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CHAPTER 12-1
TERRESTRIAL INSECTS: HABITAT AND ADAPTATIONS

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CHAPTER 12-1
TERRESTRIAL INSECTS: HABITAT AND ADAPTATIONS

Figure 1. This tiny moving moss on the back of an insect is among the many unknown wonders awaiting us among the bryophyte-insect interactions. Photo courtesy of Aline Horvath.

Mosses are useful to the insect tribe, countless numbers of which find homes among their branches, and roam about in their shades as in mighty forests, looking with their thousand eyes upon the wonders of their leaves, and sunning their wings of purple and of gold, and burnishing their shining armour upon the polished columns of their urns. Frances Tripp, British Mosses, 1888.

Bryophytes can be so unique as to be the source of as yet undescribed species (Figure 1) and even genera of insects, as will be seen in the many orders of insects discussed in the following subchapters. They harbor numerous kinds of insects as well as other arthropods (*e.g.* Takaki 1957). And they provide habitat to protect insects all over the world (Schwarz *et al*. 1993) and in all kinds of habitats (Merrifield 1994).

Bryophytes as Habitat

Bryophytes not only provide a direct habitat for insects, but they alter the soil habitat beneath them. Gerson (1969) suggested that abundance of arthropods in the Antarctic is dependent on this soil alteration. Presence of moss can moderate the soil temperature and moisture and may in some cases discourage digging by would-be predators on soil organisms.

The bryophyte habitat is subject to the climatic and microclimatic differences dictated by elevation, distance from sea, topography, and latitude, resulting in arthropod community differences (Andrew *et al*. 2003). These differences extend to such limited habitats as that of epiphyllous liverworts (Lücking & Lücking 1998). Andrew and Rodgerson (1999) found that in the Tasmanian Mountains, site scale variation (2 km or less) is the major contributor to the bryophyte faunal diversity, seemingly more important than altitude.

Drozd *et al*. (2008, 2009) found that even higher taxonomic levels formed associations that indicate interactions between the presence of bryophytes and other microhabitat features. Sampling only seven bryophyte species in the Czech Republic, they obtained more than 55,000 specimens of arthropods. They show that the presence of bryophytes, the species of bryophytes, and the moisture levels are very important determinants of arthropod abundance. Nevertheless, abundance of arthropods was greater in the litter than in the moss cushions. Since many of the arthropods are searching for prey, the density of the moss cushions limits the size and requires agility to permit the arthropods to navigate to capture prey. Instead, the bryophytes serve as a refuge for prey organisms that can find their food there. These require only limited movement, making them relatively invisible to predators. This limited movement also leads to trap bias in the pitfall traps as these insects typically do not leave the safety of the bryophyte cushions. Weikel and Hayes (1999) pointed out that while the abundance of arthropods as potential food for birds may correlate positively with bryophyte cover, the bryophytes may act as hiding places, thus rendering most of them unavailable to the birds.

Drozd *et al*. (2007) found that about 25% of the insect species in forest floor communities (litter and mosses) are present only among the mosses. Moisture was the primary factor accounting for their distribution.

But, as Drozd *et al*. (2007) pointed out, our knowledge of the mosses as a food source is all but unknown. One of the means of identifying whether bryophytes are eaten is to recognize bryophyte fragments in the faeces or frass. Matthaias Nuss (pers. comm. 16 January 2008) provided me with an image of ***Tortula truncata*** with chewed leaves and what appeared to be frass on the plant (Figure 2). But then, how often can we identify the producer of the frass?

Figure 2. Possible insect frass on ***Tortula truncata***. Matthaias Nuss of the Museum für Tierkunde / Museum of Zoology, Dresden, Germany (pers. comm. 16 January 2008) suggests that these may be sclerified head or mandible parts that have an interesting attachment to the sporophytes of these mosses. There appear to be no silk threads, ruling out moth larvae, but **Byrrhidae** (**Coleoptera**) or some **Mecoptera** are good candidates. Photo courtesy of Robin Stevenson.

Drozdová *et al*. (2009) considered mosses to be unique habitats that could provide safe sites against predators. To test this hypothesis, they used living bait in a vertical gradient (surface level, moss cushions, bushes, tree trunks). The bait was living larvae of the blowfly ***Calliphora vicina***, a common prey item. The locations included leaves of blueberries (*Vaccinium myrtillus*), mosses [***Polytrichastrum formosum*** (Figure 3), ***Polytrichum commune*** (Figure 4), and ***Dicranella*** sp. (Figure 4)], and spruce (*Picea abies*) trunks. After 30 minutes of exposure the researchers counted the attacked and missing larvae and noted the presence of predators. The dominant predators were ants and spiders, the same as the forest floor in general (Drozdová *et al*. 2009). The predation rate inside the moss cushions was about the same as that in the litter, but the taxonomic groupings of the predators differed. Millipedes were the dominant predators in cushions of ***Dicranella*** sp and ***Polytrichum commune***, with spiders and beetles (**Carabidae** and **Staphylinidae**) following. Centipedes also occurred on the ground in areas of moss cushions under the *Vaccinium myrtilloides*. The highest predation occurred inside the ***Polytrichum*** cushions, with the same rate on the terminal parts of the plants as on the tree trunks. It appears that the structure of the moss cushion – the growth form – might be an important determinant of predation risk.

Figure 3. ***Polytrichastrum formosum***, a forest moss that houses a moderate number of insects. Photo by David T. Holyoak, with permission.

Figure 4. ***Polytrichum commune***. ***Polytrichum*** cushions can be home to numerous beetle species. Photo by A. J. Silverside, with permission.

Figure 5, ***Dicranella heteromalla*** with capsules, a species that is home to millipede predators. Photo by Michael Becker, through Creative Commons.

We aren't always sure why or how bryophytes contribute to the habitat needs of insects, but there is certainly evidence that they make a difference. Pavel *et al.* (2007) used pitfall traps in the Czech Republic to compare the beetles (**Coleoptera**) in forest communities with and without a moss layer. With the caveat that there is not necessarily a cause and effect relationship, an accumulation of such studies do indicate that it is worth exploring the role of the bryophytes. In this case, two traps were placed in ***Polytrichum*** (Figure 4) cushions and two were at least 10 m away from the nearest cushions at each of three sites. In their collections, beetles reached the highest numbers among the insects, with 56 species and the greatest abundance. Overall, they found a higher insect species richness in the moss communities, with ~25% of the insect species only occurring among the mosses. Not surprisingly, moisture was the most important environmental character affecting habitat preference, but presence of a moss layer was not significant. Only one of the species was **bryophagous** (bryophyte consuming), a member of the beetle family **Byrrhidae** (Figure 6). Especially in drier regions, the insects tended to inhabit the moss cushions, behaving as **bryobionts**.

In the Spitsbergen coastal tundra, Bengston *et al.* (1974) found 268,000 insects on the wet moss tundra, compared to 518,000 on grassland. The abundance of major insect groups were similar between the Spitsbergen tundra and high alpine areas of southern Norway.

In the Czech Republic, Božanić *et al.* (2013) used heat extraction from bryophytes to determine the effects of species of bryophytes and environmental factors on the animals present. In these samples they found 45 species of invertebrates among the 15 bryophyte species examined. Surprisingly, few were insects, all in the **Formicidae** (4 species of ants). Rather, there were 9 species of centipedes, 7 of millipedes, 4 of pseudoscorpions, 6 of isopods, 4 of harvestmen, 6 of earthworms, and 5 of spiders. ***Brachythecium oedipodium*** (Figure 7) had the richest assemblages of invertebrates. These numbers are probably minimal as some bryophyte dwellers do little moving and may die before escaping the heat within the bryophyte clump in the funnel and heat separation apparatus. The ones found are all able to move rather quickly, so this may explain the absence of bugs, beetles, and other insect groups. The type of substrate and height above ground proved to be the most important factors affecting the invertebrate distribution.

Figure 6. ***Cytilus sericeus*** (**Byrrhidae**) adult on mosses. Photo by S. Rae, through Creative Commons.

Figure 7. ***Brachythecium oedipodium***, home to a rich assemblage of invertebrates. Photo by Michael Lüth, with permission.

At McKenzie Table Mountain Preserve in California, USA, Bettis (2008) found that the moss fauna on two species of **Grimmia** (Figure 8) were mostly tardigrades, mites, springtails, and midge larvae. Studies of bryophyte fauna commonly indicate that spiders (**Araneae**), springtails (**Collembola**), and mites (**Acari**) are the most common fauna (von der Dunk & von der Dunk 1979; Kinchin 1990). Even on Signy Island in the maritime

Antarctic, the mites and springtails predominate (Usher & Booth 1984). The upper, green moss communities differed from the lower, dead moss communities. The same species tended to occur in both layers, but the proportions differed.

Figure 8. ***Grimmia pulvinata*** with capsules, home to tardigrades, mites, springtails, and midge larvae in California, USA and elsewhere. Photo by Javier Martin, through Creative Commons.

Von der Dunk and von der Dunk (1979) listed the arthropods in clumps of five species of mosses in March to May, including counts (Table 1). In addition to unidentified larvae, they listed the **Collembola** ***Sminthurinus*** (Figure 9), ***Xenylla*** (Figure 10), and ***Tomocerus*** (Figure 11-Figure 12) as well as thrips.

Figure 9. ***Sminthurinus aureus*** f. ***ochropus*** on mosses, member of a springtail genus that is common among mosses in spring. Photo by Andy Murray, through Creative Commons.

Figure 10. ***Xenylla*** sp. among mosses. Photo by Andy Murray, through Creative Commons.

Figure 11. ***Tomocerus*** sp. juvenile on mosses. Photo by Andy Murray, through Creative Commons.

Figure 12. ***Tomocerus minor*** , member of a genus that is common among mosses. Photo by Andy Murray, through Creative Commons.

Table 1. Number of insects found in moss polsters in Germany in March to May. From von der Dunk & von der Dunk 1979.

	Rhytidiadelphus	***Scleropodium***	***Hypnum***	***Plagiothecium***	***Brachythecium***
Sminthurinus	46	52	-	-	-
Xenylla	4	2	7	106	-
Tomocerus	-	-	1	-	4
thrips	+	+	+		+

Nutrients in the ecosystem affect the types of plants that will grow there, and bryophytes seem to have an aversion to high nutrients. Richardson *et al.* (2002) experimented with nutrients and their effects on plant communities and their insect herbivores in a Scandinavian sub-Arctic dwarf shrub heath. After nine years of nutrient enrichment, the subordinate plant functional groups (grasses and mosses) experienced greater effects than did the dominant dwarf shrubs. The insect herbivores showed evident changes in abundance. The biomass changes in the grasses and mosses contributed more to these insect changes in biomass and species composition than did the shrubs. One moss-eating species of **Heteroptera** in the fertilized plots dropped to as little as 6% that of the control plots. The abundance of grass specialists in **Homoptera** in fertilized plots, on the other hand, reached 400% that of controls. This study emphasized the importance of the subdominant plant species in driving the insect species composition of the habitat.

Temperature Relations

Because of their construction with lots of air spaces, bryophytes can act like a fluffy winter quilt. They are able to buffer temperatures with these trapped air spaces (Soudzilovskaia *et al*. 2013). In some instances, they may remain warmer from reradiated heat from rocks or soil. In other cases their capillary water may cool them by evaporative cooling. Differences between bryophyte species comply with physical laws and can be explained by differences in mat thickness and moisture content. There are, however, few data sets to evaluate the extent of this role in a variety of ecosystems. Some of these differences are provided in Chapter 10-1 on Temperature in Volume 1.

Of course food is a problem in winter, but some insects are able to feed on alternate food sources. ***Diamesa*** sp. (**Diptera: Chironomidae**; Figure 13) is a cold-tolerant insect that lives on a glacier in the Nepal Himalayas (Kohshima 1984). This flightless insect is able to walk on the surface and in small cavities beneath the glacier. The larvae feed on Cyanobacteria and other bacteria, permitting this species to spend its entire live in the glacier. And it is still active at -16°C. While this is not a bryophyte dweller, it illustrates the ability of insects to survive in cold habitats, such as those in the Arctic and Antarctic, and to subsist on foods like bacteria and Cyanobacteria that are available among the bryophytes.

Figure 13. ***Diamesa bohemani*** larva, member of a genus in which at least one species is able to survive on glaciers and feed on Cyanobacteria and bacteria. Photo from NTNU Museum of Natural History & Archaeology, through Creative Commons.

