (Figure 24), *Methylosinus*, and *Rhizobium* (Figure 53) occurred only with *S. fallax*. The associated microbial community fulfills functions that can only be accomplished by the cooperation with the *Sphagnum* community. These include nitrogen fixation, solubilizing phosphorus, and providing carbon from peat-derived methane (Raghoebarsing *et al.* 2005; Opelt *et al.* 2007c). Bragina and coworkers considered the moss-bacterial communities to have the same close relationships that are present between *Sphagnum* and the ecology and function of the bog ecosystem.



Figure 49. *Sphagnum fallax*, a species of weakly acid mesotrophic habitats with mostly **Verrucomicrobiota** and **Planctomycetota** as bacterial associates. Photo by Hugues Tinguy, with permission.



Figure 50. *Sphagnum angustifolium*, a species that grows in weakly acid, mesotrophic situations influenced by minerotrophic groundwater. This species is colonized by a highly diverse group of **Alphaproteobacteria** in the hyaline cells of the leaves. Photo by Hermann Schachner, through Creative Commons.



Figure 51. *Caulobacter crescentus*, in a genus that occurs with *Sphagnum fallax*, but not with *S. angustifolium*. Photo by USDA, through public domain.



Figure 52. *Gluconacetobacter* cellulose biofilm, a genus that occurs with *Sphagnum fallax*, but not with *S. angustifolium*. Photo through Creative Commons.

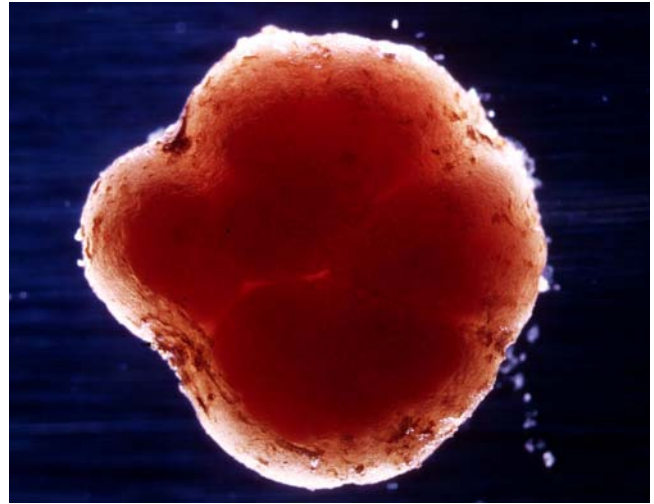


Figure 53. *Rhizobium* bacteria nodule, a genus that occurs with *Sphagnum fallax*, but not with *S. angustifolium*. Photo from CSIRO, through Creative Commons.

Bragina *et al.* (2012) also compared the bacterial diversity on *Sphagnum divinum* or *S. medium* (previously considered part of *S. magellanicum*) (Figure 54) and *S. fallax* (Figure 49) in three alpine bogs in Austria. *Sphagnum divinum/medium* characterizes strongly acid habitats with poor nutrients, whereas *S. fallax* inhabits weakly acid mesotrophic habitats. *Sphagnum divinum/medium* was inhabited mainly by **Gammaproteobacteria** (in Phylum **Pseudomonadota**), whereas associates of *S. fallax* (Figure 55) were mainly in the phyla **Verrucomicrobiota** and **Planctomycetota**. Although the bacterial colonies occurred in high abundance in the dead hyaline cells, they were always connected with living photosynthetic cells (Figure 55). Bragina and coworkers found that nutrient richness and pH were the most important determining factors for bacterial communities. They found it interesting that the bacterial diversity was transferred from the sporophyte to the gametophyte, contrasting with the transfer from the soil in tracheophyte communities. Microbial fingerprints showed that bacterial species from different bogs had a high similarity within the same bryophyte species. They considered the plant to plant transfer of bacteria, rather than through a soil intermediary, to be a possible explanation of the high specificity of *Sphagnum*-associated bacteria over long distances.



Figure 54. *Sphagnum cf. divinum*, a species of strongly acid habitats with poor nutrients, and mostly with **Gammaproteobacteria**. Photo by Michael L  th, with permission.

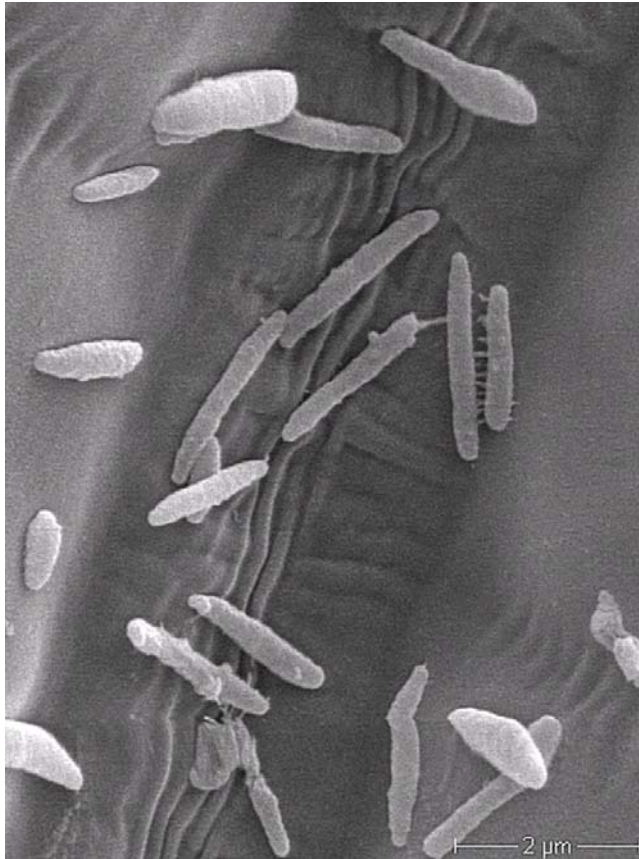


Figure 55. *Sphagnum fallax* bacteria SEM. Photo courtesy of Gabi Berg.

