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CHAPTER 18-6
CAVES – SIMILAR SECLUDED HABITATS

TABLE OF CONTENTS

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Figure 1. Zen Iwatsuki photographing fissure in lava, with bryophytes, Grjotagja, Myvatn, Iceland, 1985. Photo by Janice Glime.

Artificial "Caves"

Mine Shafts

Mines and mine shafts, in many ways, act like caves. Their cold air typically comes from lower levels rather than through channels above. They are dark, and they are usually damp. These habitats can have their own unique bryophyte flora, often influenced by the types of minerals being mined. Strip mines can in some cases resemble sink holes, but often have a much shorter history and much less moisture. But I have to wonder why I was unable to find many studies on these human-made habitats.

In Ireland, Holyoak and Lockhart (2009) found ***Cephaloziella massalongi*** (Figure 2) at the top of a copper mine shaft on rock where it was lightly shaded (Figure 3). Although it seems to always be associated with copper in Britain, ***Cephaloziella massalongi*** only occurs on acidic sites (Figure 4), and is not known from limestone sites. Cornish sites typically have *p*H levels of 5.1-5.4 and are often associated with moderate levels of both lead and zinc as well as copper. Callaghan (2011) studied the ecology of this species and found that it typically grows in shaded conditions (Figure 4) with less than 10% relative light, a level that characterizes many of the liverworts (Marschall & Proctor 2004). In an old mine adit of Wales, it grew at 2.5 lux (0.2% relative light). Callaghan suggested that ***Cephaloziella massalongi*** may be confined to such shaded conditions because of its need for moisture and inability to successfully compete elsewhere.

Figure 2. ***Cephaloziella massalongi***, a copper-tolerant liverwort. Photo by Des Callaghan, with permission.

Figure 3. ***Cephaloziella massalongi*** habitat in old metal mine. Photo by Des Callaghan, with permission.

Figure 4. ***Cephaloziella massalongi*** in Hermon Copper Bog under overhanging sod that provides it with shade. Photo by Des Callaghan, with permission.

The number of taxa in the Tongshankou Copper Mine in China is much greater than in many caves (Pen & Zhang 2005). So far 29 moss taxa, representing 7 families and 20 genera, have been identified. Pan *et al*. (2011) found a similar number of species (30 taxa) in four abandoned mercury mines in China. Bryophytes occurred within the first 10 m into the mine. The life forms were 60% short turfs, 33% wefts, and 7% mats. Among these was the luminous thallose liverwort ***Cyathodium smaragdinum*** (Figure 5).

Figure 5. ***Cyathodium smaragdinum***, a luminous thallose liverwort that is known from a copper mine in China. Photo by 楊玉鳳, through Creative Commons.

Koponen (1977) reported the mosses ***Pohlia nutans*** (Figure 6) and ***Ceratodon purpureus*** (Figure 7-Figure 10) at a depth of 176 m in a mine in Finland. But this mine was continuously illuminated by electric lights. The mosses covered an area of ~0.5 m² in this mine under a constant ~8ºC and high humidity. The mine was rich in zinc, lead, and copper. ***Ceratodon purpureus*** is a moss of a wide range of habitats, from dry roadsides to submerged in Antarctic ditches and resplendent on its boulders (Figure 9). It is not unusual to see it growing on stone ledges (Figure 10).

Figure 6. ***Pohlia nutans*** with capsules on rock, a widespread species that occurs at a depth of 176 m in a mine in Finland. Photo by J. C. Schou, with permission.

Figure 7. ***Ceratodon purpureus***, a moss that can grow at 176 m depth in a continuously illuminated mine. Photo by Michael Lüth, with permission.

Figure 8. ***Ceratodon purpureus*** with immature capsules, showing how abundant the capsules can be. Photo courtesy of Dale Sievert.

Figure 9. ***Ceratodon purpureus*** on boulders in the Antarctic. Photo courtesy of Rod Seppelt.

Figure 10. ***Ceratodon purpureus*** on a shaded ledge in Dollar Bay, Michigan, USA. Photo by Janice Glime.

Mine entrances seem to be overlooked habitats where one might find unusual species in areas where similar cave habitats are absent. On the other hand, the surface around mines is typically rich in ore and often has rare species (*e.g.* Callaghan 2018), but these areas are not similar to caves and will be discussed elsewhere.

Subways

Subways are manmade caves, but are typically illuminated and are open at both ends. They are likely to suffer from the pollution created by trains.

The granitic subway in Stockholm has lighting throughout. Established in 1970, the tunnel has a flora including **Cyanobacteria**, fungi, bacteria, diatoms, and the moss ***Eucladium verticillatum*** (Figure 11), a species not known elsewhere in Stockholm. Its occurrence on granite is unusual – it usually occurs on limestone. The subway also is home to a spider that is unknown elsewhere in Sweden.

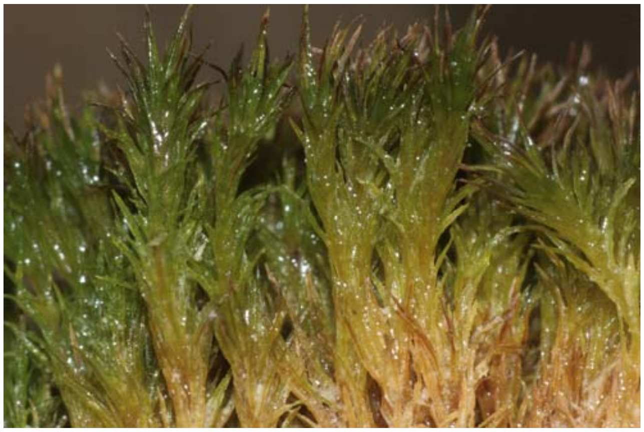

Figure 11. ***Eucladium verticillatum***, a moss that grows in a granitic subway in Stockholm. Photo by Hermann Schachner, through Creative Commons.

Small Caves and Fissures

Various fissures and cracks in rocks (Figure 1, Figure 12-Figure 13), including lava, make tiny caves and cave-like habitats that are suitable refuges for bryophytes. While

in Iceland, Yojiro Iwatsuki uncovered ***Saelania glaucescens*** (Figure 14) growing completely hidden under cracked rocks in a lava field (Figure 15-Figure 17).

Figure 12. Fissures in hard lava rock, Myvatn, Iceland, making cave-like environments. Photo by Janice Glime.

Figure 13. Fissures with hot springs at bottom and bryophytes growing on the warm, humid rocks, Myvatn, Iceland. Photo by Janice Glime.

Figure 14. ***Saelania glaucescens***, a species that grows in protected areas on cliffs or even completely under rocks in volcanic areas. Photo by Janice Glime.

Figure 15. Cracked lava that hides ***Saelania glaucescens*** north of Reykjahlid, Iceland. Photo by Janice Glime.

Figure 16. ***Saelania glaucescens*** revealed as layers of rock are removed, north of Reykjahlid, Iceland. Photo by Janice Glime.

Figure 17. ***Saelania glaucescens*** with capsules revealed from under lava crack N of Reykjahlid, Iceland. Photo by Janice Glime.

Krukowski and Świerkosz (2005) found the fern ***Vandenboschia radicans*** (Figure 18) in its easternmost locality in Europe. Its gametophytes grew in horizontal rock fissures with sparse growths of the mosses ***Schistostega pennata*** (Figure 19) and ***Distichium inclinatum*** (Figure 20). I observed the same phenomenon with ***Asplenium scolopendrium*** gametophytes growing among mosses on the vertical sides of boulders in the Upper Peninsula of Michigan, USA.

Figure 18. ***Vandenboschia radicans***, a fern species whose prothalli grow in rock crevices with mosses in Europe. Photo through Creative Commons.

Figure 19. ***Schistostega pennata*** carpet; dark green plants are upright gametophytes; yellow-green color indicates presence of the protonemata; this mat of mosses can provide suitable habitat in crevices for the fern ***Vandenboschia radicans*** in Europe. Photo by Alpsdake, through Creative Commons.

Figure 20. ***Distichium inclinatum***; this mat of mosses can provide suitable habitat in crevices for the fern ***Vandenboschia radicans*** in Europe. Photo by Hermann Schachner, through Creative Commons.

Scree

Screes (slopes covered with small loose stones; **talus**; Figure 21-Figure 22) create numerous minicaves that can act as refugia for more northern boreal and Arctic bryophyte, pteridophyte, and arthropod species (Růžička *et al*. 2012). These can even have year-round ice.

Figure 21. Scree in Switzerland, creating tiny darkened caves where bryophytes enjoy protection. Photo by Urs Kormann, through Creative Commons.

Figure 22. Talus slope at Ruby Mountains, Nevada, USA. Photo from USGS, through public domain.

In the Czech Republic, 92 bryophyte and 10 pteridophyte species were encountered among the scree. The liverworts ***Sphenolobus saxicola*** (Figure 23), ***Diplophyllum taxifolium*** (Figure 24), ***Gymnomitrion***

concinnatum (Figure 25), ***Gymnomitrion corallioides*** (Figure 26-Figure 27), and ***Barbilophozia sudetica*** (Figure 28), and mosses ***Andreaea rupestris*** (Figure 29), ***Polytrichastrum alpinum*** (Figure 30), ***Racomitrium fasciculare*** (Figure 31) and ***Racomitrium lanuginosum*** (Figure 32) have isolated populations in the Kamenec Hill of the Czech Republic, and the populations of the fern ***Cryptogramma crispa*** (Figure 33) and liverworts ***Gymnomitrion*** spp. (Figure 25-Figure 27) represent the lowest known elevational limits for the Czech Republic and Central Europe. Some species occur only near ice plots, including the liverworts ***Diplophyllum taxifolium***, ***Gymnomitrion corallioides***, and ***Lophozia sudetica*** and the mosses ***Andreaea rupestris*** and ***Polytrichastrum alpinum***. On the other hand, the liverworts ***Sphenolobus saxicola*** and ***Gymnomitrion concinnatum*** and mosses ***Racomitrium fasciculare*** and ***Racomitrium lanuginosum*** never occurred near ice.

Figure 23. ***Sphenolobus saxicola***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo through Creative Commons.

Figure 24. ***Diplophyllum taxifolium***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.

Figure 25. ***Gymnomitrion concinnatum***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Štěpán Koval, with permission.

Figure 26. ***Gymnomitrion corallioides***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Rory Hodd, with permission.

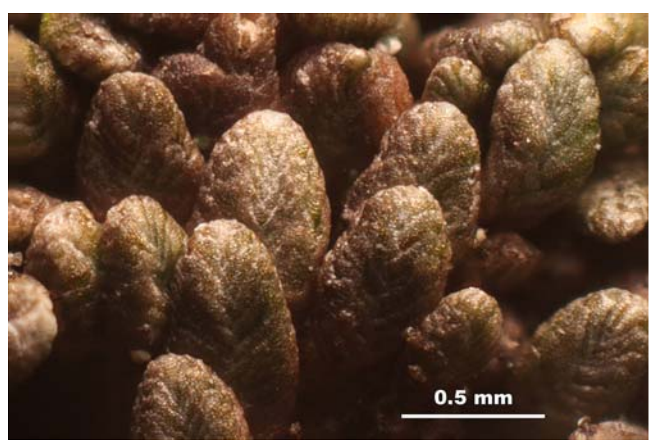

Figure 27. ***Gymnomitrion corallioides***. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Barbilophozia sudetica***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hugues Tinguy, with permission.

Figure 29. ***Andreaea rupestris***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by J. C. Schou, with permission.

Figure 30. ***Polytrichastrum alpinum***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by David T. Holyoak, with permission.

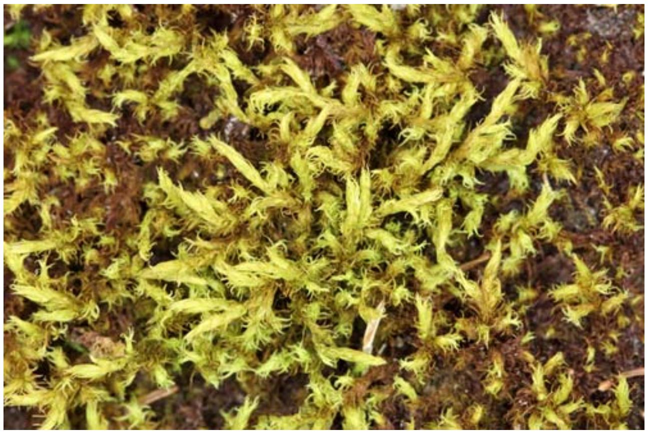

Figure 31. ***Racomitrium fasciculare***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Jean Faubert, with permission.