Preparation for Winter

As we noted in the aquatic insect chapter, insects can avoid freezing damage in two ways (Duman *et al*. 1991). The most flexible means is to obtain freeze tolerance, permitting the insect to survive formation of ice on the outside of the body. The second mechanism is to avoid freezing. The latter can be subdivided into physiological mechanisms that prevent the insect from freezing by altering the freezing point of the organism or preventing ice nucleation through manufacture of antifreeze proteins (Duman *et al*. 2004). The other is a behavioral adaptation that places the insect in a place where it is protected from freezing (Duman *et al*. 1991).

Bryophytes are often a winter refuge or site of hibernation for insects. The bryophyte offers insulation against the wind and cold. Under the snow, the dark color of most bryophytes absorbs heat from the light that is able to penetrate the snow. Nevertheless, bryophytes may be exposed to severe cold before the snow arrives or after it melts in spring. Hence, their inhabitants still require some sort of protection from the cold.

Storey and Storey (1992) listed two stresses that can prevent winter survival in terrestrial insects. The obvious one in many places is lack of food, but some insect larvae are able to feed on the bryophytes. Others may survive as eggs or pupae, stages in which there is no feeding. Some insects compensate for the lack of food by accumulating large lipid and carbohydrate reserves in the body fat in preparation for winter (Storey & Storey 1992). Others enter into a state of reduced metabolic rate (**quiescence**) or arrested development (**diapause**) in which they can rely on limited food reserves.

The second winter stress is tissue damage at low temperatures, especially freezing (Storey & Storey 1992). Insects have two options to survive in areas that attain sub-freezing temperatures: **freeze avoidance** and **freeze tolerance** (Bale 2002). Freeze avoidance includes life cycle adaptations that do not require the insect to be present during the cold period. For some, this is through migration. For others, it is finding warmer locations such as deep soil, in the water, or even among deep mosses. But insects also can have physiological means of freeze avoidance while existing in locations with sub-zero temperatures.

Protein ice nucleators (PINs) limit supercooling and induce freezing (Duman 2001). When the nucleating proteins are internal, a small size can help to prevent the formation of large crystals. In insects, freeze-tolerant species produce PINs in the hemolymph. These allow freezing in the hemolymph at temperatures just below freezing and inhibit freezing within the cells. In some cases, these PINs are "removed" in the winter, promoting supercooling. **Antifreeze proteins** (AFPs) prevent freezing. One beetle has AFPs in the hemolymph and gut that inhibit the ice nucleators in winter.

One theory of freeze avoidance in insects is that of **heterogeneous nucleation**. However Zachariassen *et al*. (2004) provide evidence that it is water volume that determines the nucleation temperatures in freeze-avoiding insects. The relationship between the aqueous solutions and the particular freeze avoidance displayed behaves more like that of homogeneous nucleated samples.

One of the strategies to survive winter is the ability to **supercool** (Holmstrup *et al*. 2002). This ability seems to have evolved at the same time as the ability for insects to retain body water in dry environments. But soil invertebrates are far less resistant to desiccation than the above ground insects. It is likely that bryophyte dwellers are more like the soil invertebrates but in some cases may find greater moisture among bryophytes. Soil invertebrates dehydrate in frozen soil; only a few degrees of supercooling causes substantial water loss which continues until the vapor pressure of body fluids equals the vapor pressure of the surrounding ice. At this point, tissue ice formation is eliminated and the invertebrate can survive subzero temperatures. But the Arctic soil invertebrates do not base their winter survival on this method of supercooling. Rather, they dehydrate to equilibrate their body-fluid melting point to that of the ambient temperature. This method works even in the extreme cooling rates of the polar soils.

For those insects that are sensitive to freezing, but still exhibit cold hardiness, their survival is typically achieved through **supercooling**, with some exhibiting supercooling points to below -25°C (Zachariassen & Husby 1982). These low non-freezing temperatures are accomplished through polyols and proteinaceous thermal hysteresis antifreeze agents that reputedly prevent the growth of ice crystals down to approximately -10°C. This prevention is increased dramatically when the crystal size is diminished. This added ability to prevent crystal formation permits them to live through temperatures as low as -30°C. In such cases, the insects can survive even in exposed areas where the snow does not accumulate.

Freeze tolerance in terrestrial insects occurs primarily among the **Coleoptera** (beetles), **Lepidoptera** (moths & butterflies), **Diptera** (flies), and **Hymenoptera** (bees & ants) (Storey & Storey 1992), whereas only the **Diptera** seem to have any tolerance to freezing in the aquatic stage (Moore & Lee 1991). Freeze tolerance may require preparation or it may be present year-round.

Freeze tolerance is energetically expensive and carries risks of ice crystal damage or other physical damage. The insect furthermore must survive osmotic stresses when water and solutes are rapidly redistributed across cell membranes during freezing and thawing periods. And part of this strategy is extracellular freezing that can damage membranes, not to mention the obstruction of oxygen flow to the body.

Freeze avoidance is the less expensive strategy and permits insects to be active under the snow where the snow provides suitable insulation (Storey & Storey 1992). Insects in cold environments further avoid freezing by the presence of hairs and dark body colors (Danks 2004), the former to insulate and the latter to absorb heat on sunny days. The insects complement these physical adaptations by behavioral adaptations – being active on sunny days and going to protected locations when it is getting cold (Danks 2004, 2005). Danks (2007) discusses their responses, including dispersal, habitat selection, habitat modification, resistance to cold, dryness, and food limitation, recognition of environmental signals, diapause, modifications to developmental rate, life cycle patterns that include multiple alternatives within the species, variation in phenology and development, and tradeoffs among these.

The behavioral escape of freezing could be to burrow into the ground below the frost line, go into decomposing material that generates heat, or find some other protected location locally. But for a few insects, this escape is a migration to a warmer climate, as is well known for the Monarch butterfly.

Bryophytes may come into the picture for some of the insects that are able to eat them. Cold induces changes in membranes and protein structure in insects due to phase changes in the molecules, changes in electrolyte concentrations and other solutes in body fluids, and changes in metabolism (Ramløv 2000). In some cases, animals switch diets prior to winter, some of which may include bryophytes (Prins 1982). This usefulness of such a behavior among insects remains unknown.

We know that bryophytes are rich in **arachidonic acids** that help to keep membranes pliable (Hansen & Rossi 1991). Insects produce little or no arachidonic acid (McPartland *et al*. 2001). Nevertheless, ladybird beetles (*Coleomegilla maculata*; Figure 14-Figure 15) have their highest proportion of arachidonic acid in the coldest part of winter (Zar 1968). Thus, a winter switch to bryophytes by some insects seems to be a reasonable hypothesis, and a potential source of arachidonic acid.

Figure 14. ***Coleomegilla maculata*** larva, a species with its highest concentrations of arachidonic acid in the coldest part of winter. Photo by Tom Murray, through Creative Commons.

Figure 15. ***Coleomegilla maculata*** adult, a species with its highest concentrations of arachidonic acid in the coldest part of winter. Photo by Tom Murray, through Creative Commons.

Whether arachidonic acids help in cold resistance for insects or not, they may help to keep membranes pliable for movement. Although Prins (1982) demonstrated a relationship with bryophytes in the diet of vertebrates, arachidonic acid, and winter survival, and we know that insects typically have quantities of the acid in their tissues (Dadd & Kleinjan 1979; Stanley-Samuelson & Dadd 1983), there does not yet seem to be research to demonstrate this relationship between arachidonic acid, winter tolerance, and insects. The closest evidence is that arachidonic acid enables the mosquito *Culex pipiens* to fly when it emerges as an adult (Dadd & Kleinjan 1979).

Arachidonic acid may not be the only chemical change in preparation for winter. Low temperatures not only affect the insects and cause different cell and membrane chemicals to initiate, the bryophytes also produce different chemicals or different concentrations when the temperatures drop. In ***Rhytidiadelphus squarrosus*** (Figure 16) and ***Eurhynchium striatum*** (Figure 17) there is a switch from 30% **arachidonic acid** (AA) and 5% **eicosapentaenoic acid** (EPA) to higher percentages of EPA, **α-linolenic acid**, and **dihomo γ-linolenic acid**, accompanied by a slight decrease in AA and **linoleic acid** (Hansen & Rossi 1991). This particular study does not support the hypothesis that AA increases in bryophytes in preparation for winter, but it is likely that the bryophytes still have higher concentrations of arachidonic acids than tracheophytes at those temperatures or any time (Herbert & Prins 1982; Hartmann *et al*. 1986; Groenewald & Van der Westhuizen 1997; Kajikawa *et al*. 2008).

Figure 16. ***Rhytidiadelphus squarrosus***, a species that decreases in arachidonic acid in winter. Photo by Michael Lüth, with permission.

Figure 17. ***Eurhynchium striatum*** with a capsule, a species that decreases in arachidonic acid in winter. Photo by J. C. Schou, with permission.

Field biologists often consider winter to be a "down" season when insects are inactive, and therefore it is not a useful season for field work. But insects must find some way to survive winter and pass their genes to the next generation. Many do this as eggs or pupae. And bryophytes seem to be an ideal place for both, at least for some insects. They provide protection against easily damaged tissues of pupae when larger animals walk or climb about, they hide them from predators, they decrease the threat of desiccation, and they provide insulation. And for active insects, they may provide food directly or through other organisms that live among the bryophytes. Surely many species spend their winters there in this bryophytic safe site.

But little literature exists on the bryophyte as an overwintering home. Not only is this season less conducive to field study, but even those who do collect are faced with a daunting task of identification. Pupae and eggs must be matched with adults to avoid the danger of creating new species for what is simply a different life cycle stage. That requires rearing to maturity, a special challenge for eggs. And someone needs to have done that already if there are to be any keys or descriptions to aid identification. Hence, even those collections that are made rarely see publication due to the lengthy process of putting names to the organisms.

Most taxonomic treatments on insects give only general habitats for the insects, and often I wonder if there wasn't a moss involved, as food or shelter, but unnoticed, or at least unreported, by the collector. Treatments of forest floor insects often compare soil and litter organisms, and even those on rocks, but no mention is made of mosses, although they are often lumped with litter.

The use of bryophytes on a phenological calendar is demonstrated by The Entomologist's Calendar (Samouelle 1819). Those arthropods living on or under mosses in January were ***Philosia muscorum*** (**Isopoda**; Figure 18), ***Cylindroiulus londinensis*** (**Diplopoda**), ***Cylindroiulus punctatus*** (Figure 19), ***Geophilus acuminatus*** (**Chilopoda**; see Figure 20), ***Siro rubens*** (**Opiliones**; see Figure 21), ***Neobisium carcinoides*** (**Pseudoscorpiones**; Figure 22), ***Cychrus caraboides*** (**Coleoptera**; Figure 23), ***Acropagus glabricollis*** (name no longer in use); in February ***Bryaxis haematica*** (**Coleoptera**; species name no longer in use; see Figure 24), ***Staphylinus morio*** (**Coleoptera**; see Figure 25); in March ***Gyrohypnus punctulatus*** (**Coleoptera**; Figure 26), ***Chlaenius prasinus*** (Figure 27), ***Tachinus analis*** (**Coleoptera**), ***Tachyporus analis*** (**Coleoptera**), ***Choleva oblonga*** (**Coleoptera**), ***Catops sericeus*** (**Coleoptera**; species name no longer in use; see Figure 28); in April ***Staphylinus aenoecephalus*** (**Coleoptera**; species name no longer in use), ***Staphylinus decorus***; species name no longer in use; in May ***Dasytes ater*** (**Coleoptera**; species name no longer in use; see Figure 29); in June – November no moss records; in December ***Tachyporus chrysomelinus*** (**Coleoptera**; Figure 30). This change from winter to summer suggests that the bryophytes offer these insects something in winter, whether it is only shelter, or there is also a food source.

Figure 18. ***Philoscia muscorum***, an isopod that can be found under mosses in January in Europe. Photo by Africa Gomez <abugblog.blogspot.com>, through Creative Commons.

Figure 19. ***Cylindroiulus punctatus***, a millipede that can be found under mosses in January in Europe. Photo by G. Drange <Biopix>, through Creative Commons.

Figure 20. ***Geophilus flavus*** (centipede) on moss protonemata. ***Geophilus acuminatus*** can be found under mosses in Europe in January. Photo by Anthony Barber, through Creative Commons.

Figure 21. ***Siro*** sp. on moss; ***Siro rubens*** occurs under mosses in January in Europe. Photo by Marshal Hedin, through Creative Commons.

Figure 22. ***Neobisium carcinoides***, a pseudoscorpion species that spends January under mosses in Europe. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 23. ***Cychrus caraboides*** adult, a species that occurs under mosses in January in Europe. Photo by Siga, through Creative Commons.