Shcherbakov *et al.* (2015) isolated bacterial populations from gametophytes of *Sphagnum* (Figure 54) from various geographic regions of Russia. Among the more than 400 strains isolated, ribosomal data indicated that the isolates were in the genera *Pseudomonas* (Figure 13) (20-57%), *Collimonas* (7-10%), *Flavobacterium* (Figure 56) (6-8%), *Burkholderia* (Figure 57) (5-6%), and *Serratia* (Figure 58) (3%). These are similar to the bacteria taxa reported for *Sphagnum* from the Austrian Alps (Bragina *et al.* 2015).



Figure 56. *Flavobacterium columnare* on gills of *Delistes luxatus*; this bacterial genus is common on Russian *Sphagnum*. Photo by S. Vanderkoo, through Creative Commons.

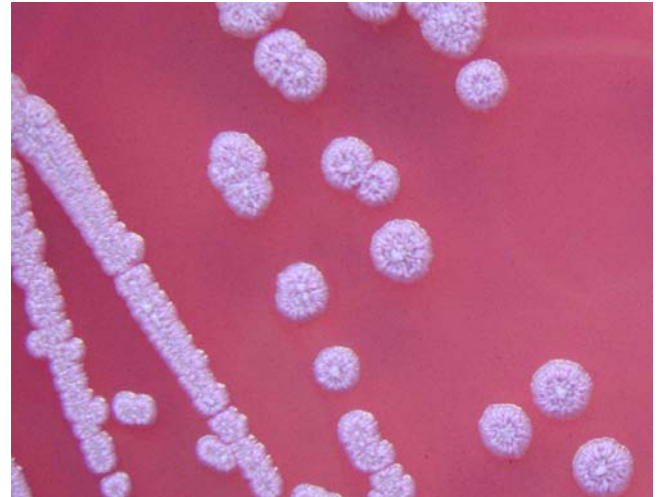


Figure 57. *Burkholderia pseudomallei*, in a genus of bacteria that are antagonistic toward bryophytes in Germany. Photo by Gavin Koh, through Creative Commons.



Figure 58. *Serratia marcescens* antibiogram, in a genus among the most common antagonists toward bryophytes in Germany. Photo by Stefan Walkowski, through Creative Commons.

Tian *et al.* (2019) compared the microbial community associated with the brown (lower) and green portions of *Sphagnum palustre* (Figure 59) peat. Alphaproteobacteria (in phylum Pseudomonadota) were dominant in all samples. Members of the phylum Acidobacteriota were abundant in the *S. palustre* peat, whereas Gammaproteobacteria (in phylum Pseudomonadota) dominated the brown layer. Cyanobacteria dominated the green portion. They considered the structural differences in the microbiome to be mainly due to microhabitat differences. The microbial communities of the *Sphagnum palustre* peat was significantly influenced by the water table and the total nitrogen content.



Figure 59. *Sphagnum palustre*, a species where **Alphaproteobacteria** is very frequent; **Gammaproteobacteria** dominates in the lower brown layer. Photo by Hugues Tinguy, with permission.

Opelt *et al.* (2007a, b) explored the bacterial relationships with *Sphagnum divinum/medium* (Figure 54) and *S. fallax* (Figure 49) from three locations in Germany and three in Norway. They particularly looked for bacteria that exhibited antagonistic activity against fungal pathogens; these comprised 48% of the isolates. *Sphagnum divinum/medium* housed 24% of the antagonists compared to only 19% for *S. fallax*. Nevertheless, *S. fallax* bacterial communities exhibited a significantly higher diversity $\{H' = -\sum_{i=1}^s [(n_i/N)\ln(n_i/N)]\}$ than did the *S. divinum/medium* associates. More of the inhabitants of *S. divinum/medium* were specific to that species. The researchers suggested that the higher nutrient levels in the *S. fallax* habitat could explain the higher bacterial diversity.

Most of the antagonists in the Germany/Norway study were in the genera *Serratia* (Figure 58) (15%), *Burkholderia* (Figure 57) (13.5%), *Staphylococcus* (Figure 7) (13.5%), and *Pseudomonas* (Figure 13) (10%) (Opelt *et al.* 2007a). Whereas most of the antagonist strains had a high moss specificity, *Burkholderia* and *Serratia* had similar molecular fingerprints on both *Sphagnum* (Figure 49, Figure 54) species. A high proportion of the antagonist strains [*Hafnia* (Figure 60), *Pantoea* (Figure 61), *Staphylococcus*, and *Yersinia* (Figure 62)] are known as facultative pathogens of humans.



Figure 60. *Hafnia alvei*, in a genus of bacteria that is antagonistic toward bryophytes in Germany and also a facultative pathogen of humans. Photo by Antoine2003, through Creative Commons.

