

CHAPTER 7-1

ARTHROPODS: HABITAT RELATIONS

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CHAPTER 7-1

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Figure 1. The epiphytic moss *Orthotrichum lyellii* that has been chewed, most likely by an arthropod, partially stripping the stems. Photo by C. Robin Stevenson, with permission.

Arthropods (Phylum Arthropoda)

The most conspicuous group of organisms living in the shelter of bryophytes are the arthropods (Bonnet *et al.* 1975; Kinchin 1990, 1992). McKenzie-Smith (1987) contended that animal densities among bryophytes often were greater than those we might expect simply on the basis of the greater surface area, implying that they provided more than just space. Yet, as Gerson (1969) so aptly pointed out, ecologists, both botanical and zoological, had dismissed the bryophyte habitat, as Cloudsley-Thompson (1962) put it, because "it is clear that moss does not form a biotope with a stable microclimate." Humph! To what were the ecologists comparing it?

Not only do the bryophytes modify their internal climate relative to the ambient conditions, they also modify the soil conditions, permitting some of the arthropod species to survive there when the ambient atmospheric conditions are extreme and uninhabitable (Gerson 1969). Acting like a spongy insulator, they buffer soil temperatures and reduce water evaporation from the soil. But they also can interfere with water reaching the soil in short spates or very light rainfall. They provide a humid

environment when the sun dries the atmosphere. And some species act like a black box, absorbing heat with dark-colored leaves and reaching temperatures higher than those in the atmosphere. With these varying conditions, we might hypothesize that bryophytes can serve as a refuge at times while being inhospitable at others, and for some, provide a source of food (Figure 1).

The abundance of arthropods among bryophytes may in part relate to their concurrent venture onto land in the early Ordovician (Anissimov 2010). Once on land, they have invaded the three main strata: subterranean, forest floor debris, and arboreal (Grimmett 1926). Among these, we will generally not be concerned with the subterranean stratum as it is rarely a habitat for bryophytes. The stratum of forest floor debris reminds us that soil scientists often consider the moss layer as part of the soil, and most certainly Grimmett included it with the forest floor debris.

Yanoviak *et al.* (2004) considered such habitats as epiphytic mosses to enhance species richness of the arboreal arthropods by increasing the available types of niches. The bryophytes provide a structural component to

the arboreal habitat and function to buffer the moisture and protect against the wind. They furthermore provide a foraging location and a place to deposit eggs (Gerson 1982; André 1983; Nadkarni 1994; Kitching *et al.* 1997; Drozd *et al.* 2009).

The bryophytes can serve as food for a wide range of arthropods and at the same time they provide excellent camouflage. Fischer (2005) estimated that 300 species of animals, many of which are arthropods, live among mosses in the Pacific Northwest and Appalachian Mountains, North America. These arthropods, in turn, can serve as food for a wide range of larger animals.

In their *Science* article, "The Forgotten Megafauna," Hansen and Galetti (2009) state that "In any given ecosystem, the largest vertebrates have ecosystem impacts that are similar on a relative scale to those of the largest vertebrates in another ecosystem: One ecosystem's mesofauna is another ecosystem's megafauna." This concept can be extended to comparing the bryophyte habitats. In this case, it would usually be the arthropods that occupy this position of megafauna. Although most of these top predators are insects, other arthropods are likewise important. As will become evident, we know almost nothing about these relationships in the bryophyte habitat.

Arthropods were so-named because they have jointed legs (Hingley 1993). Some arthropods are small enough to inhabit the water film in a leaf concavity, and small crustaceans and mites are able to live in that film between the leaves. Larger arthropods such as spiders and insects can run across the surface or navigate among the stems and leaves.

Bryophytes in all sorts of habitats house a varied arthropod fauna. Smrž (1992) studied the microarthropods inhabiting mosses on roofs. Block (1985) described arthropods in a terrestrial community on Signy Island in the maritime Antarctic. In the Antarctic, mosses modify soil moisture and temperature, permitting arthropods to live there (Gerson 1969). Curry *et al.* (1989) studied the invertebrate fauna of reclaimed peatlands in Ireland. De Graaf (1957) examined both the macrofauna such as arthropods and the microflora of a quaking bog in the Netherlands. Varga (1992) examined the communities associated with two protected moss species [*Plagiobryum zierii* (Figure 2) & *Saelania glaucescens* (Figure 3)] in Hungary and found that mosses with high lead concentrations near roads were associated with poorer bryofauna than mosses from unpolluted control sites, as already noted for micro-organisms. Protozoa, small metazoa, bacteria, organic debris, and plant material serve as food for the inhabiting arthropods, permitting the arthropods to sustain life within the protection of a bryophyte clump.