Figure 24. ***Bryaxis bulbifer*** adult; ***Bryaxis haematica*** occurs under mosses in February in Europe. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 25. ***Staphylinus*** sp. adult; ***Staphylinus morio*** occurs under mosses in February in Europe. Photo by Alvesgaspar, through Creative Commons.

Figure 26. ***Gyrohypnus punctulatus*** adult, a species that occurs among mosses in March in Europe. Photo from Naturalis, Biodiversity Centre, through Creative Commons.

Figure 27. ***Chlaenius prasinus*** adult, a species that occurs among mosses in March. Photo by Mike Quinn, through Creative Commons.

Figure 28. ***Catops tristis*** adult; ***Catops sericeus*** occurs under mosses in March in Europe. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 29. ***Dasytes plumbeus*** adult. "***Dasytes ater***" is associated with mosses in May. Photo by Sarefo, through Creative Commons.

Figure 30. ***Tachyporus chrysomelinus*** adult on bryophytes. Photo by Malcolm Storey, through Creative Commons.

Water Relations

Water is often the limiting factor for terrestrial insects (Tauber *et al*. 1998; Hayward *et al*. 2004). It can account for the importance of other variables such as elevation (Lee & La Roi 1979). Tauber *et al*. (1998) suggested that moisture was important in determining insect seasonality, stimulating diapause, modulating development and reproductive rates, and providing a cue for seasonal events. Bryophyte species are also limited by moisture, thus creating different moisture regimes available to the ground-dwelling and arboreal insects (Whittaker & Niering 1975; Slack 1977; Lee & La Roi 1979; Vitt 1991; During 1992; Wolf 1994; Li & Vitt 1995; Vitt & Belland 1997).

Fragmentation and Corridors

One of the causes of declines in species is the inability to disperse due to unfavorable habitat between suitable locations. Gonzalez *et al*. (1998) found that when patches of suitable habitat were connected by habitat corridors, they provided a rescue effect. Both abundance and distribution improved when habitats were connected. For many kinds of insects, bryophytes can provide such corridors, providing moisture and shelter even when they are unsuitable as food.

Starzomski and Srivastava (2007) experimented with landscape geometry and found that reducing the size of patches had little effect on community resilience. However, habitat loss caused complete loss of connectivity between patches. In their experiments with the microarthropod community (mostly mites and springtails) of mosses (***Polytrichum*** and ***Bryum***) on a granitic outcrop in BC, Canada, repeated disturbance caused rapid declines in species richness and abundance, altering community structure. These two arthropod groups were highly abundant, reaching 200 or more morphospecies in areas of only 20 m^2.

Insect Adaptations to Bryophytes

Insects often modify their environment to make it suitable for their homes. These include excavations in soil and other substrates, construction of feeding or resting shelters, inducing plant responses such as galls, forming aggregations, building colonial nests, and using parental care (Danks 2002). These alterations can buffer temperatures, increase moisture, and avoid flooding. Moisture needs (Danks 2004) may drive them to bryophytes, especially during summer dry spells. The excavations and shelters protect primarily against physical factors (Danks 2002). On the other hand, aggregations, colonies, and parental actions usually influence the ability to acquire resources.

Perhaps the most important characteristic of a bryophyte inhabitant is the ability to navigate within the small spaces available. This means the insects must be small, and it means their appendages must not get in the way. Hence, large insects like butterflies and moths cannot navigate as adults, and many are likewise too large as larvae to move within the mat.

Another adaptation is the ability to utilize the moss. If it is unable to use the bryophyte as a food source, it might not be worth the energy to enter the moss community.

But food is not the only reason to enter a bryophyte clump. As seen in other invertebrates, insects can seek out the moss as a safe site from the dangers of desiccation. However, they lack the ability to encyst that is beneficial to several invertebrate groups. Instead, their life cycles permit them to be inactive during the winter season, and their mobility permits them to leave when the going gets rough. Thus, pupae of insects with a **holometabolic** (having eggs, larvae, pupae, and adults) life cycle and eggs of all insects provide life cycle options to permit residency during dry or cold periods. And most likely they, like many other invertebrates, migrate vertically as moisture or temperature within the bryophyte community changes (Markkula 1981).

The bryophyte can provide camouflage. In addition to having the bryophyte create a plethora of light and dark areas with small spaces and overlying leaves and branches, the insect may itself exhibit camouflage (Lacrampe 2003), permitting it even greater protection against predators. For example, the cranefly ***Triogma*** (Figure 31) has a green and black pattern that makes it resemble a moss branch, sporting projections that resemble leaves (Figure 31). Species in this genus exist in both aquatic and terrestrial habitats, exhibiting a camouflage that suggests it evolved to survive in its mossy habitat (Alexander 1920).

Figure 31. This larva of the cranefly ***Triogma*** has green and black patterns that make it resemble the moss branches where it lives. Photo by Janice Glime.

Abundance

Invertebrates, and particularly arthropods, can be especially abundant among mosses. Peck and Moldenke (1999) found 125 morphospecies, comprising 18 orders and

5 functional groups, in their study of vine-maple (*Acer circinatum*; Figure 32) in the Willamette National Forest (Oregon, USA). The bases of shrubs exhibited the highest species richness and abundance. The composition likewise differed between the bases and tips of the shrubs. The most abundant insect was ***Sminthurus*** (Figure 33), a springtail (**Collembola**). Such abundance raises serious concerns about the harvest and export of mosses, especially in the first half meter above the ground.

Figure 32. ***Acer circinatum*** (vine maple), a species with a rich bryophyte fauna. Photo by El Grafo, through Creative Commons.

Figure 33. ***Sminthurus*** sp. with spermatophore, the most abundant species among bryophytes on the vine maple. Photo by Petter Bøckman, through Creative Commons.

The high abundance of insects in some moss communities requires special extraction techniques. Andrew and Rodgerson (1999) suggest using kerosene to float the insects because it attaches to the cuticle of the insects. The moss-insect community must first be preserved in 95% ethanol for two weeks. This preserved mix is shaken vigorously after topping off with kerosene. The insects settle to the bottom, then float at the interface between the ethanol and kerosene. The kerosene can be pipetted off and insects collected from the interface layer. I have not actually tried this method, but it would appear to work only on relatively small insects and things without legs to get caught. Further discussion of sampling methods appears later in this chapter.

Food Sources

Many researchers have considered bryophytes to be inedible for insects and other invertebrates (Haines & Renwick 2009). Others have commented on how rare bryophagy seems to be (Longton 1984). Even on Bryonet, people familiar with bryophytes marvelled at how little we know about bryophyte herbivory. Nevertheless, Paul Johnson reported studying several groups of insects that feed on mosses or liverworts, many of which are strict **bryophages** (organisms that feed on bryophytes). Kathy Merrifield reported finding much evidence of grazing on mosses that grow in the cracks of tree bark. Several members have provided images that evidence the bryophage damage, as will be seen in succeeding subchapters of terrestrial insect interactions. It is likely that the presence of bryophagy has been largely overlooked.

Nevertheless, some of the oddities among growth forms seem to be the result of **bryophagy** (see Ghullam & Stevenson 2013; Figure 35). Since a dense cluster of apical filaments is an oddity among members of ***Zygodon rupestris*** (Figure 34), those clusters (Figure 35) observed by Robin Stevenson (pers. comm. 2 June 2016) seem to be produced in response to herbivory. The herbivore is unknown. Normal gemmae (Figure 36) of this species were present along the stem, but these terminal filaments (Figure 37-Figure 38) seemed to be the result of damage to the terminal bud (pers. comm., Robin Stevenson 2 June 2016). ***Fontinalis*** produces similar filaments (protonemata) when the apex of the stem is removed (Figure 39). And could it be that the herbivore deposits a hormone such as that used to produce galls in tracheophytes? Stevenson suggested that the normal axillary gemmae may be dispersed by hares and deer that brush against the tree trunks where the moss lives. It is possible that these terminal filaments might likewise be dispersed and serve as propagules. Anomalies such as these should provide an interesting area for research on development and evolution.

Figure 34. ***Zygodon rupestris*** growing normally with no terminal clusters of filaments. Photo by David T. Holyoak, with permission..

Figure 35. Chewed ***Zygodon rupestris***. Note that several of the apices lack the gemmae clusters. Photo courtesy of Robin Stevenson.

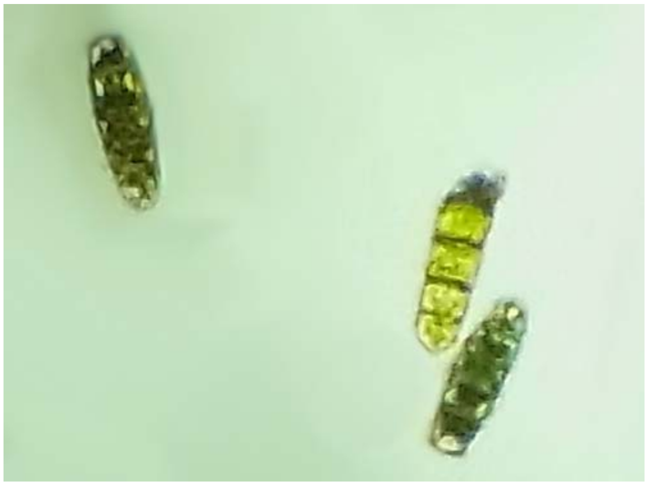

Figure 36. ***Zygodon rupestris*** normal axillary gemmae. Photo courtesy of Robin Stevenson.

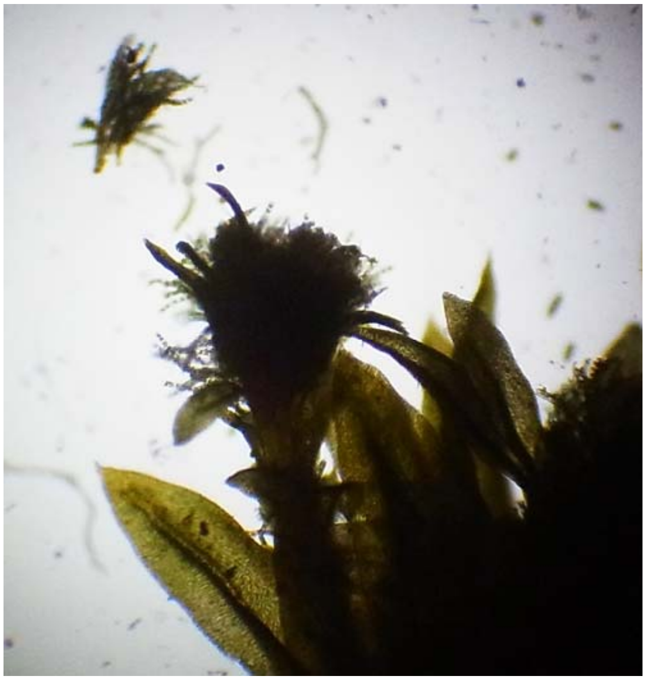

Figure 37. ***Zygodon rupestris*** with apical threads produced after herbivory. Photo courtesy of Robin Stevenson.

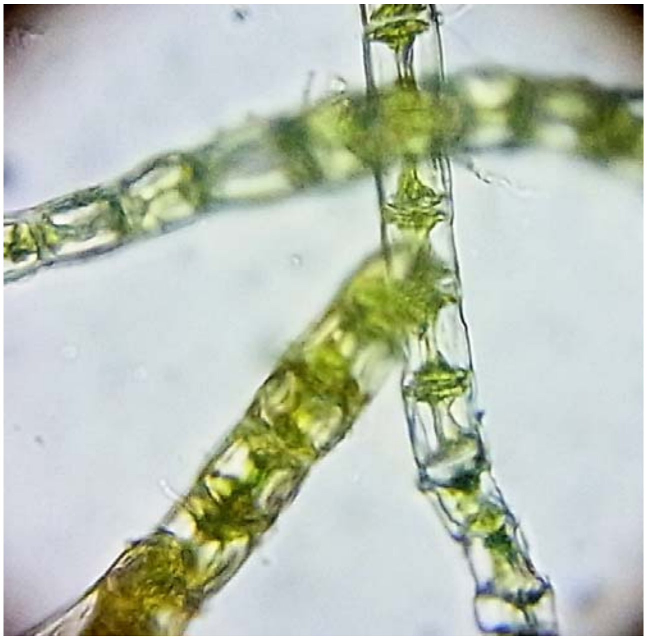

Figure 38. ***Zygodon rupestris*** apical threads produced after herbivory. Photo courtesy of Robin Stevenson.

Figure 39. ***Fontinalis hypnoides*** filaments (protonemata) produced after the stem apex was broken. Photo by Janice Glime.