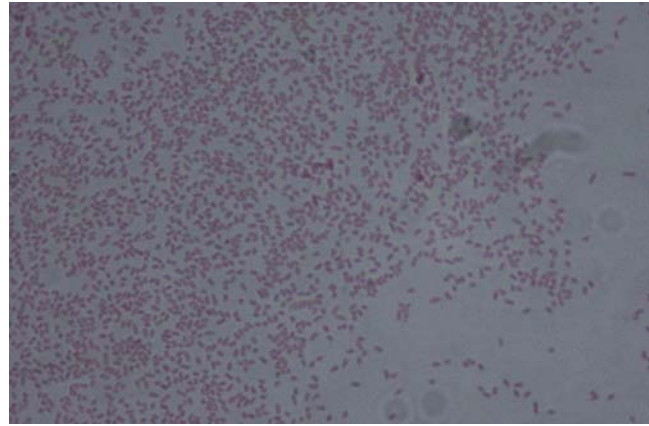


Figure 61. *Pantoea agglomerans* Gram stain, in a genus of bacteria that is antagonistic toward bryophytes in Germany and also a facultative pathogen of humans. Photo by Dr. Sahay, through Creative Commons.

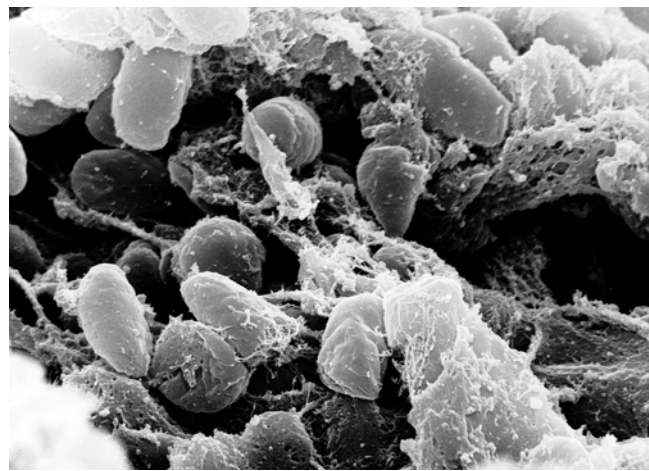


Figure 62. *Yersinia pestis* in gut of flea, in a genus among the most common antagonists toward bryophytes in Germany. Photo from CDC, through Creative Commons.

Antibiotic Role

Bacteria associated with bryophytes often serve as protectors, providing the antibacterial or antifungal compounds needed to protect the bryophytes. Whereas Opelt *et al.* (2007c) found a high proportion (26%) of antifungal bacteria, they found only 0.4% antibacterial strains. Among these antagonists, there was a high diversity of *Burkholderia* (Figure 57) isolates in the **endophytic** (living within cell) and **ectophytic** (living on plant surface) habitats of *Sphagnum* (Figure 49, Figure 54). The researchers suggested that these antagonistic bacteria could account for the high level of antimicrobial activity of *Sphagnum*. It seems likely that the high level of antimicrobial compounds in at least some *Sphagnum* species could account for the specificity of the bacteria that grow there. The researchers also found a high diversity of nitrogen-fixing bacteria, especially inside *Sphagnum*.

Because of these antagonistic properties, Sarolta *et al.* (2010) sought new types of medically useful antagonists in the Borsáros Raised Bog in Romania. They explored the communication forms that make the bacterial antagonism successful, analyzing the biofilm formation of single strains and co-cultures.

Szentes *et al.* (2011) found that rhizobacteria produced plant-growth-promoting substances that interacted in various ways, including competing with pathogens for nutrients. This research team found *Bacillus* (Figure 10-Figure 11), *Cedecea*, *Delftia* (Figure 63), *Lysinibacillus* (Figure 64), *Pseudomonas* (Figure 13), *Serratia* (Figure 58), *Stenotrophomonas* (Figure 65), and *Viridibacillus*. *Bacillus*, *Pseudomonas*, and *Serratia* were the dominant bacterial genera associated with bryophytes. *In vitro* cultures showed that a high number of the isolates inhibited the growth of fungal and bacterial plant pathogens such as *Pectobacterium carotovorum* (Figure 66) or produced secondary metabolic substances with biocontrol properties. *Serratia fonticola* BB17 (see Figure 58) and *Pseudomonas fluorescens* (Figure 67) BE8 were the most efficient against plant pathogens, with effectiveness up to 48.28% and 55.17% respectively.

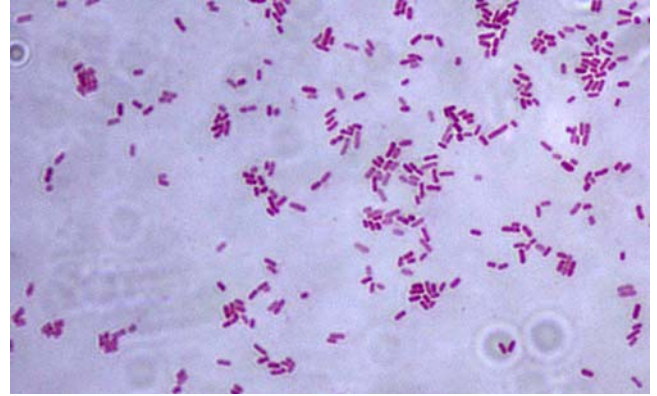


Figure 65. *Stenotrophomonas maltophilia*, in a genus that can be among the dominant bacteria associated with bryophytes in peatlands. Photo by Riraq25, through Creative Commons.