Figure 32. ***Racomitrium lanuginosum***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.

Figure 33. ***Cryptogramma crispa***, a species that reaches its lowest elevation in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Joan Simon, through Creative Commons.

These scree habits likewise provide a deep labyrinth where arthropods and other organisms find refuge (Růžička *et al*. 2010). In NE Bohemia, Czech Republic, deep vertical spaces among the scree provide microhabitats for montane bryophyte species such as the liverwort ***Diplophyllum taxifolium*** (Figure 24), and the mosses ***Dicranum elongatum*** (Figure 34) and ***Pohlia drummondii*** (Figure 35) occur. Living among these are numerous arthropods, with spiders and beetles being the most numerous. A total of 304 species of arthropods were identified in the study.

Figure 34. ***Dicranum elongatum*** with capsules, a species that lives in deep cavities among the scree in NE Bohemia, Czech Republic. Photo by Jean Faubert, with permission.

Figure 35. ***Pohlia drummondii***, a species that lives in deep cavities among the scree in NE Bohemia, Czech Republic. Photo by David T. Holyoak, with permission.

In Iceland, the mosses ***Distichium capillaceum*** (Figure 36-Figure 37), ***Mnium marginatum*** (Figure 38), and ***Pohlia cruda*** (Figure 39), and the fern ***Cystopteris fragilis*** (Figure 40), grow over the **loess** (silt-sized sediment formed by accumulation of wind-blown dust) deposits inside the scree cavities, surviving with reduced light but buffered microclimate (Blažková 1973). Similar associations also occur in crevices on loess in the Czech Republic (Hesselbo 1918; Šmarda 1947).

Figure 36. ***Distichium capillaceum*** with capsules, under grass cave; this species grows over the loess deposits inside in karst cavities and at the bottom of the deep karstic Macocha Chasm in the Czech Republic. Notice the lines of reddish brown capsules. Photo by Michael Lüth, with permission.

Figure 37. ***Distichium capillaceum***. Photo by Hermann Schachner, through Creative Commons.

Figure 38. ***Mnium marginatum***, a species that grows over the loess deposits in karst cavities. Photo by Hermann Schachner, through Creative Commons.

Figure 39. ***Pohlia cruda***, a species that grows over the loess deposits in karst cavities. Photo by Hermann Schachner, through Creative Commons.

Figure 40. ***Cystopteris fragilis*** among mosses on rock, a species that grows over the loess deposits in karst cavities. Photo by Bryant Olson, through Creative Commons.

Similar cavities occur in lava fields (Figure 41). Blažková (1973) described these from northern Iceland. Aeolian sediments accumulate on the bottom of these cavities. Light intensity is greatly reduced and the microclimate is buffered from the extremes at the surface. Blažková reported 12 bryophyte species from these. In very dark parts of the cavities mainly liverworts occur, including ***Blepharostoma trichophyllum*** (Figure 42), ***Mesoptychia collaris*** (Figure 43-Figure 44), and ***Sauteria alpina*** (Figure 45-Figure 46). Close to the openings where it is well illuminated, one can find ***Polytrichum juniperinum*** (Figure 47-Figure 48) and especially ***Timmia austriaca*** (Figure 49).

Figure 41. Sheep near lava rock at Myvatn, northern Iceland, showing the tumbled arrangement of rocks that creates minicaves. Photo by Janice Glime.

Figure 42. ***Blepharostoma trichophyllum***, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 43. ***Mesoptychia collaris***, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Mesoptychia collaris*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Sauteria alpina***, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Michael Lüth, with permission.

Figure 46. ***Sauteria alpina*** with archegoniophores. Photo by Hermann Schachner, through Creative Commons.

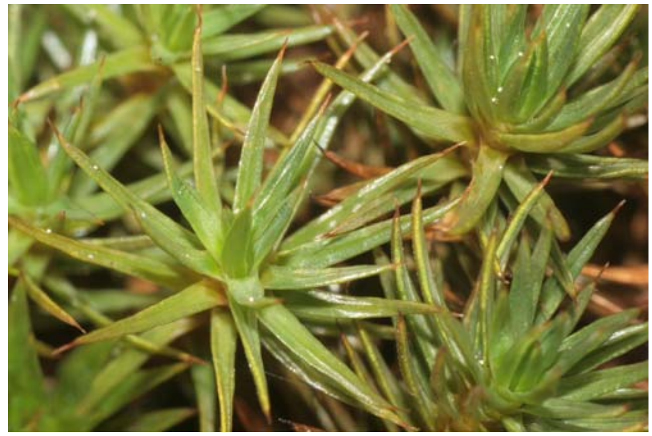

Figure 47. ***Polytrichum juniperinum***, a species that grows close to the openings of cavities among lava stones where it is well illuminated. Photo by Hermann Schachner, through Creative Commons.

Figure 48. ***Polytrichum juniperinum*** with male splash cups. Photo by Ian Sutton, through Creative Commons.

Figure 49. ***Timmia austriaca***, a species that grows close to the openings of cavities among lava stones where it is well illuminated. Photo by Jean Faubert, with permission.

Bjarnason (1991) considered every cavity around a boulder at Hekla (Figure 50), southern Iceland, to be

different, thus making all the holes different in ecological character. The moss ***Racomitrium lanuginosum*** (Figure 32) frequently grows on these rocks and covers the cavity (Figure 51-Figure 52), making the area somewhat dangerous for walking. The very deep, narrow lava clefts (Figure 53-Figure 54) support vegetation similar to that of the holes, with ***Conostomum tetragonum*** (Figure 55), ***Pohlia drummondii*** (Figure 35), ***Pohlia wahlenbergii*** (Figure 56), and ***Polytrichastrum sexangulare*** (Figure 57-Figure 58). The vegetation in these narrow lava cavities at Hekla has a very different flora from those in northern Iceland (Figure 41). Some species prefer the holes in the Hekla area, but are not restricted to them: the liverworts ***Blepharostoma trichophyllum*** (Figure 42) and ***Nardia geoscyphus*** (Figure 59) and the mosses ***Isopterygiopsis pulchella*** (Figure 60), ***Mnium stellare*** (Figure 61), ***Oligotrichum hercynicum*** (Figure 62), and ***Pohlia cruda*** (Figure 39). Many species also occupy the crags, including the liverworts ***Diplophyllum albicans*** (Figure 63) and ***Mesoptychia gillmanii*** (Figure 64) and the mosses ***Encalypta ciliata*** (Figure 65) and ***Plagiothecium cavifolium*** (Figure 66-Figure 67). Others occur in small ruptures in the main surface (Figure 54), including the liverwort ***Cephaloziella divaricata*** (Figure 68-Figure 69) and mosses ***Dicranoweisia crispula*** (Figure 70), ***Diphyscium foliosum*** (Figure 71), and ***Pohlia drummondii***. As in northern Iceland, ***Racomitrium lanuginosum*** (Figure 32, Figure 51-Figure 52) is common near the openings of the holes, infrequently accompanied by ***Andreaea rupestris*** (Figure 29) and ***Schistidium apocarpum*** (Figure 72) (Bjarnason 1991). As in northern Iceland, the moist, sandy bottom (40-60 cm) supports small patches of liverworts; mixed with larger bryophytes such as the moss ***Bartramia ithyphylla*** (Figure 73) and liverwort ***Plagiochila porelloides*** (Figure 74). In wide, shallow holes the number of species is greater at this sandy bottom, including ***Brachythecium albicans*** (Figure 75), ***Polytrichum juniperinum*** (Figure 47-Figure 48), ***Rhytidiadelphus squarrosus*** (Figure 76), and ***Timmia austriaca*** (Figure 49).

Figure 50. Hekla, Iceland, cairns and various rock sizes. Photo by cogdogblog, through Creative Commons.

Figure 51. ***Racomitrium*** mounds, Iceland. Photo by Janice Glime.

Figure 52. Lava beds of Nass Valley, British Columbia, with ***Racomitrium***, illustrating the cavities and multiple formations created. Photo by Darren Kirby, through Creative Commons.

Figure 53. Fissure in hard lava rock, with the lichen ***Cetraria*** and bryophytes, Myvatn, Iceland. Photo by Janice Glime.

Figure 54. Fissure with mosses in its small rupture, N. Myvatn, Iceland. Photo by Janice Glime.

Figure 55. ***Conostomum tetragonum*** with capsules, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Pohlia wahlenbergii***, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 57. ***Polytrichastrum sexangulare***, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Tomas Hallingbäck, with permission.

Figure 58. ***Polytrichastrum sexangulare***. Photo by Hermann Schachner, through Creative Commons.

Figure 59. ***Nardia geoscyphus***, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Rayna Natcheva, with permission.

Figure 60. ***Isopterygiopsis pulchella*** with capsule, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Michael Lüth, with permission.

Figure 61. ***Mnium stellare***, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Oligotrichum hercynicum***, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Štěpán Koval, with permission.

Figure 63. ***Diplophyllum albicans***, a species that occupies the crags in the Hekla area of Iceland. Photo by David T. Holyoak, with permission.

Figure 64. ***Mesoptychia gillmanii***, a species that occupies the crags in the Hekla area of Iceland. Photo by Tomas Hallingbäck, with permission.

Figure 65. ***Encalypta ciliata*** with capsules, among rocks, a species that occupies the crags in the Hekla area of Iceland. Photo by Tony Frates, through Creative Commons.

Figure 66. ***Plagiothecium cavifolium*** on shale, a species that occupies the crags in the Hekla area of Iceland. Photo by Bob Klips, with permission.

Figure 67. ***Plagiothecium cavifolium***. Photo by Christian Berg, through Creative Commons.

Figure 68. ***Cephaloziella divaricata***, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.

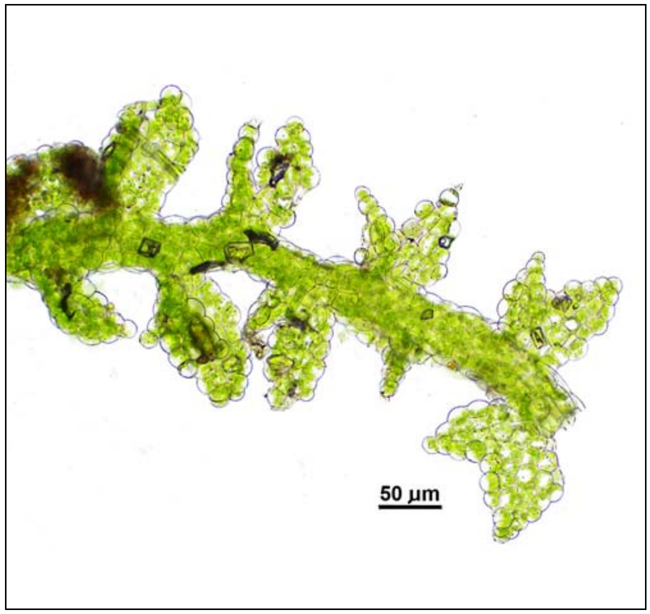

Figure 69. ***Cephaloziella divaricata*** branch. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 70. ***Dicranoweisia crispula*** with capsules, on rock, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 71. ***Diphyscium foliosum*** capsules, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 72. ***Schistidium apocarpum*** with capsules, a species that occurs near the opening of an ice cave in Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 73. ***Bartramia ithyphylla*** with capsules on vertical rock, a species that occurs on the moist, sandy bottoms (40-60 cm) of small caves in Iceland. Photo by Štěpán Koval, with permission.

Figure 74. ***Plagiochila porelloides*** on vertical bank, a species that occurs on the moist, sandy bottoms (40-60 cm) of small caves in Iceland. Photo from Botany Website, UBC, with permission.