Biologists have considered three classes of mechanisms to provide barriers to bryophagy: chemical defenses, low digestibility, and low nutrient content. But just as in tracheophytes, not all bryophytes are the same. Some are eaten while others just beside them are not, suggesting chemical defenses (Swain 1977). Haines and Renwick (2009) compared four bryophyte species by examining pre- and post-ingestive defenses by the bryophytes, all of which were mosses. Using the generalist caterpillar ***Trichoplusia ni*** (Figure 40-Figure 41), a generalist caterpillar, they found that mosses were consumed much less than lettuce or wheat germ. Of the four mosses tested [(***Bryum argenteum*** (Figure 42), ***Climacium americanum*** (Figure 43), ***Leucobryum glaucum*** (Figure 44), and ***Sphagnum warnstorfii*** (Figure 45)], only ***Climacium americanum*** was consumed in sufficient quantity to evaluate post-ingestive responses by the caterpillars. Extracts of ***Leucobryum glaucum*** placed on discs showed that this moss, the least eaten, contained a deterrent. Haines and Renwick suggested that preingestive mechanisms are more important than post-ingestive mechanisms, but much more study is needed before such a generalization is well supported.

Figure 40. ***Trichoplusia ni*** caterpillar, a species that prefers lettuce over mosses, and avoids mosses even when only mosses are offered as food. Photo by Phil Bendle, with permission.

Figure 41. ***Trichoplusia ni*** adult, a species whose larvae prefer lettuce over mosses, and avoids mosses even when only mosses are offered as food. Photo by Kurt Kulac, through Creative Commons.

Figure 42. ***Bryum argenteum***, a food source that is less preferred by ***Trichoplusia ni*** than is lettuce. Photo by Michael Becker, through Creative Commons.

Figure 43. ***Climacium americanum***, a food source that is less preferred by ***Trichoplusia ni*** than is lettuce, but it is eaten. Photo by Alan S. Heilman, through Creative Commons.

Figure 44. ***Leucobryum glaucum***, a food source that is less preferred by ***Trichoplusia ni*** than is lettuce. Photo by James K. Lindsey, with permission.

Figure 45. ***Sphagnum warnstorfii***, a food source that is less preferred by ***Trichoplusia ni*** than is lettuce. Photo by Jouko Rikkinen, through Creative Commons.

Longton (1984) reviewed the literature on the role of bryophytes and concluded that the energy content of bryophytes is generally slightly lower than that of associated plants. Wielgolaski and Kjelvik (1975) demonstrated this for Scandinavian tundra Communities. Lewis Smith and Walton (1973) demonstrated it for a sub-Antarctic island and Bliss (1962) for an alpine tundra. But is this true in warmer habitats? Gorham and Sanger (1967) found it likewise to be true in Minnesota, USA, but that is still a relatively cold climate, at least in winter.

There does seem to be an increase in caloric content with latitude (Forman 1968, 1969; Rastorfer 1976), as there is for flowering plants, with a range of 3.7-4.8 Kcal g^{-1} for bryophytes. Longton (1984) suggests that the lower energy content in bryophytes results from lower concentrations of carbohydrates, proteins, and lipids. This was true at least for proteins and readily soluble carbohydrates in a Norwegian alpine tundra (Skre *et al*. 1975).

Lawrey (1987) challenged the notion that bryophytes had little nutritional value. Some researchers have argued that they are lower in calories than tracheophytes (Forman 1968; Pakarinen & Vitt 1974), but others consider them to fall into the same range as those of tracheophytes (Bliss 1962; Forman 1968; Pakarinen & Vitt 1974; Rastorfer 1976). Davidson *et al*. (1990) compared uneaten gametophytes to edible sporophytes and found that the ash-free caloric values did not differ, further suggesting that caloric values are not a limiting factor. On the other hand, Skre *et al*. (1975) found that both their protein and carbohydrate content is typically low in alpine bryophytes compared to tracheophytes. And levels of potassium and magnesium tend to be lower in mosses than in tracheophytes (Prins 1982).

The sugars in bryophytes are the same as in tracheophytes, although some additional ones occur. Spores are especially high in lipids and may account for consumption by ants (Plitt 1907). Pelser *et al*. (2002) even reported that some mosses [***Catharomnion ciliatum*** (Figure 46), ***Canalohypopterygium tamariscinum*** (Figure 47)] produce oils. They considered that the oil may have an energy storage function, but rather than considering it to be a food source for invertebrates, they suggested that it could serve to repel invertebrates, fungi, or bacteria.

Figure 46. ***Catharomnion ciliatum***, a species that produces oils that may be a deterrent to herbivory. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 47. ***Canalohypopterygium tamariscinum***, a species that produces oils that may be a deterrent to herbivory. Photo by Pieter B. Pelser, with educational permission.

Sveinbörnsson and Oechel (1991) questioned the carbohydrate and lipid changes in tundra mosses as the seasons changed. Using ***Polytrichum commune*** (Figure 4) and ***Polytrichastrum alpinum*** (Figure 48), they samples three times per year. On the raised polygon rims, both lipid and carbohydrate concentrations were higher in ***Polytrichum commune*** than in ***Polytrichastrum alpinum***. The green parts of the plants had significantly higher concentrations of lipids than did rhizomes in ***Polytrichum alpinum***, but this relationship was not true in ***Polytrichastrum alpinum***. Sugar concentrations were higher in green parts in both species, whereas starch concentrations were highest in the rhizomes.

Only ***Polytrichum commune*** demonstrated seasonal variation in starch and sugar concentrations (Sveinbörnsson & Oechel 1991). There was a significantly strong negative relationship between sugars and starches. On the other hand, there was a significant positive relationship between lipids and starch+sugar. The seasonal relationship of these two **Polytrichaceae** mosses is like that of evergreen tracheophytes.

Figure 48. ***Polytrichastrum alpinum***, a polygon rim species in the Arctic. This species has high sugar content in green parts and high starch content in the rhizomes. Photo by David T. Holyoak, with permission.

Chapin *et al*. (1986) found that seasonal fluctuations in carbohydrate concentration varied between moss species in the Alaskan tundra. Brown parts of ***Aulacomnium*** spp. exhibited greater seasonal differences than did species of ***Polytrichum*** and ***Pogonatum***. Lipids increased in autumn in brown tissues of mosses and declined in summer. Surprisingly, mosses had the greatest levels of lignin-like substances when compared with tussock graminoids (grasses & sedges), deciduous shrubs, evergreen shrubs, deciduous forbs (non-graminoid herbs), and lichens; *Eriophorum* (cottongrass) and lichens had the least. The preferences of the eight generalist herbivores in the study responded to nutrient levels, preferring higher levels of nitrogen, phosphorus, and potassium but lower levels of lipid and cellulose in the plants.

Russell (1979) found that the liverworts preferred by ***Caurinus dectes*** actually had a low nutrient content (Table 2), particularly for nitrogen, an important component of protein. But he pointed out that the ***Caurinus*** was able to extract the nutrients from the cells without having to eat and digest the cellulose that is so abundant in some bryophyte leaves, thus making the concentrations higher than that indicated in the table.

Table 2. Macronutrient concentrations (% dry weight) in the gametophytes of some bryophytes collected in ***Caurinus dectes*** habitat at Marys Peak, Oregon, USA. From Russell 1979.

		P	N	Na	K	Ca	Mg
Mosses							
Dicranum fucescens	Figure 49	.142	.932	.038	.546	.418	.145
Rhizomnium glabrescens	Figure 50	.251	2.083	.043	1.125	.972	.261
Eurhynchium oreganum	Figure 51	.146	.829	.056	.741	.518	.190
Isothecium spiculiferum	Figure 52	.142	.949	.034	.512	.516	.177
Antitrichia curtipendula	Figure 53	.151	.686	.028	.631	.430	.170
Rhytidiadelphus loreus	Figure 54	.164	.727	.072	.770	.440	.171
mean		**.166**	**1.034**	**.045**	**.721**	**.551**	**.186**
Liverworts							
Scapania bolanderi	Figure 55	.072	.748	.035	.659	.275	.111
Porella navicularis	Figure 56	.155	.890	.026	1.040	.426	.156
Frullania tamarisci ssp. *nisquallensis*	Figure 57	.107	.874	.030	.904	.515	.134
mean		**.111**	**.834**	**.030**	**.868**	**.405**	**.134**

Figure 49. ***Dicranum fuscescens***, the species with the lowest concentrations of several macronutrients among the nine bryophytes tested (Table 2). Photo by Michael Lüth, with permission.

Figure 50. ***Rhizomnium glabrescens***, the species with the highest concentrations of P, N, K, Ca, and Mg among the nine bryophytes tested (Table 2). Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 51. ***Eurhynchium oreganum***, the species with the highest concentration of Mg of the nine species tested (Table 2). Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 52. ***Isothecium spiculiferum***, the species with the lowest concentrations of P and K among the nine bryophytes tested (Table 2). Photo by Ben Carter, through Creative Commons.

Figure 53. ***Antitrichia curtipendula***, the species with the lowest concentrations of N and Na among the nine bryophytes tested (Table 2). Photo by Hermann Schachner, through Creative Commons.

Figure 54. ***Rhytidiadelphus loreus***, the species with the highest concentration of Na among the nine species of bryophytes tested (Table 2). Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 55. ***Scapania bolanderi*** with capsules, a species with the lowest concentrations of P, Ca, and Mg among the nine species tested (Table 2). Photo by Chris Wagner, with permission.

Figure 56. ***Porella navicularis***, the species with the highest concentration of P and N among the liverworts tested (Table 2). Photo by Rosemary Taylor, with permission.

Figure 57. ***Frullania tamarisci***, the species with the highest concentration of Ca among the liverworts tested (Table 2). Photo by Tim Waters, through Creative Commons.

Rather than low nutrients, it seems likely that antiherbivore compounds may contribute to the avoidance of bryophytes by herbivores (Clymo & Hayward 1982; Davidson 1988; Davidson *et al*. 1989; Liao 1993). Lawry (1987) suggests that the same compounds already known for their antibiotic activity (Madsen & Pates 1952; Pates & Madsen 1955; Ramaut 1959; McCleary *et al.* 1960; Wolters 1964a,b; McCleary & Walkington 1966; Gupta & Singh 1971; Banerjee & Sen 1979) may serve also as antiherbivore compounds. For example, phenolic compounds and other related bio-active compounds have been demonstrated multiple times (Markham & Porter 1978, 1983; Asakawa 1981, 1982, 1984, 1990; Wilschke & Rudolph 1988; Harborne 1988; Zinsmeister & Mues 1988; Davidson *et al*. 1989; Xie & Lou 2009).

Ferulic acid in shoots (but not young capsules) of ***Mnium hornum*** (Figure 58) may account for avoidance of the shoots; ferulic acid, one of the hydroxycinnamic acids, is considered a primitive defense against herbivores in flowering plants (Swain 1977; Fry 1983). These cell wall components would be likely to discourage organisms that chew and grind, but may have no effect on those that pierce and suck, explaining the high incidence of such invertebrates (Longton 1992). In liverworts, it seems that the oil bodies store terpenoids and lipophilic aromatic compounds that have strong antifeedant activity, as shown against the African army worm ***Spodoptera exempta*** (**Lepidoptera**; Figure 59-Figure 60) (Asakawa 1990).

Thus far there is no evidence that insects take an **offensive approach** to bryophyte herbivory (Karban & Agrawal 2002). Karban and Agrawal suggest that offensive behavior includes choices for feeding and oviposition, enzymes that make it possible to digest or assimilate certain foods, sequestration of toxins, *etc*., morphological adaptations, symbionts, induction of plant galls, and induced plant susceptibility. Isopods seem to have such offensive tactics that enable them to eat and assimilate bryophytes (see Chapter 10-3 in this volume). However, special enzymes, bacteria, or other mechanisms permitting insects to digest and assimilate bryophytes seemingly remain to be discovered.

Figure 58. ***Mnium hornum***, a species that produces ferulic acid, a known antiherbivore compound. Photo by Tim Waters, through Creative Commons.

Figure 59. ***Spodoptera exempta*** larva, a species that avoids liverworts with oil bodies that store terpenoids and lipophilic aromatic compounds that have strong antifeedant properties. Photo from the University of Arkansas, through Creative Commons.

Figure 60. ***Spodoptera exempta*** adult, a species whose larvae avoid liverworts as food. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Both algae (Ceh *et al*. 2005) and tracheophytes have inducible antiherbivore compounds (*e.g.* Fowler & Lawton 1985; Kruidhof *et al*. 2012). The brown alga ***Sargassum asperifolium*** (Figure 61) and red alga ***Hypnea pannosa***

(Figure 62-Figure 63) both exhibited lower grazing levels on individuals that had been grazed previously than on those with no previous grazing, suggesting that these algae produced antiherbivore compounds in response to grazing.