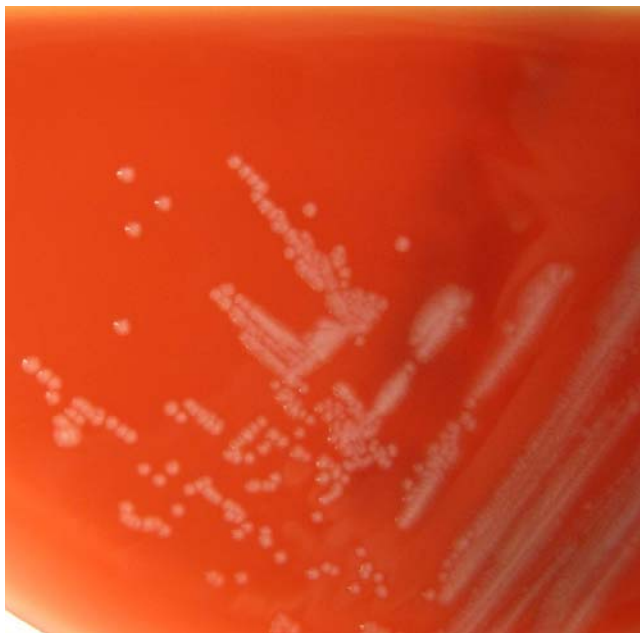


Figure 63. *Delftia*, a genus that can be among the dominant bacteria associated with bacteria. Photo by mostly harmless, through Creative Commons.



Figure 66. *Pectobacterium carotovorum*, a species that is inhibited by many bacterial isolates from bryophytes. Photo by Paul Bachi, through Creative Commons.

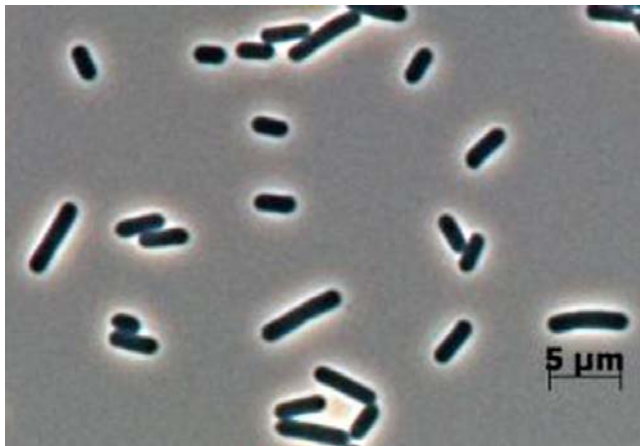


Figure 64. *Lysinibacillus*, a genus that can be among the dominant bacteria associated with bacteria. Photo from Leibniz-Institut DSMZ, through Creative Commons.

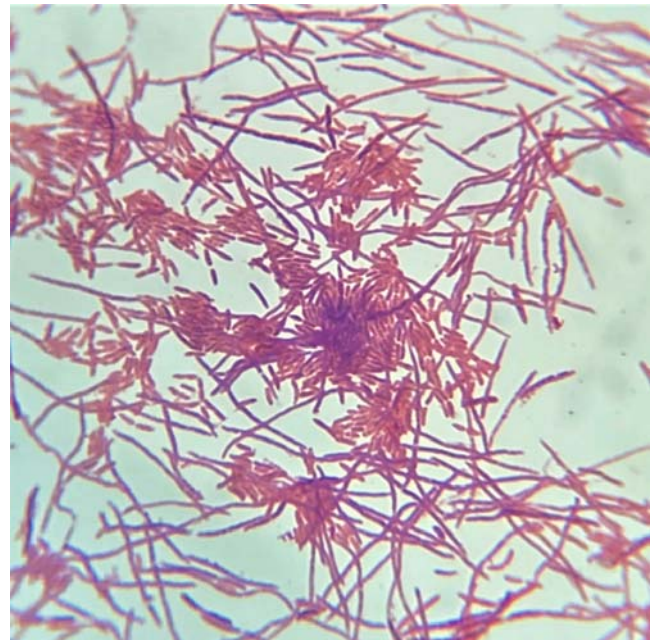


Figure 67. *Pseudomonas fluorescens* Gram stain, one of the most efficient bryophyte bacteria against plant pathogens. Photo by B. Domangue, through Creative Commons.

Ecosystem Roles

Robroek *et al.* (2021) approached the "rewiring" of peatland plant-microbe interactions and communities using a network approach. They found that the prokaryotic communities differed between sites. This was manifest in a more rapid turnover in the plant-microbial interactions than in the communities they inhabited. They found that the turnover in the bacterial network composition was driven mostly by the establishment of new interactions between the plant community and that of the microorganisms, a phenomenon that was shared among all the sites.

Wicaksono *et al.* (2021a, b) produced evidence that the tracheophytes tended to have specific bacteria, whereas the bryophytes presented greater bacterial species richness and diversity. Nevertheless, Bragina *et al.* (2015) was able to demonstrate that the plants and lichens of bogs shared a core microbiome over the entire ecosystem, forming a transkingdom metacommunity. All of these bog organisms are connected to the keystone *Sphagnum* (Figure 49, Figure 54) species through the microbial species such as *Burkholderia bryophila* (see Figure 57). This bacterial species was associated with a wide array of host plants and provides a beneficial plant-microbe interaction.

Bragina *et al.* (2014) were among the early researchers attempting to unravel the roles of the symbiotic and protocoeoperation effects of the *Sphagnum* (Figure 49, Figure 54) microbiome. It appears that the microbiome is important in facilitating survival in the extreme conditions found in the *Sphagnum* habitats. The microbiome provides abundant subsystems that facilitate coping with oxidative and drought stresses, resistance to detrimental environmental factors, repair, and self-controlling mechanisms. Microbe-microbe and plant-microbe interactions are important in biofilm formation, interaction via quorum sensing (see Chapter 19-1 of this volume), and nutrient exchange. Their involvement in the nitrogen cycle and recycling of organic material are important contributions to the nutrient supply.