Figure 75. ***Brachythecium albicans***, a species that occurs in the shallow bottom of wide, sandy holes in Iceland. Photo by Kristian Peters, through Creative Commons.

Figure 76. ***Rhytidiadelphus squarrosus***, a species that occurs in the shallow bottom of wide, sandy holes in Iceland. Photo by Johan N, through Creative Commons.

Ice Caves

Bryophytes in ice caves (Figure 77) are much more uncommon. Jakab (2000) found ***Heterocladium heteropterum*** (Figure 78-Figure 79) and ***Cyrtomnium hymenophylloides*** (Figure 80) in ice caves in Romania. But outside, the caves can cause a **temperature inversion** (reversal of normal decrease of air temperature with altitude). Other bryophytes seem to benefit from the conditions emanating from these caves, permitting more Arctic species to survive here.

Figure 77. Ice cave in natural glacier. Photo by Serge J. F., through Creative Commons.

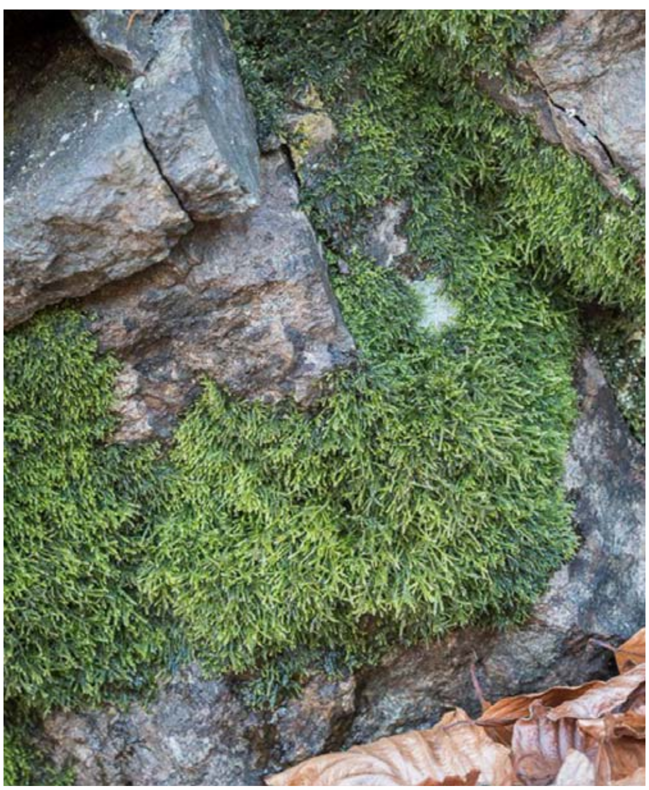

Figure 78. ***Heterocladium heteropterum*** on rock, a species that occurs in an ice cave in Romania. Photo by Štěpán Koval, with permission.

Figure 79. ***Heterocladium heteropterum*** branch showing large stem leaves and smaller branch leaves. Photo by Štěpán Koval, with permission.

Figure 80. ***Cyrtomnium hymenophylloides***, a species that occurs in an ice cave in Romania. Photo by Michael Lüth, with permission.

Windholes

Windholes (Figure 81-Figure 83, Figure 88) are also known as **Kaltluftlöcher**, **Kondenswassermoore**, and **ventaroles (**Wolfgang Karl Hofbauer, pers. comm. 26 July 2021). Natural windholes are made by the wind in sandstone formations as a result of centuries of wind and weather, making the rock formations pock-marked with windholes and caves. In summer, these cool the surrounding area with cool air that blows out, but during winter the air from the windholes is milder than that of the surrounding area (Kong *et al* 2011). These can be categorized as talus (Figure 84), cave (Figure 81-Figure 83), and sink types of windholes. Like caves, these can provide refugia for plants that normally occur at higher elevations or closer to the poles (Kong *et al*. 2012).

Figure 81. Algific talus slope with windholes in northeastern Iowa, USA. photo courtesy of Beth Lynch.

Figure 82. Algific talus slope with windholes obscured by mosses and other vegetation, northeastern Iowa, USA. Photo courtesy of Beth Lynch.

Figure 83. Algific cave opening (windhole) in Fillmore County, Minnesota, USA. Photo by S. C. Zager, MN DNR, through public domain.

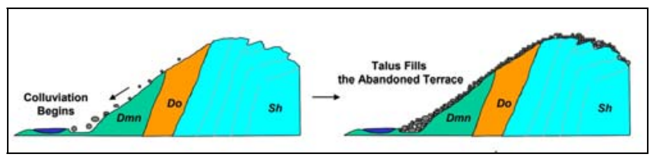

Figure 84. Algific slope cave formation, Ice Mountain, West Virginia, USA. Modified from Kevin M. Andrews, MS thesis 2003.

Harald Zechmeister (pers. comm. 26 July 2021) described the windholes in Austria. These have channels that are over 100 m long. This permits them to reach interior temperatures that are just slightly above 0ºC, often creating ice cores at the openings that persist through the summer. This favors the growth of Arctic-alpine liverworts like ***Protochilopsis*** (=***Schistochilopsis***) ***grandiretis*** (Figure 85), ***Odontoschisma macounii*** (Figure 86), or ***Tritomaria scitula*** (Figure 87) at low altitudes. He reports more than 100 bryophyte species associated with the surroundings of approximately 20 windholes.

Figure 85. ***Protochilopsis grandiretis***, an Arctic species that grows in windholes in Austria. Photo by Vadim Bakalin, with permission.

Figure 86. ***Odontoschisma macounii***, an Arctic species that grows in windholes in Austria. Photo from Earth.com, with permission.

Figure 87. ***Tritomaria scitula***, an Arctic species that grows in windholes in Austria. Photo by Tomas Hallingbäck, with permission.

Bakalin *et al*. (2017) describe these as formations in East Manchuria of Russia as places where the wind enters large holes tens of meters above, then goes underground, where it passes among wet stones and cliffs in areas with much lower temperatures due to evaporation of water from the stones. Therefore, at the exit hole, the air temperature may be about 10ºC below that of the surrounding environment.

In the Wisconsin Driftless Area, USA, Christy and Meyer (1991) similarly reported disjunct species that are restricted to the "refrigerated" windholes (Figure 88). Among these, the tiny moss ***Seligeria donniana*** (Figure 89) was new to Wisconsin. Among the 39 species of bryophytes identified from four of the largest algific slopes, one third were restricted to these cold air vents. These included the liverworts ***Marchantia polymorpha*** (Figure 90), ***Porella platyphylla*** (Figure 91), and ***Preissia quadrata*** (Figure 92), and the mosses ***Abietinella abietinum*** (Figure 93)**,** ***Anomodon attenuatus*** (Figure 94), ***Anomodon rostratus*** (Figure 95), ***Bartramia pomiformis*** (Figure 96), ***Brachythecium oxycladon*** (Figure 97), ***Koponeniella graminicolor*** (Figure 98), ***Bryoerythrophyllum recurvirostrum*** (Figure 99), ***Campylium chrysophyllum*** (Figure 100), ***Ceratodon purpureus*** (Figure 7-Figure 10), ***Climacium americanum*** (Figure 101), ***Didymodon fallax*** (Figure 102), ***Entodon seductrix*** (Figure 103), ***Eurhynchium hians*** (Figure 104), ***Hylocomiadelphus triquetrus*** (Figure 105), ***Mnium marginatum*** (Figure 38), ***Mnium stellare*** (Figure 61), ***Plagiomnium cuspidatum*** (Figure 106), ***Plagiomnium medium*** (Figure 107), ***Pohlia wahlenbergii*** (Figure 56), ***Rhodobryum ontariense*** (as ***Rhodobryum roseum***; Figure 108), ***Seligeria campylopoda*** (Figure 109), ***Seligeria donniana***, ***Thuidium delicatulum*** (Figure 110), and ***Thuidium recognitum*** (Figure 111).

Figure 88. Algific caves (windholes) in Wisconsin, USA. Photo by Ryan O'Connor, Wisconsin DNR, through public domain.

Figure 89. ***Seligeria donniana*** with capsules, a species that occurs in windholes in the algific slopes of the Driftless Area of Wisconsin, USA. Photo by Tom Neily, with permission.

Figure 90. ***Marchantia polymorpha***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Brenda Dobbs, through Creative Commons.

Figure 91. ***Porella platyphylla***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 92. ***Preissia quadrata***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 93. ***Abietinella abietinum*** on rock, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 94. ***Anomodon attenuatus***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Dendrofil, through Creative Commons.

Figure 95. ***Anomodon rostratus***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 96. ***Bartramia pomiformis*** with capsules, on rock ledge, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by David T. Holyoak with permission.

Figure 97. ***Brachythecium oxycladon***, on rock ledge, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 98. ***Koponeniella graminicolor***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 99. ***Bryoerythrophyllum recurvirostrum*** with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 100. ***Campylium chrysophyllum***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 101. ***Climacium americanum***, a common species in moist habitats, occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Rafael Medina, through Creative Commons.

Figure 102. ***Didymodon fallax***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Jean Faubert, with permission.

Figure 103. ***Entodon seductrix***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 104. ***Eurhynchium hians***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Wayne Lampa, through Creative Commons.

Figure 105. ***Hylocomiadelphus triquetrus***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by J. C. Schou, with permission.

Figure 106. ***Plagiomnium cuspidatum*** branch, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 107. ***Plagiomnium medium*** with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 108. ***Rhodobryum ontariense***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 109. ***Seligeria campylopoda*** with capsules showing tropism, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo from Earth.com, with permission.

Figure 110. ***Thuidium delicatulum*** with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 111. ***Thuidium recognitum***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Sture Hermansson, with online permission.

Beth Lynch (pers. comm. 29 July 2021) finds a few bryophyte species that are common around the windhole vents of northeastern Iowa, USA (Figure 81-Figure 82), but are very infrequent or absent in the surrounding areas. Presumably due to these microclimatic conditions, ***Hylocomium splendens*** (Figure 112) and ***Hylocomiadelphus triquetrus*** (Figure 105) can be relatively common on the algific slopes, but are absent in other cool, moist microsites in the area. It is interesting that, like most caverns, these areas seem to be devoid of leafy liverworts.

Figure 112. ***Hylocomium splendens***, a northern species that can be found around windhole vents in Iowa, USA. Photo by Hugues Tinguy, with permission.

Higuchi (1991) reported that the montane mosses ***Dicranum elongatum*** (Figure 34) and ***Pohlia drummondii*** (Figure 35) and liverwort ***Diplophyllum taxifolium*** (Figure 24) occur in windhole areas of the Senpoku-gun in Japan.

The unusual microclimate near the windholes can bring surprises for curious bryologists (Choi *et al*. 2020). Choi *et al*. (2020) found ***Mannia fragrans*** (Figure 113) and ***Mannia androgyna*** (Figure 114) in windholes near the Donggang River, the first find of these species in Korea. Borovichev and Bakalin (2016) similarly reported ***Mannia triandra*** (Figure 115) from the windhole area of Magadan Province and the Korean Peninsula.

Figure 113. ***Mannia fragrans***, a species that occurs in windholes in Korea. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 114. ***Mannia androgyna***, a species that occurs in windholes in Korea. Photo from Earth.com, with permission.

Figure 115. ***Mannia triandra*** with archegoniophores among rocks, a species that occurs in windholes in Korea. Photo by Oliver Dürhammer, through Creative Commons.

Shirasaki (1990) investigated the ecological distribution of bryophytes in the windhole areas of Mt. Naeba, Niigata and Nagano Prefectures, Japan. Shirasaki (1998) found that the moss ***Trachycystis flagellaris*** (Figure 116) sometimes grows on the ground under shrubs where there are cool sites maintained by windholes that provide a temperature below 10ºC and a high air humidity in warmer seasons.

Figure 116. ***Trachycystis flagellaris***, a species that grows on the ground under shrubs where there are cool sites maintained by windholes in Japan. Photo by Misha Ignatov, with permission.

Hitoshi and Masaji (2003) found that in the windhole area of Niigata Prefecture, Japan, one could find ***Pogonatum urnigerum*** (Figure 117) and ***Polytrichastrum formosum*** (Figure 118) growing together. Elsewhere, ***Pogonatum urnigerum*** is able to grow at higher elevations than those of ***Polytrichastrum formosum***, whereas their distribution on a flat map is similar. ***Pogonatum urnigerum*** often has caducous leaves, as known in the Arctic (Long 1988) and in northern New York, USA (McDaniel & Miller 2000).