Figure 61. ***Sargassum*** sp., a brown alga that seems to have inducible antiherbivore compounds. Photo through Creative Commons.

Figure 62. ***Hypnea pannosa***, a red alga that seems to have inducible antiherbivore compounds. Photo by Ria Tan, through Creative Commons.

No one has attempted to show whether these secondary compounds are ever induced in bryophytes. Karban and coworkers considered the advantages of inducible antiherbivore compounds (Karban & Baldwin 1997; Karban *et al*. 1997). Whereas most ecologists had argued that the inducible compounds saved costs, empirical data failed to support this argument (Karban *et al*. 1997). Karban and coworkers suggested that instead it was the variability that was important – "maximal levels of defense are constrained, variability will increase the effectiveness of a given level of investment in defense."

Gerson (1969, 1982) reports that some members of **Collembola**, **Diptera**, **Hemiptera**, **Hymenoptera**, **Orthoptera**, **Cryptostigmata**, and **Prostigmata** (**Acarina**) feed on mosses. But it is likely that the number is far greater than we suppose. Certainly **Lepidoptera** must be added to the list (Chapman 1894; Tillyard 1926). We have found that Isopods can do considerable damage to mosses, but their feeding occurs at night. A number of insects are night active, hence avoiding visibility to birds that feed on them.

Figure 63. ***Hypnea pannosa***, a red alga that seems to have inducible antiherbivore compounds. Photo by Cal Photos, through Creative Commons.

Antiherbivore compounds in liverworts have been greatly elaborated by Asakawa (1981, 1982, 1984, 1990). Despite the widespread presence of these compounds, some liverworts are still eaten. For example, Robin Stevenson sent me an image of ***Marchantia polymorpha*** (Figure 64) with evidence of herbivory on the gemmae cups.

Figure 64. ***Marchantia polymorpha*** showing gemmae cups where the gemmae have apparently been eaten; the bottom of the cup is eaten through to the soil. Photo courtesy of Robin Stevenson.

A common pattern of bryophyte consumption is for the insect to strip the leaf lamina cells while avoiding the costa and border cells (Wyatt & Stoneburner 1989; Davidson *et al*. 1990). Other insects avoid the cell wall problem by using a straw-like stylet, such as those of aphids and mites, sucking out the contents without the necessity of digesting cell walls.

Loren Russell (pers. comm.) observed the locations and food habits of insects in western Oregon and Washington, USA, and researched their food habits through published feeding observations and gut analyses. He found at least 26 species of **bryophagous** insects (those eating bryophytes). Among these, only three species were reported as associated with liverworts. To the list of liverwort consumers, he added **Tipulidae** larvae and ***Lioligus striolatus*** (a member of the bryophyte-dwelling beetle family **Byrrhidae**; Figure 65).

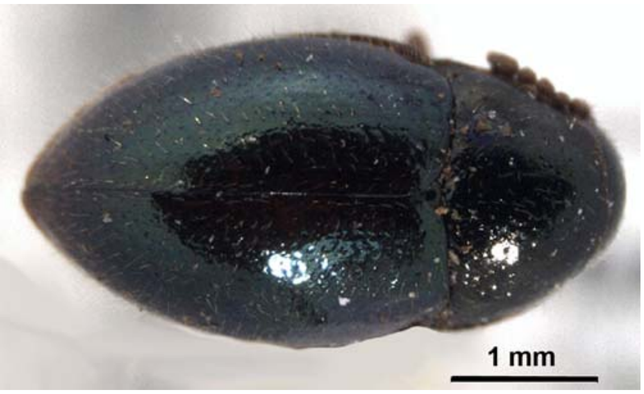

Figure 65. ***Lioligus nitidus*** adult, a bryophyte dweller and liverwort consumer. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Bryophyte herbivory may have been more extensive among early bryological evolution. As insects and other herbivores became more abundant and diverse, those that survived were more likely to be those protected by antiherbivore compounds, tough tissues, lack of nutrients, or inconspicuous locations. To shed light on early herbivory, Labandeira *et al*. (2014) examined fossil evidence from the late Middle Devonian liverwort ***Metzgeriothallus sharonae*** (Figure 66) from eastern New York state shale fragments. Using microscopic analysis, they detected an "extensive repertoire" of arthropod herbivory. This represented three functional feeding groups and nine types of damage by arthropods. They considered the oil bodies were similar to those of modern liverworts and probably provided chemical defense against the arthropod herbivory on this species. The evidence suggested that these early herbivores were significantly smaller than those of the later Palaeozoic and that they had an important role in early terrestrial ecosystems.

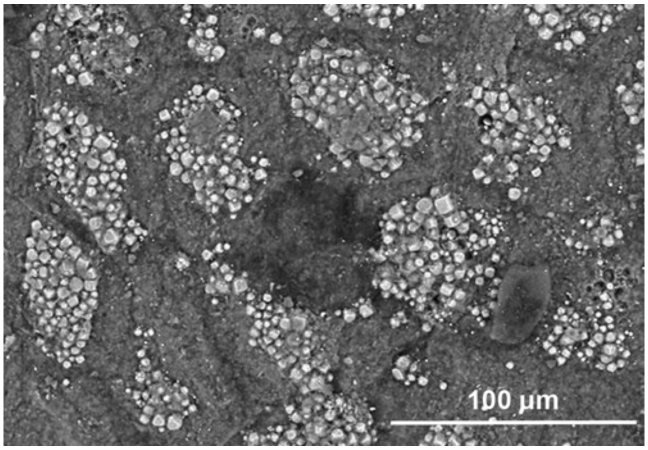

Figure 66. ***Metzgeriothallus sharonae*** fossil showing cells. This fossil species is known to have provided food for at least three feeding groups. Photo by Susan Tremblay, with permission.

It is now clear that bryophytes are eaten, but that this is not widespread among the members of the animal kingdom. Claudio Delgadillo (pers. comm. 30 March 2016) was surprised when a student discovered bryophyte tissue in a sea urchin gut. One had a liverwort and one had a moss! And most of us have probably seen capsules with holes in their sides, indicating something had been nibbling. Sometimes only the stems remain, and in the image of ***Orthotrichum affine*** (Figure 67) sent to me by Robin Stevenson. It remains a challenge to match the identity of the bryophages with their food organisms.

Figure 67. ***Orthotrichum affine*** eaten by some sort of terrestrial invertebrate, most likely an insect or isopod. Photo courtesy of C. Robin Stevenson.

Bryophytes as Pesticides

Since many bryophytes have been refused in feeding trials, and many bryologists consider their secondary compounds with antifeedant properties to be important in deterring potential feeders, it should be no surprise that some enterprising bryologists and their colleagues have attempted to use these compounds in pesticides (Singh *et al*. 2015). Singh and coworkers found the enzyme thiaminase from ferns and mosses exhibited insect resistance activity. They were able to patent crude protein extracts of several ferns and mosses that caused 70-100% mortality and reduced growth in caterpillars of the Noctuidae *Spodoptera frugiperda* (fall army worm) and *Helicoverpa zea* (corn earworm), neither of which is known to eat mosses. Such pesticides may be a boon to agriculture by decreasing destruction. Since they are natural compounds, they are probably already avoided by birds. Nevertheless, their safety as a pesticide must be evaluated, particularly in regard to pollinators.

Sampling Methods

Field Collection

A common method of field collection for soil and bryophyte invertebrates is the use of **pitfall traps**. Drozd *et al*. (2009) were surprised to find that the total abundance for arthropods was higher in the litter samples than from the moss cushions. As they point out, conclusions of this sort should be evaluated carefully based on the methods. Bryophyte dwellers may seek refuge there and may be relatively immobile. They also may be species that tend to desiccate easily, hence their retreat into the more moist bryophyte cushions. Their nighttime movements may be vertical rather than horizontal, hence never going near the pitfall traps. In the daytime they retreat into the protective cushion of bryophytes where it is harder for predators to see them and they are more protected from desiccation. This same protection in a dense moss cushion prevents rapid movement. The arthropod surface activity may be mostly that of predators in search of dinner. Those within the bryophyte clump may be species that feed on bryophytes or the collected detritus and microorganisms, hence having no need to move from the clump at all.

If these problems concern you, then the best method of collection is to sample bryophyte clumps. Andrew and Rodgerson (1999) recommend 2.5 x 2.5 cm clumps. Unfortunately, this method is destructive and should never be done with rare bryophyte species or fragile ecosystems.

One method I have not tried is to use a **sugar flotation** technique with live bryophyte cushions (see Pask & Costa 1971 below). After floating off the insects, clean the cushion well in rainwater or stream water and return it to its original position. If the clump is kept intact, it may survive. But I don't know if it will survive the sugar solution, and the effectiveness of extracting the insects without disturbing the integrity of the moss clump needs to be tested.

Extraction

Heat gradients are common methods for extracting invertebrates from soil and bryophytes. Tuf and Tvardik (2005) used a Tullgren funnel with a heat source (lamp) above the mosses in the funnel. Invertebrates are then captured in a jar of alcohol or other preservative below the funnel. This is biased against slow-moving organisms that desiccate easily.

In mosses as dense as some ***Sphagnum*** (Figure 45) mats, behavioral extraction (also a heat technique) may be beneficial (Fairchild *et al*. 1987). But Fairchild and coworkers added another gradient – dissolved oxygen. Both the heat and oxygen form a vertical gradient in a column of water with the ***Sphagnum*** immersed at the top. Mean sorting time was reduced from >16 hr to <2 hr per sample. This method was effective for insects and other invertebrates, but was intended for aquatic invertebrates. Its usefulness for emergent bog species remains to be tested. The method takes advantage of the need for oxygen and the avoidance of warmer temperatures among the aquatic organisms.

Temperature gradients have their problems for extracting insects. Some are slow-moving or might burrow deeper into the bryophytes to avoid the heat. Others may become desiccated by the heat and no longer be able to move.

Preserved samples permit the researchers to do the extractions at their convenience. This is sometimes a necessity for extended field work. Pask and Costa (1971) recommend preserving the samples in 10% formalin, but this is highly carcinogenic and should be avoided. Using 70% ethanol (or 95% for aquatic samples) works well. A few drops of glycerine can protect the organisms if too much alcohol evaporates (pers. experience). Pask and Costa compared preserved vs unpreserved samples using extraction with a sucrose solution of 1.12 sp. gr. They found a mean recovery of 90.8% for persevered samples compared to 83% from unpreserved samples. Furthermore, the unpreserved samples yielded much greater variability in efficiency of recovery than did the preserved samples. And some groups seemed to be easier to recover in the preserved samples (**Zygoptera**, **Hemiptera**, **Trichoptera**, and **Chironomidae**). No group was under-represented in the preserved samples.

Andrew and Rodgerson (1999) tested two common insect extraction methods: **Tullgren funnels** (*e.g.* Tuf & Tvardik 2005) and **sugar flotation** (Pask & Costa 1971), and compared these to a new technique using kerosene phase separation. They found that the kerosene extraction recovered significantly more invertebrate individuals than did the sugar extraction and represented similar numbers of orders.

Kerosene phase separation (Andrew & Rodgerson 1999; Andrew *et al*. 2003)**:** Upon collection in the field (2.5 x 2.5 cm samples), the bryophyte-invertebrate samples should be placed in 95% ethanol for 2 weeks before extraction. For densely tufted bryophytes, pre-washing samples in 95% ethanol may be useful because there is more interference by the bryophytes. In the **kerosene phase separation**, the kerosene attaches to the insect cuticle to facilitate flotation:

1. First put the bryophyte-insect mix into 2 large test tubes (2 cm wide X 17 cm long).
2. Then fill the test tube 3/4 full of sample with ethanol and top it off with 1 cm of kerosene.
3. Shake this mix vigorously to fully mix the solutions.
4. After 10-15 minutes of settling, roll each tube to release trapped bubbles from the sides and bottom.
5. When the tubes are then kept upright, a distinct interface will form between the ethanol and kerosene; insects will collect onto the interface layer. Pipette off the kerosene to within 1 mm of the interface layer.
6. Then pipette off remaining kerosene plus interface.
7. Wash the sides of the tube with 95% ethanol to dislodge the kerosene stuck to the sides and repipette and collect.
8. Repeat the whole process to get remaining invertebrates (increases total number by about 16%).
9. Push the invertebrates in the kerosene layer into the ethanol, using a fine brush, to dislodge the kerosene from the cuticle.
10. Examine the interface mix in a Petri dish with a binocular microscope under a fume hood for your own safety. Collect and sort the invertebrates.