In addition to the products produced by the bacteria that are associated with *Sphagnum* (Figure 49, Figure 54), the bacteria can alter the response to a change in physical growth conditions as well. With the threat of global warming looming over the cold-climate peatlands, the ability of bacteria to rapidly acclimatize may promote the survival of *Sphagnum* through host-microbiome acquired thermotolerance (Carrell *et al.* 2021). First the researchers showed that elevated temperatures decreased the growth of sterile *Sphagnum* without addition of microbes. The addition of a microbiome from a thermal habitat matching the experimental temperatures returned the *Sphagnum* to its pre-warming growth rates. Warming changed the structure of the microbiome and induced a plant heat shock response. They suggested that the thermally conditioned microbiomes provided thermal conditioning to the *Sphagnum* host. The same results occurred when the microbiomes were isolated from *Sphagnum* warming experiments in Iceland, Sweden, and France.

But we may have barely scratched the surface of the interactions in the peatland community. As reported by Dedysh (2011) in her review, these uncultivated and unidentified bacteria form a large proportion of the microbial communities in acidic, cold, nutrient-poor, and water-saturated peatlands, hiding from us unknown physiologies and roles in the peatland ecology. New genetic techniques are permitting us to enumerate the number of strains present, and our culturing techniques are improving for these more elusive organisms.

Decomposition

Sphagnum litter has a very slow decomposition, with first year loss of mass ranging 0.1-25% (Clymo 1965; Aerts *et al.* 2001; Scheffer *et al.* 2001; Dedysh 2011). This has been attributed to acidity (that favors fungi more than bacteria), phenolic compounds and waxes (mostly from shrubs) that are highly resistant to decay (Verhoeven & Liefveld 1997; Dedysh 2011), low nutrient content, especially N and P in *Sphagnum*, low temperatures, and anoxic conditions (Dedysh 2011). When decay occurs, the end-products are transferred into methane. This methane diffuses into the living, aerobic parts of the peat where Methanobacteria oxidize it and release CO₂.

Bacteria affect the decay of *Sphagnum* (Figure 49, Figure 54), or more accurately, its near absence. Using *Sphagnum fallax* (Figure 49) from a fen woodland, Brock and Bregman (1989) found that after 12 months, the original N and P content associated with the moss had diminished little. Furthermore, the cells lacked much damage and had poor colonization by bacteria.

Patra (2020) reminded us of the role of *Sphagnum* (Figure 49, Figure 54) in secreting acids, making acid conditions that are unfavorable for the growth of most decomposing bacteria. The decomposition is further slowed by the absence of oxygen in the lower peat layers, causing an accumulation of dead material we know as peat.

Xeric

Liu *et al.* (2014) investigated the endophytic bacterial community in the xerophytic moss *Grimmia montana* (Figure 68). Using a 212 sequence library, they identified 54 genera of bacteria in 4 phyla (*Pseudomonadota*, *Bacillota*, *Actinomycetota*, and *Cytophaga/Flexibacter/Bacteroids*). As in many other bryophyte bacterial communities, the *Pseudomonadota* were dominant (45.9%), with *Bacillota* being second (27.6%). The most abundant genera included *Acinetobacter* (Figure 69), *Aeromonas* (Figure 70), *Enterobacter* (Figure 71), *Leclercia*, *Microvirga*, *Paenisporosarcina*, *Planococcus*, *Planomicrobium*, *Pseudomonas* (Figure 13), and *Rhizobium* (Figure 53). They did not determine the role of the bacteria in the association, but some were known to have beneficial effects on their hosts. Some of the genera isolated differed from those detected by the molecular method, thus emphasizing that our methods may often miss important genera and species due to inappropriate culture conditions. At the same time, some taxa may not be in the molecular library.



Figure 68. *Grimmia montana* with capsules, a rock-dwelling species with 54 known genera of bacteria in its cells, spanning 4 phyla, with *Pseudomonadota* being dominant. Photo from Earth.com, with permission.

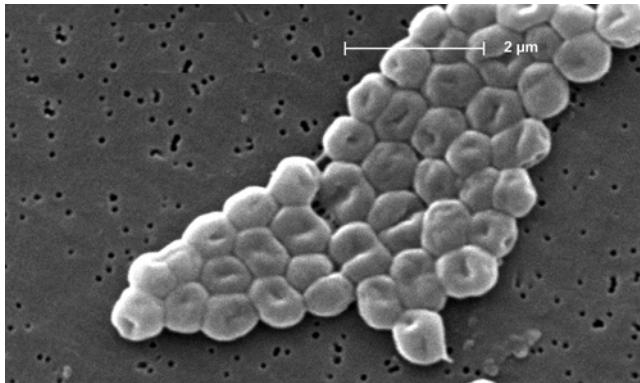


Figure 69. *Acinetobacter baumannii*, in one of the more abundant genera on *Grimmia montana*. Photo by Janice Carr, through Creative Commons.



Figure 70. *Aeromonas hydrophila*, in one of the more abundant genera on *Grimmia montana*. Photo by Nathan Reading, through Creative Commons.



Figure 71. *Enterobacter cloacae*, in one of the more abundant genera on *Grimmia montana*. Photo from CDC, through public domain.