Figure 117. ***Pogonatum urnigerum*** with capsules, among rocks, a species that grows in windhole areas of Japan. Photo by Claire Halpin, with permission.

Figure 118. ***Polytrichastrum formosum***, a species that grows in windhole areas of Japan. Photo by Leonhard Lenz, through Creative Commons.

At the Bixby State Park and Preserve in Iowa, USA, Kleinman and Blisard (2018) reported 68 bryophyte species from the algific talus slopes near cold air vents. Of these, 16 moss species and 1 liverwort species are uncommon elsewhere in the Bixby park.

Sinkholes

Sinkholes (cenote, sink, sink-hole, sink hole, swallet, swallow hole, or doline; Figure 119-Figure 121) are large depressions in the ground due to collapse of the underlying substrate. This collapse is often caused by karstic processes that dissolve underlying carbonate rocks.

Figure 119. Sinkhole along Rio Camuy, Puerto Rico, aerial view. Photo from US Geological Survey, through Creative Commons.

Figure 120. Looking out of deep sinkhole at Gouffre-v-hdr in France, showing vegetation at the bottom. Photo through Creative Commons.

Figure 121. Sinkhole with bryophytes in Wilson County, Tennessee, USA. Photo by Brian Stansberry, through Creative Commons.

Linares *et al*. (2017) demonstrated the correlation between drought and the formation of sinkholes. This has occurred repeatedly in the karst of the fluvial valley of northeastern Spain (Figure 122), and it has been widely visible in Florida, USA (Figure 123), due to the emptying of aquifers by water usage and periods of drought.

Figure 122. Sinkhole Chinchón dolina c, collapse sinkhole in Spain. Photo through Creative Commons.

Figure 123. Sinkhole, Dover, Florida, USA, collapsed during a winter freeze event. Photo by Ann Tihansky, USGS, through public domain.

Sinkholes encompass some of the same characteristics as caves, especially high humidity and reduced light intensity (Maheu 1926). Because they are sunken, they tend to be more moist than the surrounding forest, with humidity increasing toward the base (Maheu 1926; Li *et al*. 2020b). The additional moisture is at least a contributor to lower temperatures. Maheu noted that the same dominant genera of mosses occurred in the sinkholes as in caves: ***Anomodon*** (Figure 94-Figure 95), ***Eurhynchium*** (Figure 104), ***Mnium*** (Figure 38, Figure 61). Perhaps this is in part due to their ease of starting protonemata from stems and leaves of these mosses. Maheu also considered that the protonemata of the mosses could enter in symbiosis with fungi. The modifications in these conditions are likewise similar to those of cave bryophytes: sterility, leaf elongation, longer internodes, elongation of cells, and disappearance or attenuation of the rib or costa.

The sinkhole often has greater bryophyte diversity than does the surrounding surface forest, but it also can increase the diversity of the adjoining forest. Li *et al*. (2020a) reported 71 taxa of bryophytes from a sinkhole forest in southeastern China, whereas the forest at the surface had only 29, and farther from the sinkhole only 22 taxa were present (Figure 124). Furthermore, the sinkholes were more favorable to liverworts, with 22 taxa compared to only 2 in the adjoining surface forest. In this study, 93% of the sinkhole bryophytes were absent from the surface forest. Li and coworkers found that in the sinkholes the dominant families were **Brachytheciaceae** (Figure 75, Figure 104), **Fissidentaceae** (Figure 128), **Plagiochilaceae** (Figure 74), and **Hypopterygiaceae** (Figure 125). The sinkhole bryophytes, by importance, were ***Conocephalum conicum*** (Figure 126), ***Homaliodendron montagneanum*** (see Figure 127), ***Fissidens cristatus*** (Figure 128), ***Leucobryum glaucum*** (Figure 129-Figure 130), ***Makinoa crispata*** (Figure 131), ***Plagiomnium rhynchophorum*** (Figure 132), ***Claopodium aciculum*** (see Figure 133), ***Eurhynchium laxirete*** (see Figure 104), ***Claopodium gracillimum*** (see Figure 133), and ***Fissidens hyalinus*** (Figure 134). The surface families were completely different, with the exception of **Brachytheciaceae**.

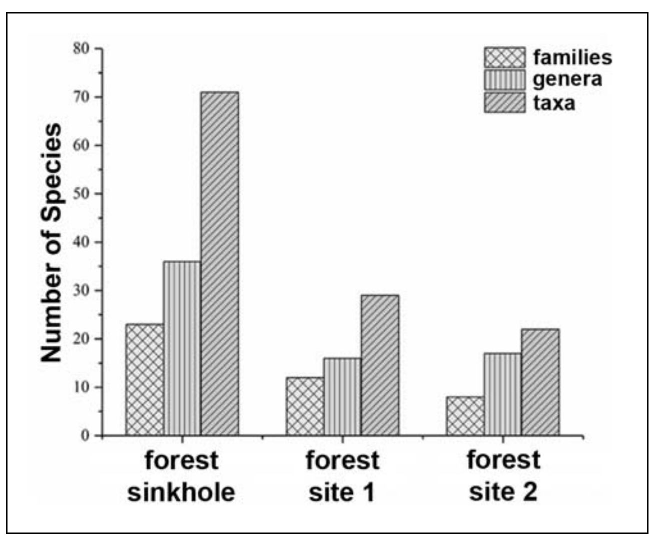

Figure 124. Sinkhole diversity vs forest diversity at 2 distances from sinkhole. Modified from Li *et al*. 2020a.

Figure 125. ***Hypopterygium filiculaeforme***, a member of the family **Hypopterygiaceae**, a family that is among the dominant families occurring in sinkholes in China. Photo by Sara Smerdon, through Creative Commons.

Figure 126. ***Conocephalum conicum*** with archegoniophores, most important bryophyte associated with sinkholes in sinkhole forest in southeastern China. Photo by Claire Halpin, with permission.

Figure 127. ***Homaliodendron flabellatum***; ***Homaliodendron montagneanum*** is among most important bryophytes associated with sinkholes in forest in southeastern China. Photo by Chris Alice Kratzer, through Creative Commons.

Figure 128. ***Fissidens cristatus***, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Brad von Blon, through Creative Commons.

Figure 129. ***Leucobryum glaucum*** habitat on cliff, Canyon Falls, Michigan, USA, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Janice Glime.

Figure 130. ***Leucobryum glaucum***. Photo by Janice Glime.

Figure 131. ***Makinoa crispata*** with capsules, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by 楊玉鳳, through Creative Commons.

Figure 132. ***Plagiomnium rhynchophorum***, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Paul Davison, with permission.

Figure 133. ***Claopodium*** sp.; ***Claopodium aciculum*** and ***C. gracillimum***, both among the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by John Game, with permission.

Figure 134. ***Fissidens hyalinus*** (whitish green), one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Ivanov, with permission.

In the Guda Sinkhole in China, Li *et al*. (2020b) found 75 species of bryophytes. They recorded the highest bryophyte diversity and abundance in the middle and upper sections, with the lowest in the top section and in the base. Furthermore, the most rapid turnover of species occurred in the two middle sections, presumably in response to a rapidly changing gradient of conditions of light and moisture. On the other hand, Váňa *et al*. (2014) found the liverworts ***Riccardia insularis*** (see Figure 135) and ***Calypogeia fissa*** (Figure 136) on both the floor and wall of a sink-hole cave on Ile Amsterdam in the South Indian Ocean.

Figure 135. ***Riccardia multifida***; ***Riccardia insularis*** occurs in a sink-hole cave on Ile Amsterdam in the South Indian Ocean. Photo by Hermann Schachner, through Creative Commons.

Figure 136. ***Calypogeia fissa***, a liverwort that occurs on both the floor and walls of a sink-hole cave on Ile Amsterdam in the South Indian Ocean. Photo by Claire Halpin, with permission.

In the large (280 m deep, 300 m diameter) Monkey-Ear sinkhole in China, Li *et al*. (2018) found 71 species of bryophytes. The greatest diversity was on tree trunks (41 species), followed by forest land > stone surfaces > carrion > leaf surfaces. There are 10 different life forms, 88% of which are typical of dark, humid habitats, whereas only 12% are adapted to bright light and dry conditions. The dissimilarity with surface bryophyte communities is high. Light, humidity, and temperature all influence the distribution of species, but light had the most influence.

In their study of Karst Mountain Sinkhole of Southeastern China, Li *et al*. (2020a) found that the number of life forms diminished from the sink hole to the first forest site and diminished more to the second (farthest) forest site (Figure 137).

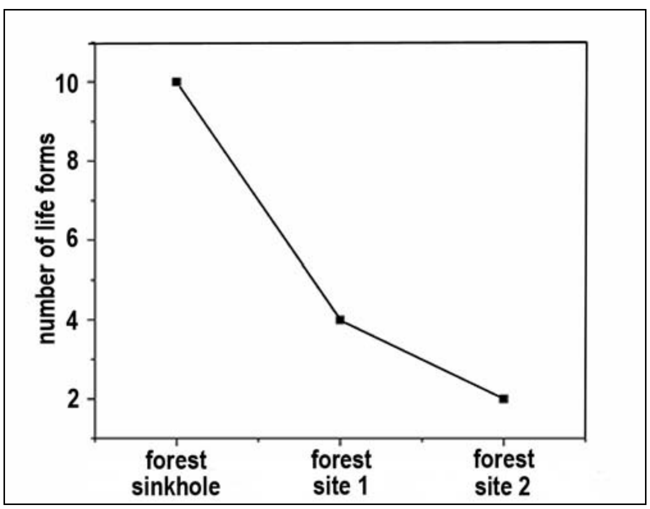

Figure 137. Sinkhole vs forest life forms in Karst Mountain Sinkhole of Southeastern China. Modified from Li *et al*. 2020a.

Thus, like caves, sinkholes provide refugia for species that are unable to live in that geographic region outside the sinkhole (Li *et al*. 2020a). Enclosing cliffs reduce the rate of water loss, thus increasing the humidity within the sinkhole. And these same cliffs can contribute to shading that reduces the temperature as well as the light levels. Furthermore, at least in the sinkhole studies in southeastern China, the nutrients are in greater supply in the sinks (Figure 138), although one would think this would be more beneficial to tracheophytes than to bryophytes.

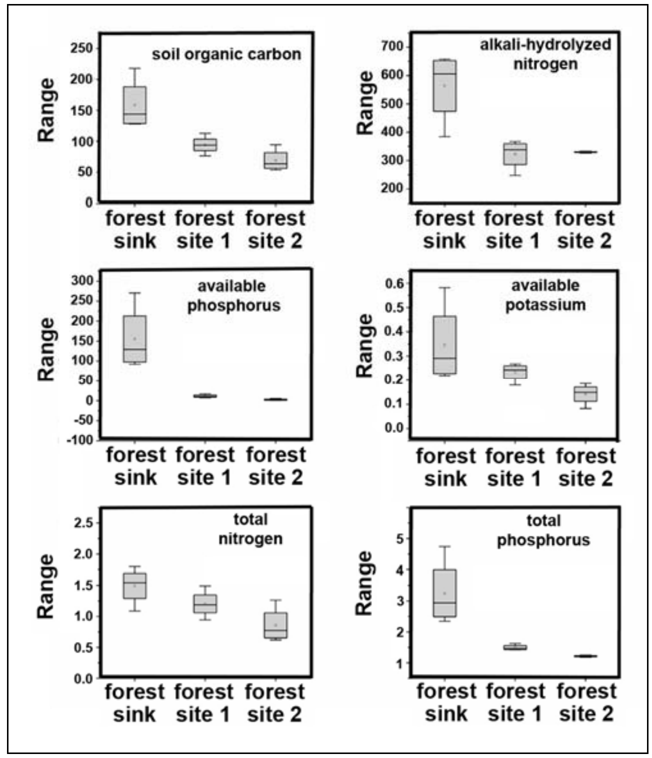

Figure 138. Soil nutrients in sinkhole forest and two surface forests. Bottom and top sections of the box plots indicate the inner quartile ranges. Horizontal bar within the box represents median. Whiskers indicate spread. Modified from Li *et al*. 2020a.