Habitats

Many practices of humans threaten the bryophytes on the planet Earth. Perhaps the greatest of these in purely terrestrial ecosystems is the management practices of forests. Management for timber threatens the forest floor bryophytes, not to mention those that live on the trees themselves. A major problem is the imposed dispersal limitation to recolonize cut forests, and the larger the cut and isolation, the greater the problem for recolonization (Fenton & Frego 2005). Islands of trees provide refugia where at least some bryophytes may survive long enough to recolonize. Temperature, total daily photosynthetically active radiation, and vapor pressure deficit were significantly different between areas with remnant canopy and those without. If bryophytes are unable to colonize or survive, the insects that depend on them for moisture, food, and refuge from predators are vulnerable and their mortality increases, often to their local extinction.

Bogs and Wetlands

Data would suggest that bogs and wetlands have the highest populations of insects living among bryophytes. This is at least in part due to the greater biomass of mosses, a ratio of 1.6:1 in a Stordalen mire when compared to tracheophytes (Rosswall *et al*. 1975). Since they are also the habitats with the greatest cover of bryophytes, this high population of insects should probably be expected. Nevertheless, there seems to be little evidence that the bryophytes are used as food. Of nine species of **Nematocera** (midge) larvae, Smirnov (1961) found that only ***Psectrocladius*** from the ***psilopterus*** group (Figure 68-Figure 69) had eaten ***Sphagnum***, and then it constituted only 16% of the food volume. Rather, algae and detritus among the bryophytes formed the main food for the herbivorous members of the group. The **Collembola** (springtails) eat the fungi that grow on decomposing ***Sphagnum***. Thus, the ***Sphagnum*** provides the substrate needed to make the food available.

Figure 68. ***Psectrocladius*** sp. larva, a genus that includes one species that eats ***Sphagnum***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 69. ***Psectrocladius psilopterus*** adult, species group where some larvae eat ***Sphagnum***. Photo by NTNU Museum of Natural History and Archaeology, through Creative Commons.

Insects in boreal peat bogs may be more distinctive. Spitzer and Danks (2006) found that these bogs have not only the generalists that seem to be common in many bogs, but also distinct **tyrphobionts** (species restricted to bogs) and **tyrphophiles** (species frequenting bogs but not restricted to them). One reason for the great diversity in some bogs is the topographic diversity of bogs, including hummocks that can become dry and hollows that are underwater, with the opportunity to migrate short distances vertically to find suitable moisture levels. Especially in boreal regions, many bogs may be hundreds and some thousands of years old, preserving relict communities that are well established. The isolation of bogs from each other has permitted them to develop unique insect communities.

Brink and Wingstrand (1949) found that the four species considered typical for bogs (Krogerus 1939, 1947) were also present in the Virihaure area of Swedish Lapland. These were the beetles (**Coleoptera**) ***Agonum consimile*** (**Carabidae**) and ***Elaphrus lapponicus*** (**Carabidae**) and the flies (**Diptera)** ***Dolichopus fraterculus*** (**Dolichopodidae**) and ***Delia lineariventris*** (**Anthomyiidae**). They also considered **Staphylinidae** beetles ***Anthobium lapponicum***, ***Stenus hyperboreus***, ***S. umbratilis***, the **Linyphiidae** spiders ***Erigone capra*** and ***Bathyphantes setiger***. On the other hand, Agrell (1941) was unable to find any **Collembola** that were characteristic bog species.

Forests

Biomass production of bryophytes in forests can be high. In oak woodlands, Rieley *et al*. (1979) reported that bryophytes contributed 90% of the ground vegetation green biomass compared with only 60% of the annual production, providing a standing crop (green + brown) of 200-640 g m^{-2} in pine forests and mires.

Garry Oak trees sport a variety of bryophytes, providing habitat for various invertebrates (pers. comm. Wynne Miles 12 January 2008). Miles found tufts of ***Orthotrichum*** (Figure 70) that were missing their sporophytes and only the broken setae remained. In another case, a collection of epiphytes, including ***Tortula*** (Figure 71), was grazed while in its collecting bag.

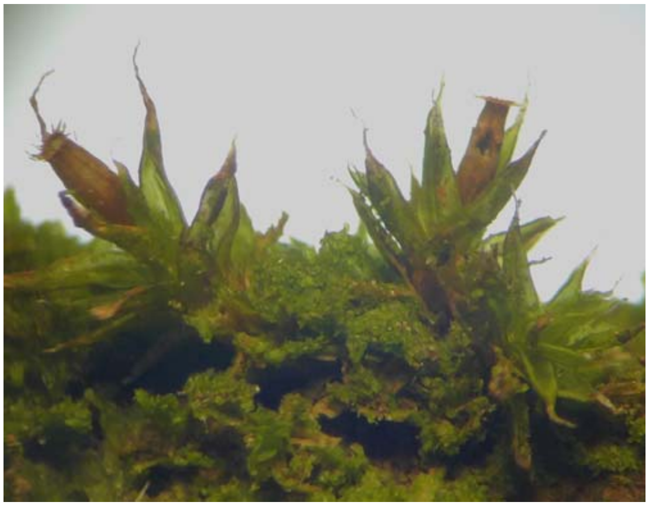

Figure 70. ***Orthotrichum diaphanum*** with a chewed capsule (on right) similar to that observed by Wynne Miles. Photo courtesy of Robin Stevenson.

Figure 71. Larva (**Lepidoptera**) on ***Tortula*** sp. This inadvertently collected larva grazed a collection of epiphytic mosses that had been growing on a large Garry Oak. Photo courtesy of Wynne Miles.

Forest ecosystems offer a diversity of habitats to insects. Because of their ability to fly as adults, the adult habitat can differ significantly from that of the larvae. The habitats of eggs and pupae – immobile stages – are typically the same as those of the larvae. But once the adult emerges, it is able to move from the food habitat of the larva to the feeding habitat of the adult, or in some cases, the adult does not feed. For many of the adults mating is the first and only priority.

In boreal forests, the bryophytes can often form 100% cover (Oechel & Van Cleve 1986). Although they are a minor part of the biomass, they perform a major portion of the primary productivity and ground cover. Hence, they also provide a major function in determining the invertebrate communities.

Drozd *et al.* (2009) used pitfall traps in a submountain and mountain forest ecosystem of the Czech Republic amid ***Polytrichum commune*** (Figure 4), ***Polytrichastrum formosum*** (Figure 3), ***Sphagnum teres*** (Figure 72), ***Sphagnum girgensohnii*** (Figure 73), ***Sphagnum fallax*** (Figure 74), ***Bazzania trilobata*** (Figure 75), ***Pleurozium schreberi*** (Figure 76), ***Eurhynchium angustirete*** (Figure 77), and ***Oligotrichum hercynicum*** (Figure 78). The traps followed a moisture gradient in moss cushions and in litter with no moss (controls). Drozd and coworkers suggested that the relationship with the mosses seemed to have broader implications than just that of a substrate, *i.e.*, the data indicate interaction between moss presence and other microhabitat features. The great number of insects in these forest floor habitats was indicated by the 55,000 specimens collected (66 traps, 5 locations), averaging 850 individuals per trap. Drozd and coworkers found that moss species, as well as moss presence, was important in determining both total abundance and taxon diversity (Figure 79). But moisture was important as well, perhaps contributing to moss species preference. Nevertheless, trapped arthropod abundance was greater in the litter samples.

Figure 72. ***Sphagnum teres***, a forest moss that houses a moderate number of arthropods. Photo by A. Neumann <www.biopix.org>, with online permission.

Figure 73. ***Sphagnum girgensohnii***, a forest moss that houses large numbers of arthropods, including insects. Photo by Mark Melton (Noah Project), with permission.

Figure 74. ***Sphagnum fallax***, a forest moss that houses a small number of arthropods. Photo by Michael Lüth, with permission.

Figure 75. ***Bazzania trilobata***, a forest liverwort that houses a moderate number of arthropods with few being insects. Photo by Bernd Haynold, through Creative Commons.

Figure 77. ***Eurhynchium angustirete***, a forest moss species that houses insects. Photo by Marko Vainu, through Creative Commons.

Figure 76. ***Pleurozium schreberi***, a forest moss species with a moderate number of insects. Photo by Sture Hermansson, with online permission.

Figure 78. ***Oligotrichum hercynicum***, a forest moss species that houses insects. Photo by Hermann Schachner, through Creative Commons.

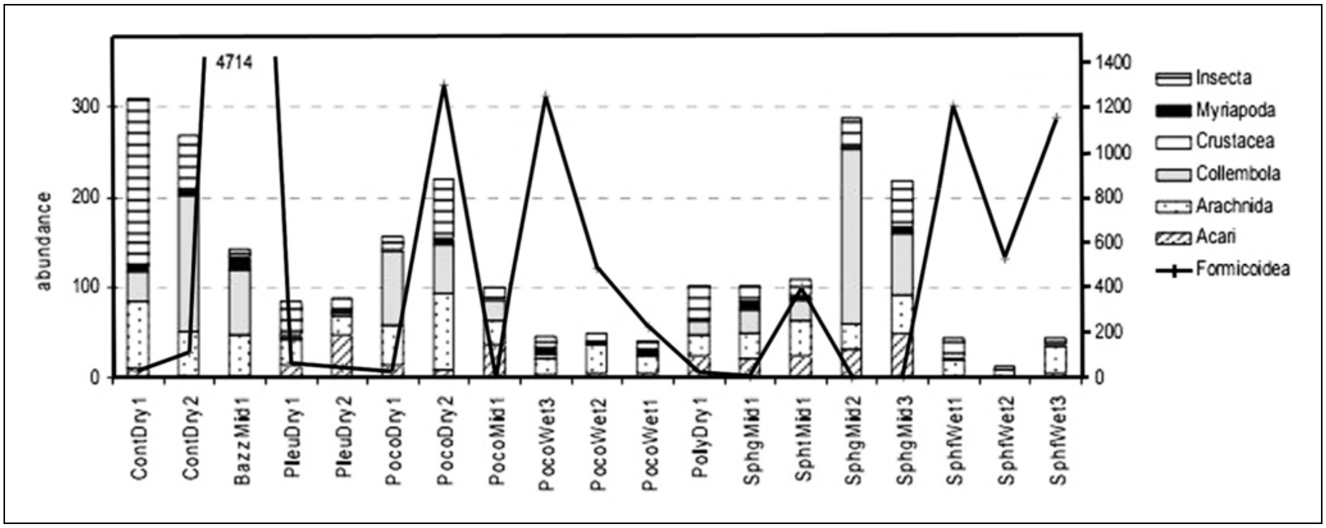

Figure 79. Arthropods from mosses in the Podolánky area of the Czech Republic. Poco = ***Polytrichum commune***, Poly = ***Polytrichastrum formosum***, Spht = ***Sphagnum teres***, Sphg = ***Sphagnum girgensohnii***, Sphf = ***Sphagnum fallax***, Bazz = ***Bazzania trilobata***, Pleu = ***Pleurozium schreberi***, Eurh = ***Eurhynchium angustirete***, Olig + ***Oligotrichum hercynicum***, Spha = ***Sphagnum*** spp., Cont = litter; moisture Wet = high, Mid = middle, Dry = low. Modified from Drozd *et al.* 2009.

As Drozd and coworkers (2009) pointed out, bryophages and detritivorous arthropods "have no reason to move about," potentially causing a low capture rate in traps that require movement. But these researchers also suggested that bryophytes may serve only as shelter and a temporary place to prevent desiccation, referring to the oft held view that the bryophytes are low in nutrients. This latter assumption, however, has been contested, as you will seen earlier in this chapter.

Few studies have attempted to find the uses made by the bryophyte inhabitants (Drozd *et al*. 2009). Rather, most have simply enumerated species, perhaps correlating them with other physical factors such as temperature and moisture.

One of the few studies that elaborates on the relationship between bryophyte species and the invertebrate inhabitants is that of Božanić *et al*. (2013). In this case, ***Brachythecium curtum*** on a decaying tree housed the greatest number of species. The layers of the forest were important, with type of substrate and height above ground proving to be the most important factors to determine the invertebrate distribution.

Figure 80. ***Brachythecium curtum***, a species with a rich fauna of arthropods. Photo by Janice Glime.

Montane Tropical Rainforests

In the Atlantic Forest of Brazil, Maciel-Silva and dos Santos (2011) found a number of insects associated with the mosses ***Hypopterygium tamarisci*** (Figure 81) and ***Lopidium concinnum*** (Figure 82). These include **Lepidoptera** larvae, leafhoppers, aphids, and **Psocoptera**, as well as isopods, snails, mites, and spiders.

Figure 81. ***Hypopterygium tamarisci***, home to several orders of insects. Photo by Peter Woodward, through Creative Commons.