Soil Crusts

Soil crusts are a community of organisms that together colonize and stabilize soil surfaces. These are most common in dry areas where their ability to survive long periods of drought permit them to survive with little competition (Weber *et al.* 2019). These crusts occupy approximately ~12% of the terrestrial surface of the planet Earth (Weber *et al.* 2019). It is important that we understand these processes as they relate to ecosystem processes, especially in cryptogamic soil crusts (Deane-Coe & Stanton 2017), as our Earth remains in a state of continuous change.

The biocrusts may be dominated by **Cyanobacteria**, lichens, or bryophytes (Warren *et al.* 2019; Weber *et al.* 2019). The communities differ significantly from each other (Maier *et al.* 2018). Their organisms include free living, lichenized, and mycorrhizal fungi, **Cyanobacteria**, chemoheterotrophic bacteria, diazotrophic bacteria and archaea, eukaryotic algae, and bryophytes (Warren *et al.* 2019; Weber *et al.* 2019). The organisms are characterized by desiccation and extreme temperature tolerance, production of various soil-binding chemistries, almost exclusive dependency on asexual reproduction, pattern of aerial dispersal over impressive distances, and universal vulnerability to a wide range of human-related perturbations (Warren *et al.* 2019).

The role of bacteria in the bryophyte-lichen matrix of soil crusts remains poorly known. Weber *et al.* (2019) found that bacterial community composition changed in a stepwise manner along with biocrust succession, while bare soil communities were completely different. As the climate changes and land use destroys these communities, it is important that we understand the role of interactions, including those between the bacteria and bryophytes.

Weber *et al.* (2012) explored the soil crusts in the succulent Karoo of South Africa. They found that leaching from mosses may cause the high rates of soil respiration. The leaching creates microsites with high nutrient levels, favoring the growth of the microorganisms.

Moquin *et al.* (2012) examined the bacterial diversity in bryophyte-dominated soil crusts. They found the dominant phyla to be **Acidobacteriota**, **Bacteroidota**, and **Pseudomonadota**. Although tracheophytes are not a common member of the crusts, they found bacterial root associates, especially in the family **Oxalobacteraceae**. The presence of **Bacteroidota** suggests that the bacterial community in these crusts is affected by high carbon availability. The bacterial communities of soils and the **Cyanobacteria**-dominant crusts differed from those of the bryophyte-dominated ones. Bamforth (2008) noted that the microorganisms are important in the nutrient cycling of the crust community and subsequently contribute nutrients to the underlying soils.

In southwestern China, Cao *et al.* (2020) found that not only moss species, but also the types of karst rocky desertification, affect the microbial communities. Mosses were by far the more impacting factor, with changes in moss species bringing drought-resistant factors that affected the bacterial community, or *vice-versa*. The bacteria were able to provide proline content, superoxide dismutase activity, and peroxidase activity. These compounds are closely related to the drought adaptability of mosses.

Maier *et al.* (2018) found that alpha diversity of the crust community increases as succession progresses, with a concomitant shift from more generalized to more specialized organisms. At the same time, the CO₂ gas exchange exhibits significantly larger respiration rates in later successional stages. The NO and HONO emission patterns also change during succession. Thus, as the photosynthetic organisms change, they facilitate specific microbial communities, and these microbial changes in turn influence the physiological properties of the biocrusts and their contributions to both local and global nutrient cycles. The three dominance types of biocrusts have significantly different communities.

In the *Didymodon rigidulus* (Figure 72) community, there are endophytic bacteria, including *Bacillus cereus* (Figure 73), *Bacillus pumilus*, *B. subtilis* (Figure 10), *Bacillus* sp., *Neobacillus niacini*, *Peribacillus simplex* (see Figure 74), and *Priestia aryabhatai* (all previously in *Bacillus*; see Figure 9) (Ma *et al.* 2017b). The dominant species was *B. subtilis*. They found that at the test concentrations of petroleum ether, ethyl acetate, and n-butyl alcohol extracts, *B. cereus* and *B. subtilis* did not significantly alter the bryophyte spore germination. On the other hand, the protonema growth was inhibited to varying degrees by the same extracts. Hence, we know that bacteria can use their secondary metabolites to affect the development of bryophytes and alter the community composition.

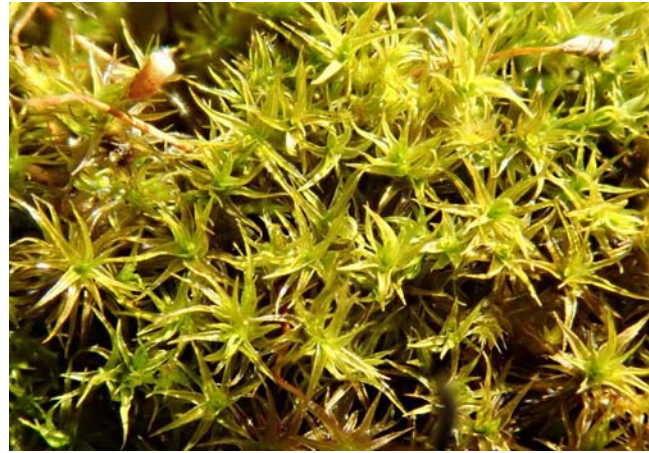


Figure 72. *Didymodon rigidulus*, a species with a number of endophytic bacteria; *Bacillus subtilis* is dominant. Hugues Tinguy, with permission.