Rosseló and Ginés (1980), referring to them as potholes, reported 36 species of bryophytes in 23 sinkholes of Mallórca. They considered ***Eucladium verticillatum*** (Figure 11), ***Fissidens cristatus*** (Figure 128), ***Homalia lusitanica*** (Figure 139), ***Mnium*** sp. (Figure 38, Figure 61), and ***Thamnobryum alopecurum*** (Figure 140) to be "regular inhabitants." These species are likewise known from caves.

Figure 139. ***Homalia lusitanica***, a common species in sinkholes of Mallórca. Photo by Hugues Tinguy, with permission.

Figure 140. ***Thamnobryum alopecurum*** with capsules, a common species of sinkholes of Mallórca. Photo by David T. Holyoak, with permission.

Fergusen and Knobloch (1998) likewise found a high plant diversity in the Pliocene sinkhole of Willerhausen, Germany. Herrero-Borgonon and Puche (1987) found 26 moss species in the sinkholes of the Valencia region, Spain. In the Apuseni Mountains of Romania, Sass-Gyarmati *et al*. (2009) identified 21 liverwort and 59 moss species in sinkholes, compared to 43 species of **Cyanobacteria** and 50 of lichens.

Sinkholes can often present interesting species that are not found in other habitats of the area and, like caves, may provide conditions suitable for species of more polar or higher elevation habitats (Luo & Zhang 2017). Li *et al*. (2020c) explored the third largest sinkhole in the world – Haolong sinkhole in China. They identified 183 species, of which 26 are endemic to China.

Reyes-Colón and Sastre-D.J. (2000) reported 50 bryophyte species two sinkholes in the north-central karst region of Puerto Rico. They found that the bryophyte flora of the sinkholes was very different from that of the Puerto Rican forests and considered them to be centers for diversity in the area. Pérez and Jesús (2009) reported new bryophyte species from sinkholes in old-growth forest fragments in Puerto Rico. Allred (1998) rediscovered the tiny moss ***Fissidens littlei*** (Figure 141) in a sinkhole in New Mexico, USA.

Figure 141. ***Fissidens littlei***, a rare, tiny moss found in a sinkhole in New Mexico, USA. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Other rare surprises may delight the explorer. In the Alpena, Michigan, USA, limestone sinks, Robinson and Wells (1956) found ***Mannia sibirica*** (see Figure 113-Figure 115), ***Seligeria calcarea*** (Figure 142-Figure 143), and ***Tritomaria scitula*** (Figure 87), all new for Michigan. In all, there were 110 species of bryophytes in six sinks. Later Miller and Vitt (1970) found ***Orthotrichum pallens*** (Figure 144) in sinkholes in Alpena County – a new species for the eastern part of North America. Priwer (1979) reported that bryophytes were dominant in number of species in these sinks, and that she did not find rare species of tracheophytes.

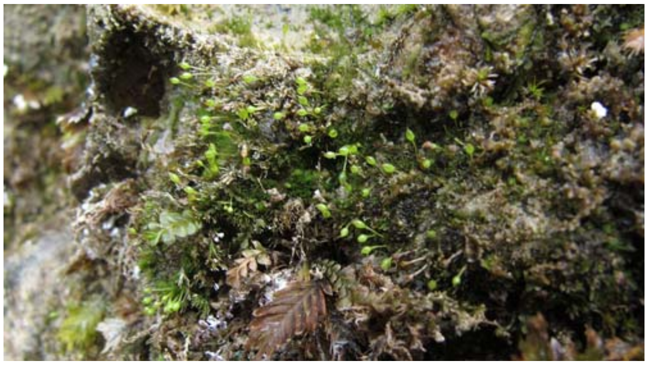

Figure 142. ***Seligeria calcarea*** with capsules, a species that occurs in the Alpena limestone sinks, Michigan, USA. Photo by Michael Lüth, with permission.

Figure 143. ***Seligeria calcarea*** with capsules, on stone. Photo by Brian Eversham, with permission.

Figure 144. ***Orthotrichum pallens*** with capsules; its occurrence in sinkholes in Alpena County, Michigan, USA, represented a new species for the eastern part of North America. Photo by Hermann Schachner, through Creative Commons.

In New Zealand, ***Timmia norvegica*** (Figure 145) occupies sinkholes on rock where there is seepage and calcareous detritus over marble (Horton & Bartlett 1983). This species is one of the bipolar species whose distributions are hard to explain.

Figure 145. ***Timmia norvegica***, a species that occurs on seepage rocks in calcareous sinkholes in New Zealand. Photo by Hermann Schachner, through Creative Commons.

Cao *et al*. (2020) described the relationship of the bryophytes to the microbial communities of sinks in the Guizhou Province, China. They found 145 species of bryophytes in the sinks, five of which were highly drought tolerant, including ***Eurohypnum leptothallum***, ***Hyophila involuta*** (Figure 146-Figure 147), and ***Racopilum cuspidigerum*** (Figure 148). They found that both moss species and the karst rocky desertification types affect the microbial communities, but that the moss species had the much stronger effect on the microbial diversity. Bacteria species composition changed strongly between mosses and drought resistance factors. Hence, bryophytes play a strong role in these communities.

Figure 146. ***Hyophila involuta*** wet, a highly drought-tolerant moss found in karst sinks in Guizhou Province, China. Photo by Bob Klips, with permission.

Figure 147. ***Hyophila involuta*** dry, a drought-tolerant species that survives on dry vertical rock surfaces. Photo by Bob Klips, with permission.

Figure 148. ***Racopilum cuspidigerum***, a highly drought-tolerant moss found in karst sinks in Guizhou Province, China. Photo by Andrew Thornhill, through Creative Commons.

Like so many of the richest bryophyte sites, sinkholes are subject to human disturbance (Liu *et al*. 2019). As refugia, the sinkholes play a crucial role in retaining many rare species, at least at the local level. As you might expect, the number of species in undisturbed sinkholes was considerably higher than in those affected by tourism or farming. Others, sadly, are used as garbage dumps.

Karstification

Karst (type of topography formed from dissolution of soluble rocks such as limestone, dolomite, and gypsum; characterized by underground drainage systems with sinkholes and caves) topography provides a variety of cave-like small and large spaces where bryophyte can live.

Šmarda (1947) recorded the presence of ***Distichium capillaceum*** (Figure 36-Figure 37) and ***Timmia bavarica*** (Figure 149) at the bottom of the deep karstic Macocha Chasm in the Czech Republic, thriving in little light but a moist environment with basic soil.

Figure 149. ***Timmia bavarica***, a species that grows at the bottom of the deep karstic Macocha Chasm in the Czech Republic. Photo by Hugues Tinguy, through Creative Commons.

Jia *et al*. (2014) explored the role of karst bryophytes and their local occupancy. They found 33 bryophytes in their study area in a Guizhou mountain area of China. In particular, they found that bryophytes were important in storing water, becoming saturated at 849-1474% of dry weight. Soil absorption ranged 464-1025%. Furthermore, they absorbed the heavy metals Pb, Zn, and Cd, with concentrations 2.25, 3.98, and 2.49 times that in their substrates, respectively. The concentrations in the bryophytes were not significantly correlated with that in their substrate. The researchers concluded that bryophytes had an important role both in providing a water reserve and in absorbing heavy metals from automotive exhaust. The water absorption helps to stabilize the road slopes in the karst area. Wu *et al*. (2019) described the vertical distribution of the **Hypopterygiaceae** and the environmental factors influencing that distribution in a karst sinkhole in China.

Bryokarst

That's right. Bryophytes contribute to karstification (Meng *et al*. 2019). Meng and coworkers explained that bryophytes can act as physical forces, including expansion, curling, freezing, and thawing (Figure 150-Figure 151). These are most evident under alternating wet and dry conditions and can destroy rock. They also can destroy rocks through metabolic secretions and the H_2CO_3 formed using the CO_2 expelled in respiration.

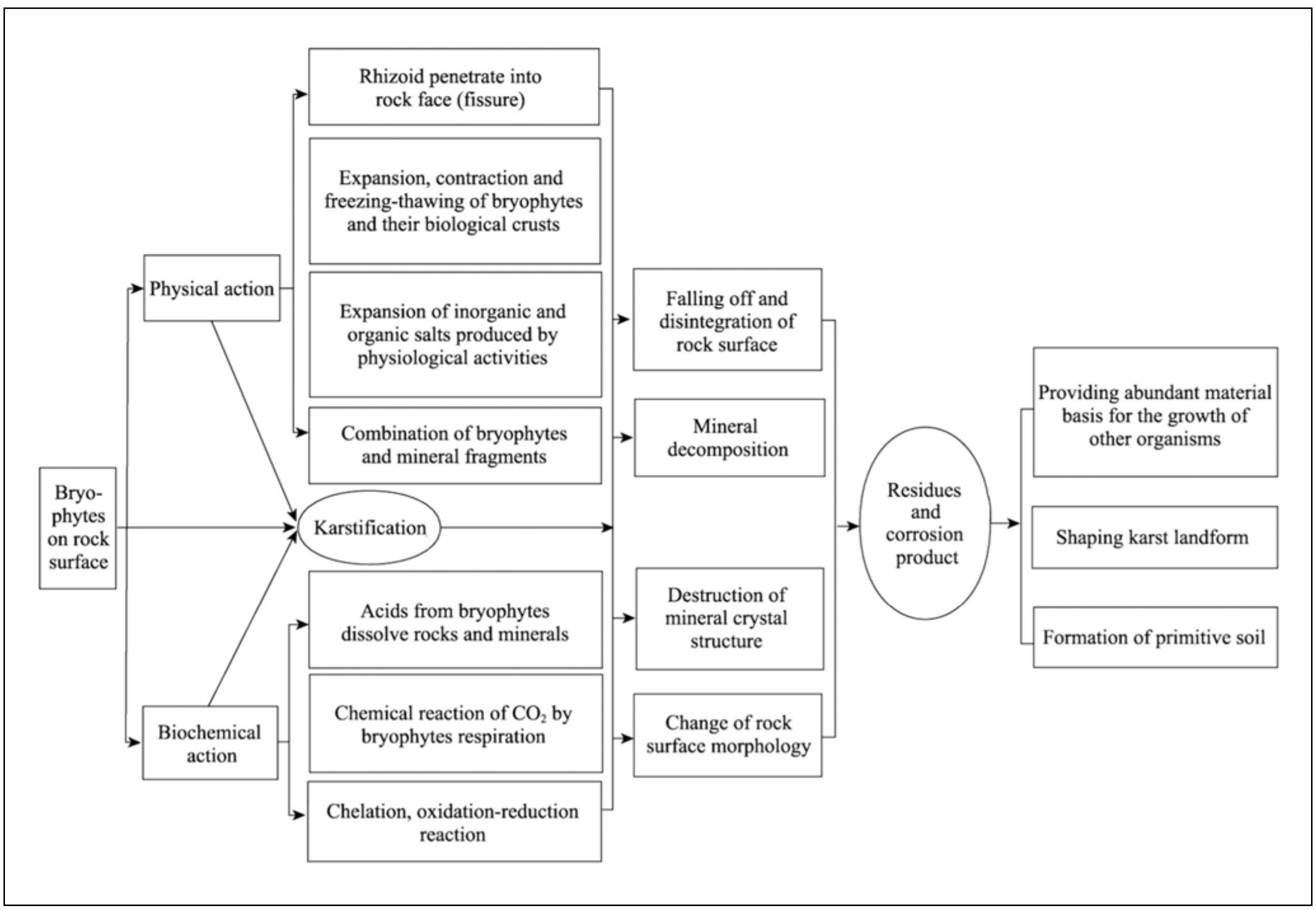

Figure 150. Flowchart showing bryophyte role in karstification. Mosses on the rock surface use physical and biochemical action to destroy and corrode the rock, change the rock surface morphology, and form the karst microtopography. The dissolved products are deposited to form the original soil. Modified from Meng *et al*. 2019.