Figure 82. ***Lopidium concinnum***, a habitat for several orders of insects. Photo by Juan Larrain, through Creative Commons.

Epiphytes

A number of species of arthropods are associated with the epiphytes, including several groups of insects. Miller *et al*. (2008) compared the epiphyte arthropod fauna at three heights on red maple (*Acer rubrum*; Figure 83) trees in the Acadian forest of Maine, USA. They found that there was a close association between springtails and spiders and suggested that the spiders were there because of the abundance of springtail prey. When the bryophytes diminished following gap harvesting, the spiders and springtails did as well. One surprise was the abundance of **Diptera** associated with the epiphytes. Fifteen families of these flies were represented. Overall, the numbers of morphospecies was positively correlated with bryophyte abundance except for the springtail family **Isotomidae**. Abundance of the other springtail morphospecies were correlated with dense bryophyte cover at the bases of trees.

Figure 83. ***Acer rubrum***, a species that supports arthropods living in epiphytic bryophytes. Photo by Jean-Pol Grandmont, through Creative Commons.

In the Pacific Northwest of North America, the epiphytic bryophyte mats in the subcanopy likewise house numerous insects. In collections of over 143,000 individuals, Peck and Moldenke (2011) recovered 205 morphospecies from 337 moss mats (less than 25 kg of mosses, fresh weight). These mosses were collected to determine the impact of moss harvesting on the insect community, but they also provide us with information on community structure. The faunal morphospecies composition between moss mats from the two shrubs, vine maple (***Acer circinatum***; Figure 84) and huckleberry (***Vaccinium parvifolium***; Figure 85) did not differ. Likewise, the fauna of the vine maple did not differ between the bases and branch tips of these shrubs, differing from their results in the Willamette National Forest (Peck & Moldenke 1999). Instead, the invertebrate fauna composition correlated with elevation, stand age, and vertical distance to water.

Figure 84. ***Acer circinatum***, a shrub that supports growths of mosses that are often commercially harvested, with their accompanying invertebrate fauna. Photo by El Grafo, through Creative Commons.

Figure 85. ***Vaccinium parvifolium***, a species with moss mats that hold arthropods. Photo by Walter Siegmund, through Creative Commons.

In the tropics, canopy bryophytes may be especially important for some of the invertebrates. Pócs (1982) estimated an excess of 1000 g m^{-2} of bryophytes in the elfin forests. Trees in Costa Rican montane forests build canopy soils (including bryophytes) that house mites, amphipods, isopods, beetles, springtails, ants, and insect larvae as the dominant invertebrate groups (Nadkarni & Longino 1990). The ground fauna had a mean density of 2.6 times that of the canopy. Only ants did not fit this pattern. However, it is difficult to assess these tropical mats because the mosses are typically only a minor component. Instead, the mats are primarily leafy liverworts and filmy ferns (Yanoviak *et al.* 2007). Yanoviak and coworkers found that these insect assemblages resembled the fauna of the soil mosses and accompanying humus layer. These are dominated by mites, springtails, ants, and minute beetles (Yanoviak *et al.* 2003, 2004). Unfortunately, the fauna of mosses in the canopy may be under-sampled because the fogging method used in many studies of canopy invertebrates is ineffective for sampling the tiny insects that inhabit the canopy bryophytes (Yanoviak *et al.* 2003).

Even within a mat of epiphytic bryophytes and other plants, vertical differences exist (Yanoviak *et al.* 2004). In a Costa Rican lower montane forest, the green portion of the mat housed twice as many individuals and species per gram dry mass compared to the brown portion. Morphospecies composition was similar, but some taxa differed significantly in relative abundance. Predators were randomly distributed in the larger patch sizes (up to 50 cm^2). They found that interspecific interactions were more important than the environmental variables in determining the distribution of the mat fauna in small patch size (20 cm^2).

Cryptogamic Crusts

The cryptogamic crusts are those habitats in arid ecosystems that are comprised of algae, bacteria, fungi, lichens, and bryophytes. These crusts are of major importance in these ecosystems, covering as much as 70% of the soil (Brantley & Shepherd 2004).

The arthropod fauna make use of the crusts for retreats and homes. In piñon-juniper woodland in central New Mexico, the crusts differ little in major groups from bryophyte habitats in other ecosystems, with tardigrades, nematodes, springtails, small insects, mites, and spiders predominating (Brantley & Shepherd 2004). Of the 38 taxa identified in the study, 27 occurred on mixed lichen and moss patches and 29 on moss patches. Only 21 were found on pure lichen patches. Of the three types of crusts, 15 arthropod taxa occurred on all three. Not only did the mosses have the highest number of arthropod species, but they also had the greatest abundance of arthropods. In this very dry climate, the greatest arthropod richness and abundance occurred in winter.

Altitude

Altitudinal gradients are complicated. Although the temperature tends to decrease and winds increase, moisture may be greater or less, and microhabitats abound. Vegetation changes and can increase or decrease shade. UV light may come into play.

Differences between elevations may be more due to microclimate differences than to those differences caused by elevations (Andrew *et al.* 2003). For example, Andrew and coworkers found that whereas altitude had a significant effect on diversity of insects in Tasmania and New Zealand, there was no general trend present along the altitudinal gradient. Mt. Field in Tasmania had the highest invertebrate and bryophyte diversity at 750 m. But Mt.

Rufus had low bryophyte and insect diversity throughout the altitudinal gradient. In Tasmania Mt. Otira had the highest diversity of both invertebrates and bryophytes at low altitudes, whereas Mt. Kaikoura had the highest invertebrate and lowest bryophyte diversity at the highest altitude. Clearly different factors are important for the bryophytes compared to those important for the invertebrates. Andrew and coworkers stressed the importance of scale and the need to sample both broad scale and microscale community patterns.

Tundra

Bryophytes are important ground cover in the tundra. In Spitsbergen, Bengston *et al*. (1974) found a total arthropod abundance of 268,000 individuals m^{-2} on wet moss tundra, compared to 42-63,000 on lichen tundra and 518,000 on grassland. The mites and springtails comprised 96-99% of the arthropod fauna, with small numbers of spiders, flies, and **Hymenoptera**. These major groups were similar in abundance to those of the high alpine in southern Norway.

Boreus in Norway takes advantage of mosses to provide protective space. This is a safe space in which they lay their eggs (Håvar 2001). And it appears that it might be a site of copulation, an event rarely observed on the snow. The chambered air spaces most likely also provide space for this winter-active scorpionfly. Adults of ***Boreus elegans*** (Figure 86) and ***B. californicus*** (Figure 87-Figure 88) feed on ***Racomitrium heterostichum*** (Figure 89-Figure 90); larvae and pupae of ***B. elegans*** can be found under ***Brachythecium*** (Figure 91) and other mosses (Russell 1979).

Figure 86. ***Boreus elegans*** adult, a winter-active scorpionfly that lays eggs among mosses. Photo by Megan Asche, with permission.

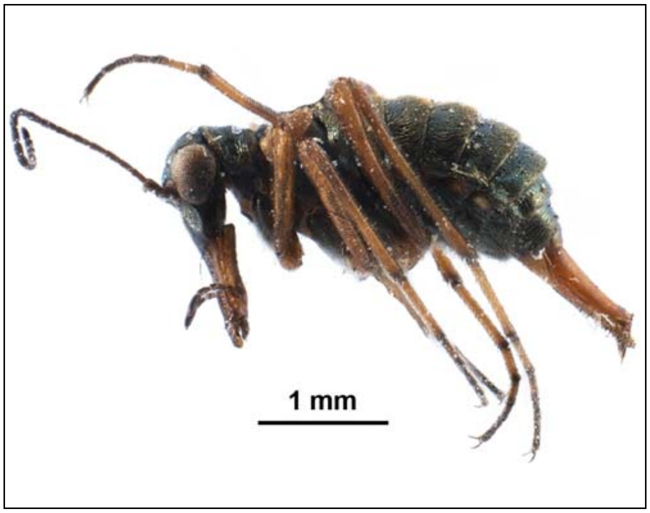

Figure 87. ***Boreus californicus*** adult female, a species that feeds on ***Racomitrium heterostichum***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

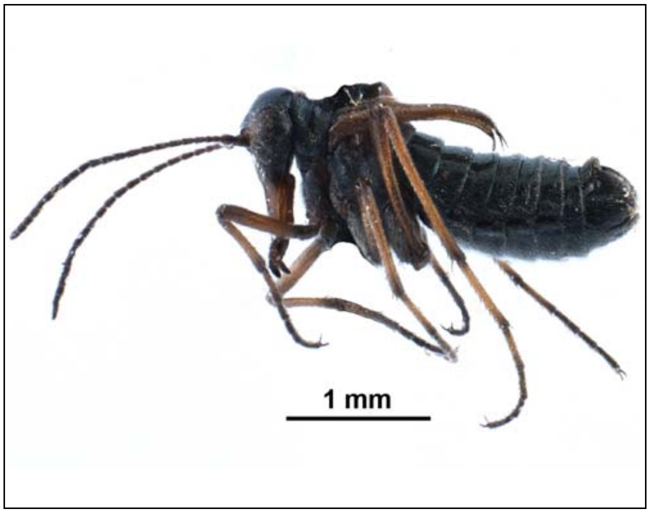

Figure 88. ***Boreus californicus*** adult male, a species that feeds on ***Racomitrium heterostichum***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 89. ***Racomitrium heterostichum*** habitat and home for ***Boreus californicus*** and ***B. elegans***. Photo by Andrew Spink, with permission.

Figure 90. ***Racomitrium heterostichum***, food for ***Boreus californicus*** and ***B. elegans***. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 91. ***Brachythecium rutabulum***, home for larvae and pupae of ***Boreus elegans***, with capsules. Photo by Tim Waters, through Creative Commons.

The family **Apteropanorpidae** has a single genus, ***Apteropanorpa*** (Figure 92), with only four species (Wikipedia 2011). These are the Tasmanian snow scorpionflies, and they live among mosses in Tasmania and southern Australia. The adults are predators, but the larvae live among the mosses.

Figure 92. ***Apteropanorpa tasmanica***, a moss dweller that is often infested with one or two species of parasitic mites. Photo by Simon Grove ©, Tasmanian Museum and Art Gallery, with permission.

The best-known species, ***Apteropanorpa tasmanica*** (Figure 92), is known to carry two species of parasitic mites (Seeman & Palmer, 2011). These are ***Leptus agrotis*** (**Erythraeidae**) and ***Willungella rufusanus*** (**Microtrombidiidae**)

Antarctic

In the Antarctic, bryophytes form the dominant vegetation and house the most arthropods (mites, springtails, insects) (Gerson 1969). Gerson reported that the ***Polytrichum-Dicranum*** (Figure 93) mats housed more arthropods than did ***Pohlia*** (Figure 94-Figure 95). The former was less wet and cold in the summer and its open texture made it easier for movement, especially of larger arthropods.

Figure 93. ***Polytrichum juniperinum*** in ***Dicranum scoparium*** mat, a species combination that is home for many arthropods. Photo by Kirill Ignatyev, through Creative Commons.

Figure 94. ***Pohlia nutans*** with capsules, a common sight in the Arctic and Antarctic. ***Pohlia*** species house arthropods there. Photo by Michael Lüth, with permission.

Figure 95. ***Pohlia nutans*** with capsules, a genus that is home to arthropods. Photo by Michael Lüth, with permission.

The Antarctic is dominated by small organisms. In that regard, bryophytes are an important habitat for invertebrates. Davis (1981) compared the invertebrates on two kinds of moss communities on Signy Island: a moss turf dominated by ***Polytrichum alpestre*** (=***P. juniperinum***; Figure 96) and ***Chorisodontium aciphyllum*** (Figure 97-Figure 98) and a moss carpet composed of ***Warnstorfia sarmentosa*** (Figure 99), ***Sanionia uncinata*** (Figure 100), and ***Calliergidium austrostramineum*** (Figure 101), with the liverwort ***Cephaloziella varians*** (Figure 102). The trophic structure, organic matter transfer, and production of primary producers (which included lichens and algae in addition to the bryophytes) were similar in these two community types, but the standing crops of **Collembola** (springtails; Figure 33) and **Acari** (mites) differed. These differences may have related to the differences observed in turnover of mosses and accumulation of dead organic matter.

Figure 96. ***Polytrichum juniperinum***, a common moss on Signy Island and home to **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Photo by Juni, through Creative Commons.

Figure 97. ***Chorisodontium aciphyllum*** in Antarctica, home to a variety of invertebrates. Photo from Polar Institute, through Creative Commons.