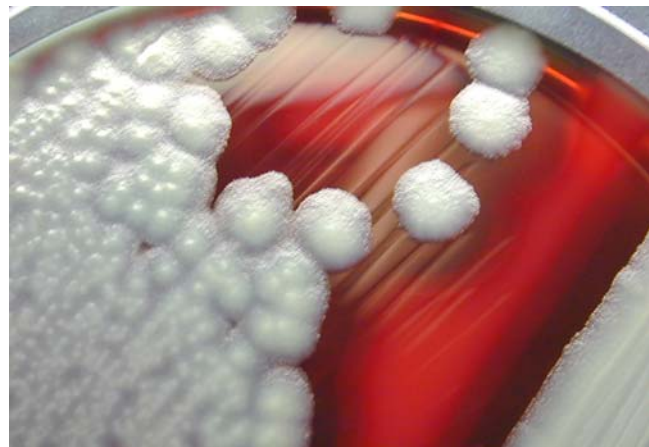


Figure 73. *Bacillus cereus* showing hemolysis on sheep blood; this is one of the endophytic bacteria found in *Didymodon rigidulus*. Photo by Larry Stauffer, through public domain.

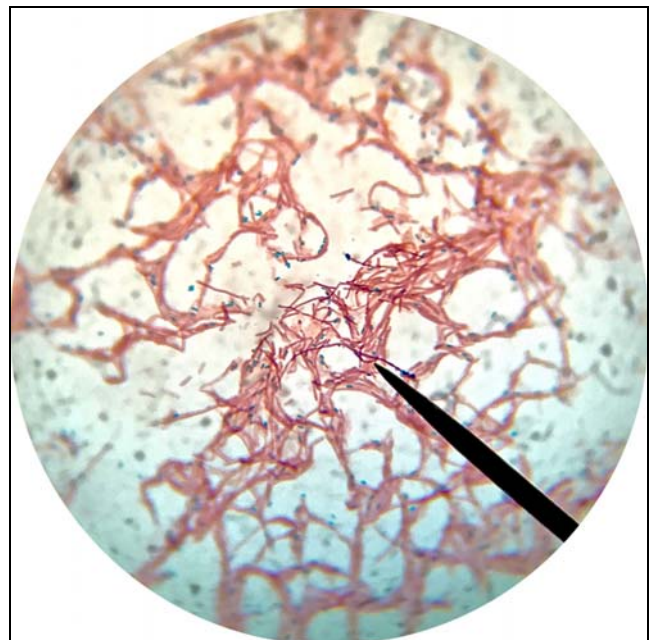


Figure 74. *Peribacillus subtilis* with endospores; *P. simplex* is one of the endophytic bacteria found in *Didymodon rigidulus*. Photo by W M Rapids, through Creative Commons.



Honeybees

Honeybees can benefit from the antibacterial activity of bryophytes against bacteria. And without honeybees, the plant community can suffer due to absence of pollination. Gahtori *et al.* (2011) identified the bacterium *Medisaccoccus plutonius* as the cause of the European foulbrood disease in honeybees (Figure 75). They extracted antibacterial compounds from three different bryophytes and tested them against this bacterium. All of the tested extracts exhibited good antibacterial activity against the foulbrood bacteria. The maximum activity derived from *Dicranum undulatum* (Figure 76) and *Marchantia polymorpha* (Figure 17) and was comparable to that of the standard drug in use against these bacteria.



Figure 75. *Apis mellifera* (honeybee) on comb. Photo by A. Szalansk, through Creative Commons.



Figure 76. *Dicranum undulatum*, a species that has compounds that are antibacterial against the foulbrood bacteria in honeybees. Photo by Robin Bovey, with permission through Dale Vitt.

Sevim *et al.* (2017) tested the antibacterial activity of 23 bryophyte species in Turkey against *Paenibacillus larvae* (Figure 77) isolates from honeybee larvae; these bacteria are responsible for the American foulbrood diseases in the honeybee larvae. Of the 23 bryophytes sampled, they found 10 [liverwort *Metzgeria conjugata* (Figure 78); mosses *Calliergonella cuspidata* (Figure 79), *Calliergonella lindbergii* (Figure 80), *Grimmia alpestris* (Figure 81), *Isoetecium alopecuroides* (Figure 82),

Polytrichastrum formosum (Figure 83), *Polytrichum commune* (Figure 84), *Syntrichia calcicola* (Figure 85), *Syntrichia intermedia* (Figure 86), *Tortella densa* (Figure 87)] that exhibited good antimicrobial activity against *P. larvae* isolates.



Figure 77. *Paenibacillus larvae*, a bacterium in honeycombs that affects the larvae of the honeybee. Photo from Georgia Department of Agriculture, through Creative Commons.



Figure 78. *Metzgeria conjugata*, a liverwort that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.



Figure 79. *Calliergonella cuspidata*, a wetland moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hugues Tinguy, with permission.



Figure 80. *Calliergonella lindbergii*, a wetland moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.



Figure 83. *Polytrichastrum formosum*, a soil-dwelling moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Kent Brothers, Botany Website, UBC, with permission.



Figure 81. *Grimmia alpestris*, a rock-dwelling moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.



Figure 84. *Polytrichum commune*, a wetland moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Riken Mon, through Creative Commons.



Figure 82. *Isoetecium alopecuroides*, a rock-dwelling moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.



Figure 85. *Syntrichia calcicola*, a xerophytic moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.



Figure 86. *Syntrichia intermedia*, a xerophytic moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Acta Plantarum, through Creative Commons.