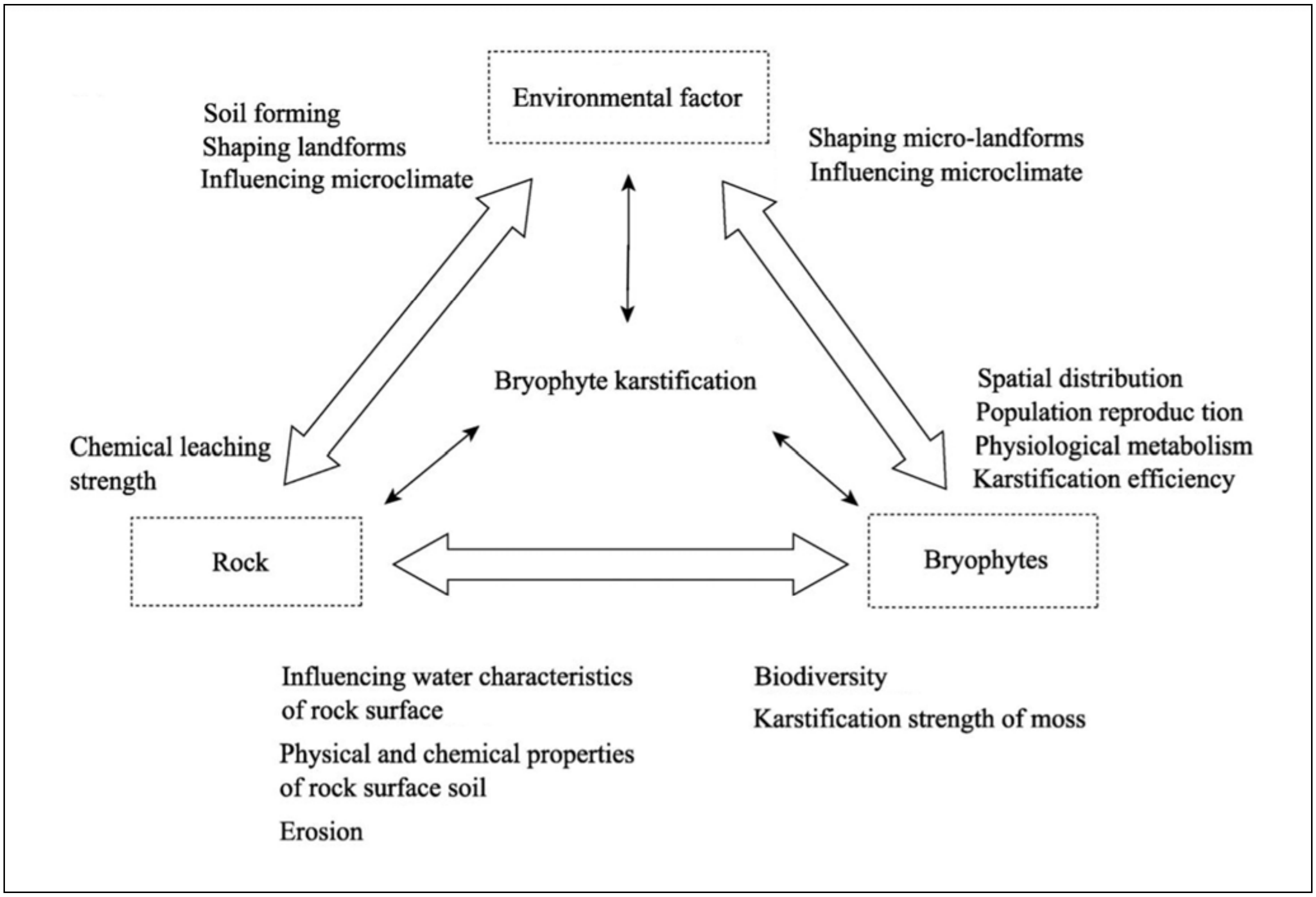

Figure 151. Three-way circulation interaction modified from Meng *et al*. (2019). The bryophytes, environmental factors, and rock promote and restrain each other in the karstification process. The environmental factors and rock affect the karstification process and its efficiency by controlling the community characteristics, morphology, physiological processes, genes, and other bryophyte factors. The resulting lithology, composition, occurrence of rock, and the improvement of the bryophytes on the rock surface microhabitat (temperature, humidity, light, soil fertility, microbes) are closely related to the rate of karstification.

Zhang *et al*. (1996) described four types of **bryokarst** deposition from caves (drop bryophytes-tufa, waterfall bryophyte-tufa, seasonal river bryophyte-tufa, and phototropism bryophytes-scale) in the Huangguoshu area of China, based on light, water availability, and bryophyte growth. They also identified four forms of bryophyte corrosions: corrosional hole, corrosional spot, corrosional block, and corrosional filament. These caves had 59 species of bryophytes in 43 genera.

Pentecost (1987) enumerated the annual growth rates of some mosses associated with tufa formation: ***Palustriella commutata*** (Figure 152), 1-4 mm; ***Eucladium verticillatum*** (Figure 11), 2-3 mm; ***Hymenostylium recurvirostrum*** (Figure 153-Figure 155), 1-3 mm; ***Platyhypnidium riparioides*** (Figure 156), *ca.* 30 mm. Pentecost (1996) followed this study with one on the role of photosynthesis vs other factors in the karstification process. ***Palustriella commutata*** and ***Eucladium verticillatum*** both deposited 6-12% of the carbonate through photosynthesis. In addition, 10-20% was deposited through evaporation and 70-80% through gas evasion.

Figure 152. ***Palustriella commutata***, a moss that grows 1-4 mm per year in tufa formation. Photo by J. C. Schou, with permission.

Figure 153. ***Hymenostylium recurvirostrum*** habit, a moss associated with tufa formation. Photo by Hermann Shachner, through Creative Commons.

Figure 154. ***Hymenostylium recurvirostrum*** on side of cliff, with icicles. Photo by Bob Klips, with permission.

Figure 155. ***Hymenostylium recurvirostrum*** showing color of lower portions and three growth regions distinguishable by color changes. This species grows 1-3 mm per year in tufa formations. Photo by Hermann Schachner, through Creative Commons.

Figure 156. ***Platyhypnidium riparioides***, a moss that grows ~30 mm per year in tufa formation. Photo by Hermann Schachner, through Creative Commons.

Lyons and Kelly (2020) pointed out the paucity of knowledge regarding deposition rate of tufa or the growth rates of involved bryophytes living in petrifying springs. Using fixed bar markers, they measured the heights of bryophytes at six petrifying springs in Ireland. They found that tufa deposits increased 20.5 ± 1.1 mm yr^{-1}. The moss ***Palustriella commutata*** (Figure 152) worked together with the surface water to increase the annual deposition of tufa by 5.7 ± 1.9 mm. Unvegetated tufa achieved a growth of only 16.5 ± 3.0 mm yr^{-1}. Thus, with an annual growth of 27.6 ± 1.9 mm, ***Palustriella commutata*** outgrows the unvegetated tufa growth. The smaller mosses ***Didymodon tophaceus*** (Figure 157-Figure 158) and ***Eucladium verticillatum*** (Figure 11) grew only 9.1 ± 1.6 mm yr^{-1} and 9.5 ± 1.3 mm yr^{-1}, respectively, thus being less important in tufa formation; they were typically displaced by ***Palustriella commutata*** through competition.

Figure 157. ***Didymodon tophaceus*** habitat at cliff base. Photo by Jean Faubert, with permission.

Figure 158. ***Didymodon tophaceus***, a tufa moss that grows at a mean of 9.1 ± 1.6 mm yr^{-1}. Photo by David T. Holyoak, with permission.

Figure 160. ***Conocephalum salebrosum*** under overhanging rocks, a common liverwort in rock canyons and behind waterfalls. Photo by Claire Halpin, with permission.

Waterfall Caves

Waterfalls often fall over ledges, creating a curtain in front of shallow caves. These caves are typically shaded and moist, with rock surfaces (Figure 159).

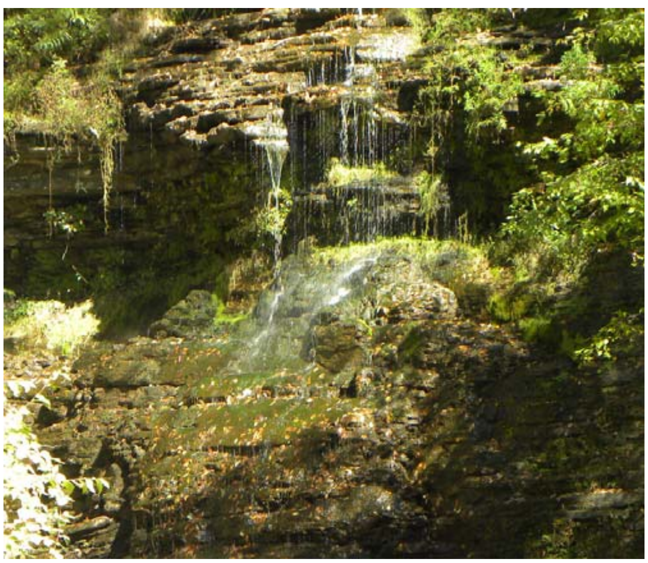

Figure 159. Waterfall in West Virginia, USA, with bryophytes and ferns growing on the ledges behind the water. Photo by Eileen Dumire, with permission.

Figure 161. ***Conocephalum salebrosum***, a common species in cool, shaded, damp places in the US. Photo by Claire Halpin, with permission.

I have seen ***Conocephalum*** (Figure 126, Figure 160-Figure 161) species several times in the shallow caves behinds waterfalls (Figure 162). Although these were usually named as ***Conocephalum conicum*** (Figure 126) in North America, we have recently realized that these are really ***Conocephalum salebrosum*** (Figure 160-Figure 161), a species with much larger thalli than those of the former. This habitat occurs in the Keweenaw Peninsula of Michigan, USA, and at Hocking Hills, Ohio, USA. The latter also has a number of small caves where the species is abundant.

Figure 162. Scot Falls, Michigan, USA, with cave behind waterfalls. Bryophytes occur on the ceiling of the cave. Photo by Janice Glime.

Higuchi *et al*. (2020) reported ***Fissidens geminiflorus***, ***F. nobilis*** (Figure 163), and ***Timmiella anomala*** (Figure 164) on wet stones in a cave behind a waterfall in Cambodia.

Figure 163. ***Fissidens nobilis***, a moss that lives on wet stones behind a waterfall in Cambodia. Photo by Janice Glime.

Figure 164. ***Timmiella anomala***, a moss that lives on wet stones behind a waterfall in Cambodia. Photo from Earth.com, with permission.

Natalie Cleavitt found ***Haplodontium macrocarpum*** (Figure 165) in Mountain Park, Alberta, Canada, where it occurs on the underside of overhangs associated with ephemeral waterfalls (Dale Vitt, pers. comm. 4 August 2021).

Figure 165. ***Haplodontium macrocarpum*** on cave wall, a species that also occurs under overhangs of ephemeral waterfalls. Photo by René J. Belland, with permission.

Townsend (2006) reported ***Epipterygium tozeri*** (Figure 166) from Kenya in a cave behind a waterfall.

Figure 166. ***Epipterygium tozeri***, a species that grows in a cave behind a waterfall in Kenya. Photo by Hugues Tinguy, with permission.

Other Bryophyte Roles

Building and destroying cave formations are not the only roles of bryophytes in caves. They increase the diversity of stalactites and stalagmites (Mulec 2018). They can be diversity hotspots. Bryophytes increase the loss of water by 81.2 times and absorption by 8.1 times, the highest compared to the algae (18.8 and 1.6) and lichens 2.9 and 19.1) (Cao & Yuan 1999). Bryophytes also prolong the period of water loss by 610%, but do not extend the period of absorption. This improves the water holding by 57.2 times! This increases the activity of the carbon cycle on the rock surface, affection rates of corrosion under the growths.

Pentecost (1999) notes the importance of bryophytes, along with algae, in stabilizing ephemeral sand ripples on steep rock surfaces in the UK. Fu and Zhang (2010) identified four types of bryophyte erosions on limestone: erosional fusion, erosional plaques, erosional bands, and erosional blocks.