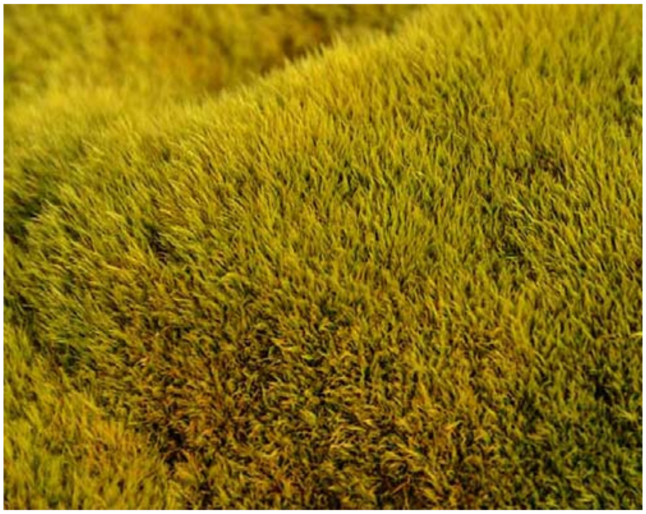

Figure 98. ***Chorisodontium aciphyllum*** in the Antarctic, a primary producer and home for the same groups of organisms as ***Polytrichum juniperinum***, but with different proportions. Photo by Zicheng Yu, through Public Domain.

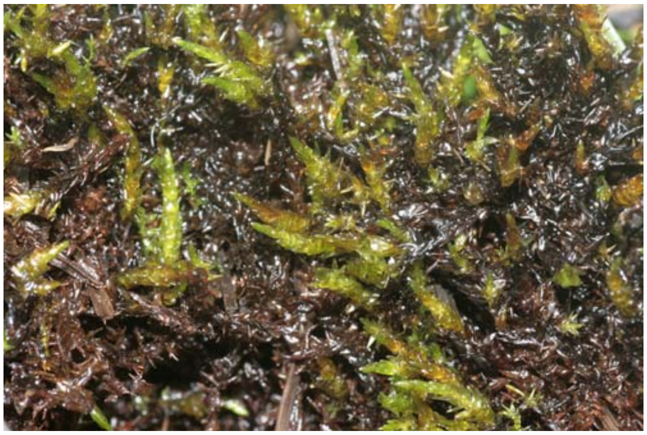

Figure 99. ***Warnstorfia sarmentosa***, home for a variety of invertebrates, including **Collembola**, on Signy Island. Hermann Schachner, through Creative Commons.

Figure 100. ***Sanionia uncinata***, home for invertebrates in the Antarctic. Photo by Hermann Schachner, through Creative Commons.

Figure 101. ***Calliergidium austro-stramineum***, home for invertebrates in the Antarctic. Photo by Bill Malcolm, with permission.

Figure 102. ***Cephaloziella varians*** with ***Polytrichum*** sp., home for invertebrates in the Antarctic. Photo by Christian Peters, with permission.

The maritime Antarctic has a flora that is predominately bryophytic (Tilbrook 1967). The invertebrate fauna has few species with any great abundance. This area produced a number of indigenous insects: only seven species of **Collembola** (springtails) and one of **Diptera** (flies), but 20 species of mites. The dominant arthropod is ***Cryptopygus antarcticus*** (**Collembola**). The highest densities of insects are among the vegetation, but some occur in areas free of permanent ice. Habitat specificity is uncommon. It is likely that the ability of bryophytes to absorb radiation and affect the microhabitat temperature, coupled with the insulation of snow, makes the bryophyte habitat a suitable habitat for the arthropods. Geothermal areas, as discussed below, further provide a bryophytic habitat that is suitable for arthropods.

Strong (1967) considered the Antarctic mosses to serve primarily as shelter and concluded that they do not provide a significant source of nourishment. Humidity seems to be the major controlling factor, with temperature playing a secondary role. Wind is an important feature that modifies temperature and humidity. The primary consumers include springtails and the midge ***Belgica*** (Figure 103). Adaptations to the climate seem to be primarily physiological rather than developmental or behavioral.

Figure 103. ***Belgica antarctica***, a moss consumer, mating. Photo, through Creative Commons.

Usher and Booth (1984) cut five sets of 96 contiguous samples from moss turf on Signy Island in the maritime Antarctic. They found only 10 taxa of arthropods, comprised of mites and springtails. Of the six species with enough abundance to analyze, they found a vertical separation of the species, with three occurring near the surface, two in an intermediate position, and one deep in the mat, resulting in many negative correlations arthropod between species at any given depth. However, when the depths were combined, there were no negative correlations, and many positive correlations were present. Even within a species the vertical distribution differed with life cycle stage. Overall, two distinct communities were present – the green moss community (0-1.5 cm) and the dead moss community (below 3 cm). Nevertheless, the two communities were composed of the same six species, but the proportions differed.

Geothermal

Cold climates are harsh and many organisms do not have the life cycle and physiological adaptations needed to survive in them. However, one habitat provides the year-round warmth for survival of more temperate organisms that are able to arrive there. These are the geothermal areas that are in polar regions of both the Antarctic and Arctic landscapes.

Bryophytes serve as buffers in these habitats. Their own depth insulates the tips of the plants from the heat beneath, and the "steam" emanating from the vents keeps the habitat moist (Glime & Iwatsuki 1990). Lichens seem unable to survive these hot but moist environments, but the bryophytes protect their own growing tips and survive at higher moist temperatures than those suitable for lichens.

Elmarsdottir *et al*. (2003) address the paucity of knowledge about the geothermal ecosystems. Most studies have been descriptive, with little attention to the interactions of this unique ecosystem. Soil temperatures dominate the limiting factors, with soil *p*H and carbon content also influencing species composition. Nevertheless, a number of bryophytes have been able to tolerate the heat or escape it by providing their own insulation through decaying lower parts. These bryophytes provide homes for invertebrates.

Historically, geothermal areas most likely served as refugia from glaciers, and once glaciers receded, these heated areas permitted recolonization of nearby non-geothermal regions. Fraser *et al*. (2014) tested this hypothesis, based on the expectation that the greatest diversity would occur closest to the geothermal areas. Using Antarctica as a test, they did indeed find the greatest diversity closest to the geothermal areas.

Convey and Lewis Smith (2006) reported that the bryophytes on South Sandwich Islands in the Antarctic had the greatest richness in geothermally influenced ground. In fact, only four of the mosses on the islands were never associated with geothermal areas; 35 moss species and 9 liverwort species were present in all. On the other hand, 8 liverwort and 50% of the mosses occurred only on heated or recently heated geothermal areas. ***Campylopus introflexus*** was the only bryophyte to tolerate the maximum temperatures (40-47°C) of the upper 0.5 cm of the bryophyte layer. The flora of the unheated ground is similar to that of the maritime Antarctic (Convey *et al*. 2000). The heated ground contains species common to both the maritime and sub-Antarctic areas, supporting the importance of the geothermal areas for successful colonization elsewhere

Given the success of bryophytes in geothermal areas, it is easy to imagine that the ubiquitous insects would likewise be represented there, likewise taking advantage of the extra warmth. Even in Hawaii, geothermal areas permit ants to extend to higher elevations than would otherwise be possible (Wetterer 1998).

Boothroyd and Browne (2006) found that the invertebrate species occupying geothermal areas of New Zealand tended to be common species. Willoughby *et al*. (2015) found that the bryophytic fauna in the Waikato Region of New Zealand did not correlate with the soil temperature.

Some studies are focussing on the impact of human activity, especially for harvesting geothermal heat and power, on the flora and fauna (Miller *et al*. 1995). Human activity poses a threat to these fragile systems. Connectivity between suitable sites is important to maintain these communities and their fauna.

Pollution Effects

Bryophytes are well known for their ability to collect air pollutants, especially heavy metals. As a result, we might expect that the bryophagous insects would also have higher concentrations than those feeding on plants that are less efficient collectors (Steiner 1994).

We might also predict that these high concentrations could be lethal for some of the inhabitants. Varga (1992) tested ***Plagiobryum zierii*** (Figure 104) and ***Saelania glaucescens*** (Figure 105) from a polluted roadside in Hungary and found higher lead concentrations in them. Concomitantly, the invertebrate fauna, including insects, was lower than that found in mosses from an unpolluted control site. Furthermore, the invertebrates from the polluted mosses exhibited high concentrations of lead.

Figure 104. ***Plagiobryum zierii*** from Europe, a moss that accumulates lead that can then accumulate in bryophagous insects. Photo by Michael Lüth, with permission.

Figure 105. ***Saelania glaucescens***, a moss that accumulates lead that can then accumulate in bryophagous insects. Photo by Michael Lüth, with permission.

Pollution can have positive or negative effects on insects. When mosses in an area polluted with heavy metals were analyzed, those from less polluted areas had more molybdenum, whereas those from the polluted areas had increased levels of cadmium and chromium (Soltes 1996). These increased Cd and Cr contents corresponded with the areas of spruce bark beetle outbreak.

Climate Change

Pollution with CO_2 is generally blamed for global climate changes. It not only means that some areas will be hotter, some will be colder, more severe storms will occur, water levels will rise, and seasons will have different periodicities, but nutrient levels will change as well.

Richardson *et al.* (2002) examined the impact of changes in nutrients and warming in a sub-Arctic heath on vegetation and insect herbivores. The bryophagous **Heteroptera** in fertilized plots was reduced to as little as 6% that of the unfertilized controls. **Homoptera** that fed on grasses became 400% more abundant. The changes in the insect community was driven primarily by the subordinate plant groups (grasses and mosses), emphasizing the importance of the mosses in this tundra habitat. Nutrients had a greater impact than the rise in temperature.

Summary

Bryophytes serve as habitat for numerous kinds of insects. They provide moisture (an important limiting factor for insects), food, shelter, refuge from predators, and a buffer against the climate. The insects that live there are limited in their adaptations, but some are wingless, have cryptic coloration, are able to eat bryophytes, and are small and flexible enough to maneuver among the bryophytes.

Those that live in northern regions often use mosses as a winter home. They may eat bryophytes to survive in winter and it is possible these bryophytes may help to adapt them to the winter cold, possibly through providing **arachidonic acids**.

Because bryophyte dwellers typically have limited mobility, their dispersal is limited. Fragmented landscapes and separated microhabitats often require corridors that connect the habitats with suitable microhabitats to permit recolonization of disturbed sites.

Although most of the bryophyte inhabitants seem to use the associated invertebrates, algae, bacteria, and fungi as food, some do eat the bryophytes and some are even liverwort specialists. Bryophytes often have secondary compounds that prevent herbivory and those insects that eat bryophytes do have preferences. Some bryophytes are so effective at deterring herbivores that they are being developed as pesticides.

Again because bryophytes have limited mobility, typical insect sampling methods are often inappropriate and biased. Using heat to cause the insects to fall into traps or using pitfall traps may miss whole taxonomic groups that fail to move away from the bryophytes. Hand sorting of bryophyte clumps is the only (nearly) unbiased method, but it is destructive and therefore limits the number of samples.

The most common bryophyte-dwelling arthropods worldwide are spiders, springtails, and mites. The typical orders of insects present include **Collembola**, **Odonata**, **Notoptera**, **Psocoptera**, **Hemiptera**, **Megaloptera**, **Neuroptera**, **Coleoptera**, **Hymenoptera**, **Trichoptera**, **Lepidoptera**, **Mecoptera**, and **Diptera**.

In bogs and wetlands, ants are common ***Sphagnum*** inhabitants making nests of the ***Sphagnum***. **Lepidoptera** are common and depend on plants that depend on the environment created by the bryophytes. Several families of beetles, especially **Carabidae**, live among the bryophytes.

Forest bryophytes have fewer species and the bryophyte fauna there seems to be less well known. In the tropical rain forests, epiphytes provide important habitats, especially for ants and springtails. In cryptogamic crusts of the desert, bryophytes provide a refuge from the hot sun and a place where moist periods last longer, but the life cycle needs to be attuned to the short moist periods or the insects must be able to burrow deep into the soil.

At high altitudes, in the tundra, and in the Antarctic, the bryophytes are the most hospitable habitat for terrestrial insects, providing a buffer against the extreme temperatures, maintaining moisture, and harboring smaller food organisms. It is also likely that they protect against UV light. Geothermal areas in these cold regions provide a haven for species normally found in warmer habitats, and the bryophytes are usually the dominant vegetation.

Bryophytes are known accumulators of air pollutants, so insects that eat them or eat other invertebrates that eat them may be seriously affected by the accumulated heavy metals. A warming climate is likely to decrease the bryophytes in northern climates and thus affect the insect herbivores. Furthermore, increases in nutrients resulting from climate warming cause decreases in bryophagous **Heteroptera** and increases in **Homoptera** that feed on grasses.

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