Figure 87. *Tortella densa*, a moss of mostly rather dry habitats that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.

But does this protection work in nature? Are honeybees able to bring mosses to the hive to prevent the growth of the bacteria? Do they have behavioral adaptations that cause them to move about among the mosses to sanitize themselves? What an interesting relationship it would be if such activities were true. But we don't know; perhaps nature was simply waiting for humans to do the sanitizing job.

Pollution Relationships

Meyer *et al.* (2010a) compared bryophyte microbial communities in rural, urban, and industrialized communities. The particulate atmospheric pollution affects the bryophyte-microorganism complexes. They found that microalgae, bacteria, rotifers, and testate amoebae biomasses were significantly higher in the rural site. The physico-chemical variables (NO_2 , relative humidity,

temperature, site) and the trace elements accumulated in bryophytes (copper, strontium, lead) explained 69.3% of the variance in the microbial community. These numbers suggest that bacteria in a community are potential biomonitors of atmospheric pollution.

Rojas *et al.* (2016) reported that bryophytes dominated control precipitates, whereas the **Basidiomycota** fungi were most abundant under reclaimed precipitates at an acid mine drainage reclamation site in central Pennsylvania, USA. Furthermore the reclaimed precipitates had more bacterial diversity than did the controls. Bacteria under bryophytes were more common under unreclaimed (control) soils.

Meyer *et al.* (2010b) found that the bryophytes did not accumulate the low concentrations of metallic trace elements. However, the **Cyanobacteria**, testate amoebae, and fungi all decreased in the microbial community in response to the particle deposition. Thus, the composition of the microbe community could serve as a useful indicator of pollution effects.

Reclamation Communities

Bryophytes can help to reclaim despoiled areas in a number of ways. Kyyak *et al.* (2020) found that they could colonize saline substrates of tailings storage, where they provide extended surface area for the accumulation of organic matter. The organic carbon under moss turfs increased 2.2-5.0 times compared to areas with no bryophytes. The dense-turf mosses *Didymodon rigidulus* (Figure 72) and *Ptychostomum pseudotriquetrum* var. *bimum* (Figure 88) accumulated the most organic matter, compared with loose turf formed by *Barbula unguiculata* (Figure 89) and *Funaria hygrometrica* (Figure 90). The moss turfs facilitate a 0.2-0.5 unit increase in acidity of the aqueous solutions of the tailings. Bacterial quantity increased significantly under mosses in reclaimed mine tailings, achieving a biomass under the moss turfs of *Didymodon rigidulus* and *Funaria hygrometrica* of 5.09-6.10 $\mu\text{g C g}^{-1}$ dry weight soil. Without mosses, bacteria reached only 3.19-11.27 $\mu\text{g C g}^{-1}$ dry weight soil.



Figure 88. *Ptychostomum pseudotriquetrum* var. *bimum* where organic matter accumulates in greater amounts than in the tailings beneath the loose moss turfs. Photo by Hugues Tinguy, with permission.



Figure 89. *Barbula unguiculata* dry, where less organic matter accumulates in the tailings beneath the moss loose turfs than in dense turf areas. Photo by Bob Klips, with permission.



Figure 90. *Funaria hygrometrica* where less organic matter accumulates in the tailings beneath the moss loose turfs than in the dense turf areas. Photo by Kurt Stueber, through Creative Commons.

The microbial biomass in the tailings beneath the moss turfs depended on the species characteristics of the mosses (Kyyak *et al.* 2020). The microbial biomass index almost doubled with the high level of salinization under turfs of *Didymodon rigidulus* (Figure 72) and *Funaria hygrometrica* (Figure 90). The moss cover also promoted a significant increase in the primary ecological and trophic groups of microorganisms (saprophytes, cellulose-degrading bacteria, oligonitrophils, and nitrogen fixers). Thus the pioneer bryophytes are important in the accumulation of organic matter, increase in acidity, improvement of the redox regime of the substrate, and promotion of development of the important soil microbiota (DeLuca *et al.* 2002; Gavazov *et al.* 2010; Stewart *et al.* 2011; Kyyak *et al.* 2020). In particular, they increased the productivity of cellulose-degrading bacteria.

Summary

It is only in the 21st century that much research has addressed the bacterial communities associated with bryophytes. It appears that these communities have important roles in the ecosystems they inhabit.

Bryophytes in rivers and streams trap organic sediments. These provide rich habitats for bacteria, which in turn provide food for invertebrates both large and small. We now know that they can cause denitrification, whereas others are important in nitrogen fixation, while at the same time converting methane to free CO₂ that is used by the bryophytes. Their role in nitrogen fixation in peatlands, the boreal forest, cryptogamic crusts, and other low-nutrient habitats is significant. They are also, at least in part, responsible for degradation, senescence, and decomposition of the bryophytes, thus contributing to nutrient cycling. However, in acidic peatlands, the decomposition is slow.

Some bacteria produce ice-binding proteins that help bryophytes, especially in the polar and alpine regions, to survive freezing by preventing large crystals from forming in the bryophyte cells.

Some communities are very similar on a number of bryophyte species in an area, while at the same time some bryophytes can have unique communities. But we do not understand what causes the bacterial community differences with bryophyte species – microhabitat needs, bryophyte secondary compounds, bryophyte structure, bacteria-bacteria interactions?

There are many habitats where the bacterial associates of bryophytes have not been assessed. Their roles in these communities could be critical for some of the vital ecosystem functions. It is likely that there are multiple connections for some of these roles and that the community composition will change with climate change, probably before we begin to understand these connections.

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