Ren *et al*. (2010) found that the rare and endangered flowering plant ***Primulina tabacum*** (Figure 167) is found

only at cave entrances of a small number of karst caves in southern China. The researchers transplanted small plants of this species to several new cave entrances. The only seedlings that survived were associated with the moss ***Gymnostomiella longinervis*** (Figure 168), performing well under the cover of the moss. It appears that the moss nurse plant is necessary for the success of ***P. tabacum***.

Figure 167. ***Primulina linearifolia*** × ***Primulina tabacum***; ***Primula tabacum*** seems to require the moss ***Gymnostomiella longinervis*** to be successful in karst cave entrances. Photo by Kenpei, through Creative Commons.

Figure 168. ***Gymnostomiella longinervis*** on bark, a moss that helps ***Primulina tabacum*** succeed in entrances of karst caves in southern China. Photo through Creative Commons.

Submerged cave bryophytes can serve as substrate for the diatom ***Pinnularia borealis*** (Figure 169) (Czerwik-Marcinkowska *et al.* 2019). The cyanobacterial ***Gloeocapsa atrata*** (Figure 170) occurs frequently on mosses on wet cave wall rocks in the Glowoniowa Nyża Cave. The latter species can contribute to nitrogen fixation, thus increasing the levels of usable nitrogen in the cave.

Figure 169. ***Pinnularia borealis***, a diatom that often uses bryophytes as a substrate in caves. Photo from BELSPO, with online permission.

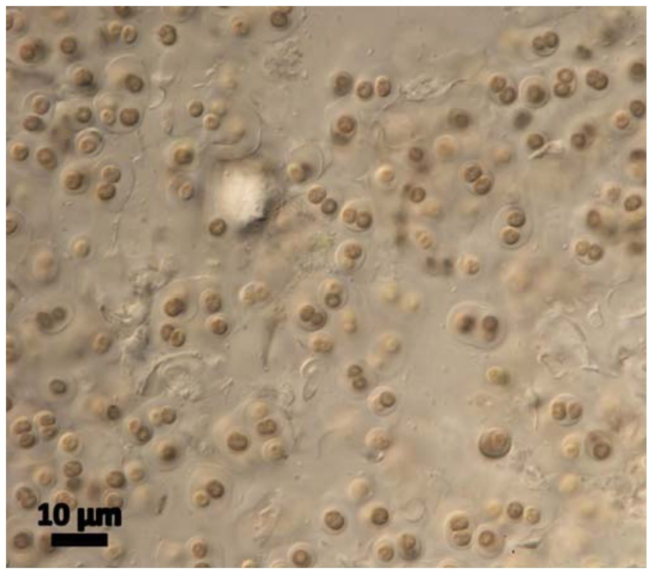

Figure 170. ***Gloeocapsa atrata***, a member of **Cyanobacteria** that fixes nitrogen and can occur on mosses in caves. Photo by Sergei Shalygin, through Creative Commons.

Cave Fauna Interactions with Bryophytes

Galas *et al.* (1996) found that the decay rates of two seed plants and of moss were all slow in a mountain cave in the Tatra Mts., Poland. They attributed this slowness to the absense of large shredders in the cave. The energy released through respiration by microorganisms on the moss was higher than that released from microorganisms on sorb and alder litter.

Cao and Yuan (1999) reported that the water holding by evaporation of carbonate rock increases 81.3 times and water absorption by 8.1 times for mosses compared to relative fresh rock samples. The amount of water holding by the rock improves 57.2 times with mosses on them.

Copepods

In Japan, Iwatsuki and Ueno (1959) found the fern ***Cyrtomium fortunei*** (Figure 171) and moss ***Fissidens geminiflorus*** (see Figure 128, Figure 134, Figure 141, Figure 163) to be dominant, sometimes obtaining a "full growth." They also found cave fauna that associated with the mosses, including the harpacticoid copepod ***Bryocamptus zschokkei*** (Figure 172), the latter occurring in a carpet of ***Fissidens geminiflorus***.

Figure 171. ***Cyrtomium fortunei***, a dominant fern in some Japanese caves. Photo by Bing Liu, Kew Plants of the World, through Creative Commons.

Figure 172. ***Bryocamptus zschokkei***, a harpacticoid copepod associated with mosses in caves in Japan. Photo by Joe Connolly, through Creative Commons.

Stoch (2000) reviewed the aquatic fauna of caves in northern Italy, including some that are part of the bryophyte fauna. Watiroyram *et al*. (2012) found 11 species of the copepod ***Bryocyclops*** (Figure 173) from wet mosses in caves.

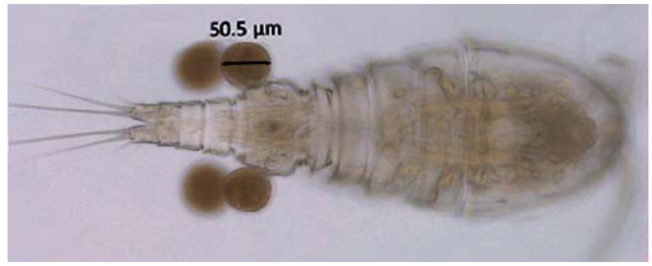

Figure 173. ***Bryocyclops*** sp.; 11 species in this genus occur among mosses caves in Italy. Photo by Watiroyram, S., through Creative Commons.

Tardigrades

One of the best places to look for tardigrades is nestled among the leaves of bryophytes. Cave-dwelling tardigrades are no exception to that (Bartels & Nelson 2007). This affinity for bryophytes, particularly mosses, includes a special adaptation for feeding on the mosses [Tardigrada (Water Bears) 2005]. Members of **Echiniscidae** are adapted to this mode of living by having a long stylet that can penetrate the moss cell wall and suck out the cell contents. In addition to eating moss cell contents, the bryophyte dwellers might eat epiphytic diatoms and bacteria from the moss surface.

Insects

In addition to the copepod, Iwatsuki and Ueno (1959) found the troglophilous fly ***Exechia*** sp. (fungus fly; Figure 174) associated with the mosses in a cave in Japan.

Figure 174. ***Exechia fusca*** adult, a fungus fly similar to those that occur with mosses in a Japanese cave. Photo by Jostein Kjaerandsen, through Creative Commons.

Even in Death Valley. California, USA, caves can serve as a refuge for insects. Hungerford (1917) reported the true bug ***Mesovelia mulsanti*** (Figure 175) from among mosses in a hot spring cave. Later, Polhemus and

Chapman (1979) reported ***Mesovelia amoena*** (Figure 176) on moss-covered rocks in hot spring caves, also in Death Valley. This species is parthenogenetic in Hawaii, a trait that might make reproduction easier in caves. Kamp (1970) reported cave grasshoppers that were associated with bryophytes in caves in the western United States.

Figure 175. ***Mesovelia mulsanti***, a true bug that occurs among mosses in a hot spring cave in Death Valley, California, USA. Photo by Matt Bertone, through Creative Commons.

Figure 176. ***Mesovelia amoena*** wingless female, a species that lives on moss-covered rocks in hot spring caves in Death Valley, California, USA. Photo by Claudia Moreno-R., Wendy Molina-J., Juliana Barbosa, and Filipe Moreira, through Creative Commons.

In icefields, ice bugs (**Grylloblattodea**) lay their eggs in the soil or mosses (Ramel 2015). They hide under stones during the ay and prefer low temperatures. These also occur in caves in Korea. These insects are extremophiles. In the Oregon Caves in the Klamath Mountains of Oregon and California, USA, Schoville (2012) found three new species of **Grylloblattodea**: ***Grylloblatta oregonensis*** (Figure 177), ***G. siskiyouensis***, and ***G. marmoreus***. This species occupies the dark zone and twilight zone of caves. Their relationships to the bryophytes in the caves is not known, but they may have the same uses for egg laying as members of the genus found in Korea.

Figure 177. ***Grylloblatta oregonensis***, a new species discovered in Oregon caves in the twilight and dark zones. Other members of the genus use mosses for egg laying, but egg laying has not been described in this species. Photo through Creative Commons.

There are two tiphiid wasp species (***Tiphia andersoni*** and ***T. nona*** – see Figure 178) that are able to hibernate beneath rocks surrounded by mosses in caves (Wynne 2013). Moss gardens in lava tubes have the most developed bryophyte communities (Lindsey 1951) and present a biologically unique bryophyte community (Lightfoot *et al.* 1994; Wynne 2013). This includes a high arthropod biological diversity (Wynne 2013).

Figure 178. ***Tiphia*** sp. Several species in the genus hibernate beneath rocks surrounded by mosses in caves. Photo by XPDA, through Creative Commons.

Other Arthropods

Importantly, this habitat has been identified as supporting at least two presumed relict species (Lightfoot *et al*. 1994, this paper) and high arthropod biological diversity (Wynne 2013).

Benedict (1979) found that the pseudoscorpion ***Apochthonius forbesi*** (see Figure 179) benefits from the mossy litter layer in sinks in Oregon, USA. This species was described as a new species based on populations in a lava tube sink where it lived at the cold air trap that

retained permanent ice but a mossy litter layer. ***Syarinus*** (Figure 180) was an accompanying species in this habitat.

Figure 179. ***Apochthonius diabolus***; ***Apochthonius forbesi*** lives in lava tube sinks with permanent ice and a mossy litter layer. Photo by Steve Taylor and Mike Slay, through Creative Commons.

Figure 180. ***Syarinus*** sp.; a species in this genus of pseudoscorpion accompanies ***Apochthonius forbesi*** in lava tube sinks with permanent ice and a mossy litter layer. Photo by P. M. Brousseau, through Creative Commons.

Wynne and Shear (2016) found a new millipede species, ***Austrotyla awishoshola*** in "cave moss gardens" in New Mexico, USA. The millipedes need mesic conditions, and these are limited in these caves to locations with mosses. As is the case for mosses, the caves serve as refugia for insects and other fauna that found refuge here following the end of the more moist Pleistocene. Such refugia are known in other parts of the world where mosses have become the restricted environment for relict species (Benedict 1979; Wynne *et al.* 2014).

For the invertebrate cave fauna, the bryophytes provide opportunities for a high diversity. They are also home to the relict spider ***Lepthyphantes turbatrix*** (Figure 181) (Wynne 2013).

Figure 181. ***Lepthyphantes turbatrix***, a spider that uses cave mosses as a home. Photo by Tom Murray, through Creative Commons.

Salamanders

Some salamanders are especially adapted to cave living. Others benefit from the cooler, more moist conditions. Gorman and Camp (1953) found the new species ***Hydromantes shastae*** (Figure 182-Figure 183) under a mossy log at a cave entrance in California, USA. The salamander ***Aneides aeneus*** (Figure 184) is known to eat mosses (Lee & Norden 1973), although it may just be the result of foraging there for ants and spiders. This salamander has occurred in Bat Cave in Rutherford County, North Carolina, USA, and is also known from Cooper's Rock, West Virginia, where small caves or cave-like habitats can occur among the rocks.

Figure 182. ***Hydromantes shastae***, a species that includes mossy logs at a cave entrance as a hiding place. Photo by James Bettaso, USFWS, through public domain.

Figure 183. ***Hydromantes shastae*** showing a color form that is well adapted to a mossy habitat. Photo by John Clare, through Creative Commons.

Figure 184. ***Aneides aeneus***, a species known to eat mosses and hangs out among boulders and in caves. Photo by Alan Cressler, through public domain.

Frogs

In the borderland between Venezuela and Brazil, Myers and Donnelly (1997) found the frog ***Eleutherodactylus cavernibardus*** (*cavernibardus* means cave singer; see Figure 185) calling during the day in local caves formed by granite boulders or on mosses. It is likely that the frogs use both of these habitats.

Figure 185. *Eleutherodactylus planirostris*; ***Eleutherodactylus cavernibardus*** calls from mosses in caves. Photo by Todd Pierson <www.discoverlife.org>, with permission.

Angulo *et al*. (2003) reported ***Stefania riae*** in a sinkhole at Sarisariñama tepui in Peru. The habitat lacked either flowing or standing water, but the walls of rocks, crevices, and caves were moist and mossy, presumably providing moisture for the frogs, as suggested by Barrio-Amorós and Fuentes (2003).

Reptiles

Little seems to be known about the role of bryophytes for cave reptiles. Storey (2006) reported that reptiles seek refuge in winter in locations such as caves, burrows, grass, or moss hummocks. It might be worthwhile to look for some of the smaller reptiles among the cave mosses in winter. If nothing else, the mosses might be a source of invertebrate food. I wonder if lizards and snakes find the older sinkholes in Florida suitable.

Birds

Even birds can benefit from bryophytes in caves. In Brazil the White-collard Swift [***Streptoprocne zonaris*** (Figure 186)] typically breeds in wet caves next to waterfalls (Figure 187) (Biancalana 2014). Nests are made mostly of bryophytes (Figure 188). The birds returned to the same nest sites in subsequent years.

Figure 186. ***Streptoprocne zonaris*** on rock wall. Photo by Amesac, through Creative Commons.

Figure 187. ***Streptoprocne zonaris*** behind waterfall, where it typically builds nests mostly of mosses. Photo by Donald Hobern, through Creative Commons.

Figure 188. ***Streptoprocne zonaris*** on nest made of mosses. Photo by Sesernam, through Creative Commons.

On the young island of Surtsey, Iceland, a Herring Gull-Glaucous Gull hybrid pair [***Larus argentatus*** (Figure 189) - ***Larus hyperboreus*** (Figure 190)] nested in a small collapsed cave, using primarily the moss ***Racomitrium*** (Figure 31-Figure 32) as nesting material (Olafsson 1982). When a Berlese funnel was used to search the nest for arthropods, only a single specimen, that of an **acarid** (mites & ticks) was revealed.

Figure 189. ***Larus argentatus***; a hybrid of this species uses ***Racomitrium*** as nesting material in the volcanic island of Surtsey, Iceland, in a collapsed cave. Photo by Kulac, through Creative Commons.

Figure 190. ***Larus hyperboreus*** and offspring; a hybrid of this species uses ***Racomitrium*** as nesting material in the volcanic island of Surtsey, Iceland, in a collapsed cave. Photo by A. Weith, through Creative Commons.

The Biscutate Swift (***Streptoprocne biscutata***; Figure 191) has been studied at its home in a cave in the Paraná State, southern Brazil (Pichorim 2002). The birds use bryophytes, among other plants and lichens, to build its nests. When the birds are nesting in the cave, the cave floor has abundant moss and lichen fragments. The birds collect these materials for nesting and at times even pull pieces of bryophytes from the vertical wall. The unusual observation was that they appeared to chew the fragments soon afterwards. Observations of a viscous substance in the moss fragments in the nests suggest that the chewing was practiced to add the saliva. Fragments in the nests included the liverworts ***Frullania brasiliensis*** (Figure 192) (most common – 14 of 23 nests), ***Herbertus*** sp. (Figure 193), ***Lejeunea flava*** (Figure 194), ***Omphalanthus filiformis*** (Figure 195), ***Plagiochila*** sp. (see Figure 74), and ***Plagiochila rutilans*** (see Figure 74), and the mosses ***Campylopus*** sp. (see Figure 196), ***Campylopus aemulans*** (Figure 196), ***Leucobryum crispum*** (Figure 197), ***Leucoloma*** sp. (Figure 198), ***Macromitrium punctatum*** (Figure 199), ***Phyllogonium viride*** (Figure 200), ***Polytrichum juniperinum*** (Figure 47-Figure 48), ***Porotrichum longirostre*** (see Figure 201), ***Rhacocarpus*** sp. (Figure 202), ***Schlotheimia rugifolia*** (Figure 203), ***Schlotheimia tecta*** (Figure 204), ***Sematophyllum subpinnatum*** (see Figure 205), ***Squamidium leucotrichum*** (Figure 206), ***Syrrhopodon prolifer*** (Figure 207), and ***Zelometeorium recurvifolium*** (Figure 208).

Figure 191. ***Streptoprocne biscutata***; when this species nests in caves in Brazil, it uses mosses available from the cave floor as nesting material. Image by Joseph Wolf and J. W. Wood, through public domain.

Figure 192. ***Frullania brasiliensis***, a liverwort used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Jan-Peter Frahm, with permission.

Figure 193. ***Herbertus aduncus*** subsp. ***hutchinsiae***; a species of ***Herbertus*** is used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by J. Barry Stewart, with permission.

Figure 194. ***Lejeunea flava***, a liverwort used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Rory Hodd, with permission.

Figure 195. ***Omphalanthus filiformis***, a liverwort used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 196. ***Campylopus aemulans***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 197. ***Leucobryum crispum***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Claudio Delgadillo-Moya, with permission.

Figure 198. ***Leucoloma*** sp., a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Shyamal L., through Creative Commons.

Figure 199. ***Macromitrium punctatum***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Maarta Luz Uribe, through Creative Commons.

Figure 200. ***Phyllogonium viride*** with capsules, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by George Shepherd, with online permission.

Figure 201. ***Porotrichum bigelowii*** branch; ***Porotrichum longirostre*** is a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Brian Starzomski, through Creative Commons.

Figure 202. ***Rhacocarpus purpurascens***; a species of ***Rhacocarpus*** is used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Jan-Peter Frahm, with permission.

Figure 203. ***Schlotheimia rugifolia***,a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Juan David Parra, through Creative Commons.

Figure 204. ***Schlotheimia tecta***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 205. ***Sematophyllum*** sp.; ***Sematophyllum subpinnatum*** is used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 206. ***Squamidium leucotrichum***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

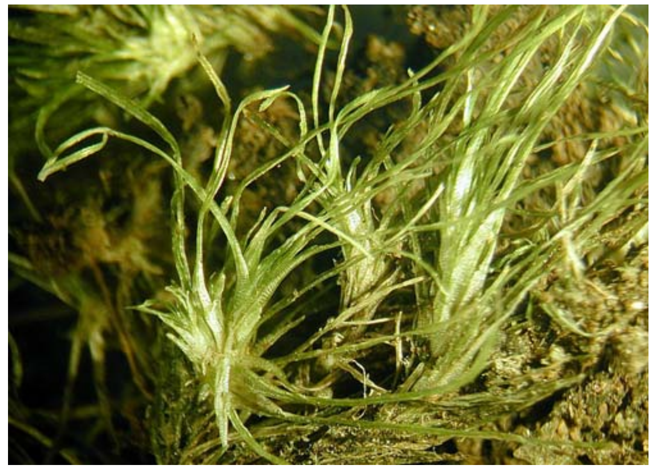

Figure 207. ***Syrrhopodon prolifer*** var. ***scaber***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 208. ***Zelometeorium patulum***; ***Zelometeorium recurvifolium*** is used in nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Mammals

Several mammals use caves as their dens. The bear has perhaps the most influence on the bryophytes. The brown bear (***Ursus arctos***; Figure 209) includes mosses to line its den (Czerwik-Marcinkowska *et al*. 2019). This can bring moss spores and fragments into the cave for possible establishment and growth there.

Figure 209. ***Ursus arctos*** (brown bear) running, a species that uses mosses to line its den in caves. Photo by Malene Thyssen, through Creative Commons.

Sampling Methods

Bryophyte sampling methods have varied among researchers. Many researchers sought only to document the flora, with no attempt to quantify species. Li *et al*. (2020a) used 8 plots, 10 x 10 m, in each section of a sinkhole, totalling 80 plots. In addition to assessing the bryophyte flora, they measured depth, *p*H, light level, humidity, temperature, and slope, making it possible to find correlations.

Although caves have more constant conditions than those found outside the cave, conditions nevertheless vary between caves and within the caves. Poulson and Culver (1969) measured evaporative rate, substrate moisture, substrate organic content, predictability and stability of food and microclimate, substrate diversity, and intensity of flooding in Mammoth Cave, Kentucky, USA. They found that arthropod diversity exhibited significant correlations with substrate diversity, substrate organic content, and intensity of flooding. To this list, light intensity must be added for photosynthetic organisms, and even for some cave animals. Thus it is instructive to measure these conditions.

Nakanishi (2002) established 14 quadrats in a light intensity gradient. The quadrats were 20 x 20 cm and restricted to clayey soils; they assessed the bryophytes using the Braun-Blanquet method.

Pakeman *et al*. (2019) used Attribute values based on the Ellenberg values (see Schaffers & Sýkora 2000) to describe the nitrogen, light, and moisture in bryophyte habitats in Scotland. These have been used in some cave studies for similar purposes.

Summary

Cave-like conditions are present in a variety of landforms. Among these are mine shafts, subways, fissures, minicaves among rocks and at the base of boulders, among scree, ice caves, windholes, sinkholes, behind water falls, and in animal burrows. These differ in available light, substrate, moisture, nutrients, *p*H, and toxic substances such as pollutants.

Mine shafts are often vertical structures with light diminishing with depth. The exposure of the substrate to the ore being mined can be a toxic factor. There are few published records of bryophytes in mines, but the presence of the ubiquitous ***Ceratodon purpureus*** is a not surprising find.

Subways are typically well lit and may have some of the same species as caves. Because the subway age is known, it can provide a suitable laboratory for studying colonization rates.

Small fissures often support surface bryophytes due to their collection of nutrients and soil and a greater moisture-holding ability than the rock surface. Larger fissures as found in lava fields, geothermal areas, and some large rock formations may support bryophytes for a short distance into the fissure, again dependent on light, moisture, and substrate type. Such fissures offer protection from direct sun, reducing sun bleaching, photoinhibition, and drying.

Among the lava rocks and fissures one can find ***Saelania glaucescens***, ***Distichium inclinatum***, and ***Schistostega pennata***, but much more study is needed to relate the bryophyte species to the cave-like locations vs the surface locations. The scree presents a similar problem, although there are more studies that list species found there. Despite the shallowness of its caves, they can provide cool refugia in otherwise hot, dry, exposed fields of rock.

Ice caves typically do not support bryophytes, but ***Heterocladium heteropterum*** and ***Cyrtomnium hymenophylloides*** are known in ice caves. On the other hand, the cool air from these caves, especially in summer, can alter the climate and bryophyte composition outside the cave. Windholes have similar effects, providing a cool cave, but also cooling the area near the cave. These cool refugia permit Arctic species to live at much lower latitudes, occurring there as disjuncts.

Sinkholes have much in common with caves, including low light and usually greater moisture. However, they experience seasonal changes much like the surrounding forest. They have many species on their walls that coincide with those in caves. Their responses to these conditions are similar to those of bryophytes in caves: sterility, leaf elongation, longer internodes, elongation of cells, and disappearance or attenuation of the rib or costa. The protection provided by the sinkhole can result in a greater species diversity than that found in the surrounding forest.

Karstification is a process of dissolution of soluble rocks, characterized by underground drainage systems with sinkholes and caves. Bryophytes can play a role in the process, creating stalactites and stalagmites by the accumulation of $CaCO_3$ around some bryophyte

species, particularly accomplished by ***Eucladium verticillatum***. The bryophytes can also destroy rock formations by exuding organic acids or holding water that makes breakdown of the rock easier.

Waterfall caves maintain a moist habitat while reducing light intensity. They seem to be an especially suitable habitat for some ***Conocephalum*** species. There are probably many records for this habitat, but they are often embedded in studies of the larger area without specific separation of the cave area.

Bryophytes in caves can serve various roles for the cave fauna. For copepods, tardigrades, insects, and other arthropods, they provide cover and moisture and sometimes food. Salamanders may forage there or sometimes use the bryophytes for cover and moisture conservation. Frogs can use them as calling locations and sources of moisture. Reptiles can occasionally be found there. Birds use them for nesting material, as do some mammals, especially bears.

Cave sampling is useful to determine gradient effects on species composition. This sampling typically uses quadrats (plots) of 10 x 10 cm or larger. A distance transect is useful for assessing gradient effects. It is useful to measure both physical and chemical parameters along these transects.

Acknowledgments

Many Bryonetters responded to my call for images for this chapter. They especially contributed to my coverage of sinkholes. Thank you to our Chinese colleagues (Wen Ye, Xinlei Guo, Yang Liu, Xiaoming Shao, and Wang Zhe) who responded to my request for the English translation of the abstract of a Chinese study.

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