Insects, the largest group of arthropods and the largest single group of animals on the planet, have many members small enough to navigate within the moss clumps, and are therefore a major component of the fauna. They can be so numerous as to require special extraction methods (Andrew & Rodgers 1999). Their abundance and diversity have earned them separate chapters in this book.



Figure 2. *Plagiobryum zierii*, a moss where lead accumulations can lead to a depauperate fauna. Photo by Michael Lüth, with permission.



Figure 3. *Saelania glaucescens*, a lead accumulator that becomes unsuitable for many invertebrates. Photo by Michael Lüth, with permission.

Habitat Relations

Since I first began, early in my career, studying arthropods associated with aquatic bryophytes, numerous studies have addressed the fauna of the protective bryophyte habitat (see Borges *et al.* 2005). Yet, the relationships of the bryological fauna to the bryophytes remains poorly known (Drozd *et al.* 2008). Drozd and coworkers (2009) were able to demonstrate that significant relationships exist between the microhabitat conditions within the bryophyte cushions and the patterns of abundance of the invertebrate community (Figure 4).

In comparison to litter habitats, Drozd *et al.* (2009) were surprised to find that nearly all arthropod groups were in greater abundance in the litter than in moss cushions ($p = 0.0003$; *e.g.* Figure 5). But as they identify species, we may find this relates to available space for larger organisms that cannot navigate well among the bryophytes. Drozd *et al.* (2009) found that moss presence, moss species, and moisture were very important in determining arthropod abundance.

Much remains for us to understand about the arthropod fauna of these unique habitats.

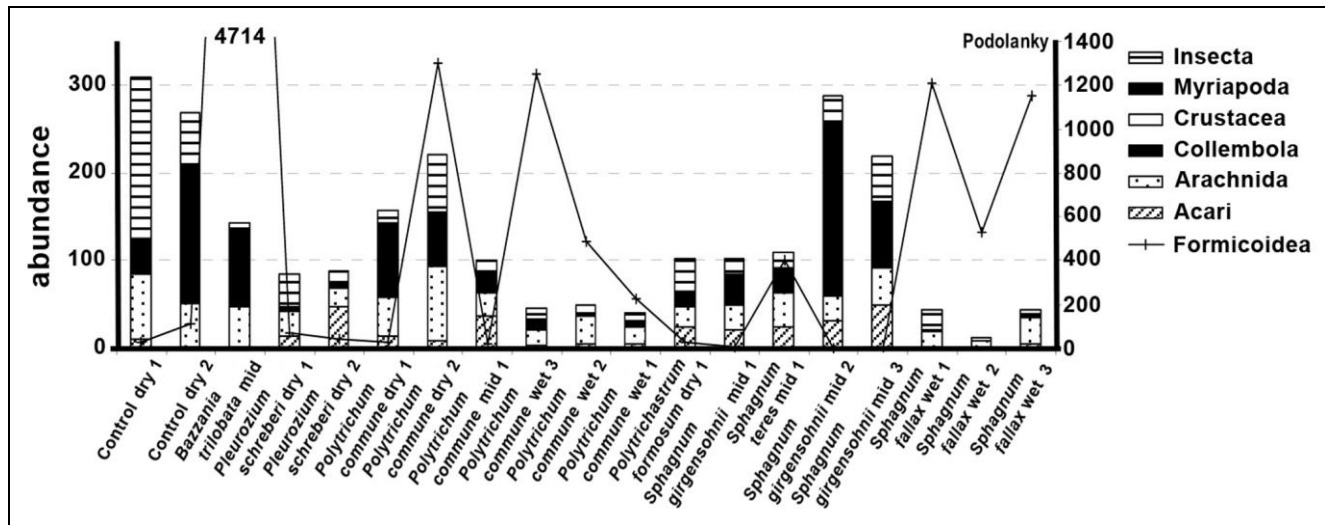


Figure 4. Abundance of arthropod taxonomic groups in pitfall traps in the mountains of the Czech Republic. Ants (Formicoidea) from Podolánky were drawn separately because of their high numbers. Control = litter; moisture categories are wet (high), middle, and dry (low). Redrawn from Drozd *et al.* 2009.

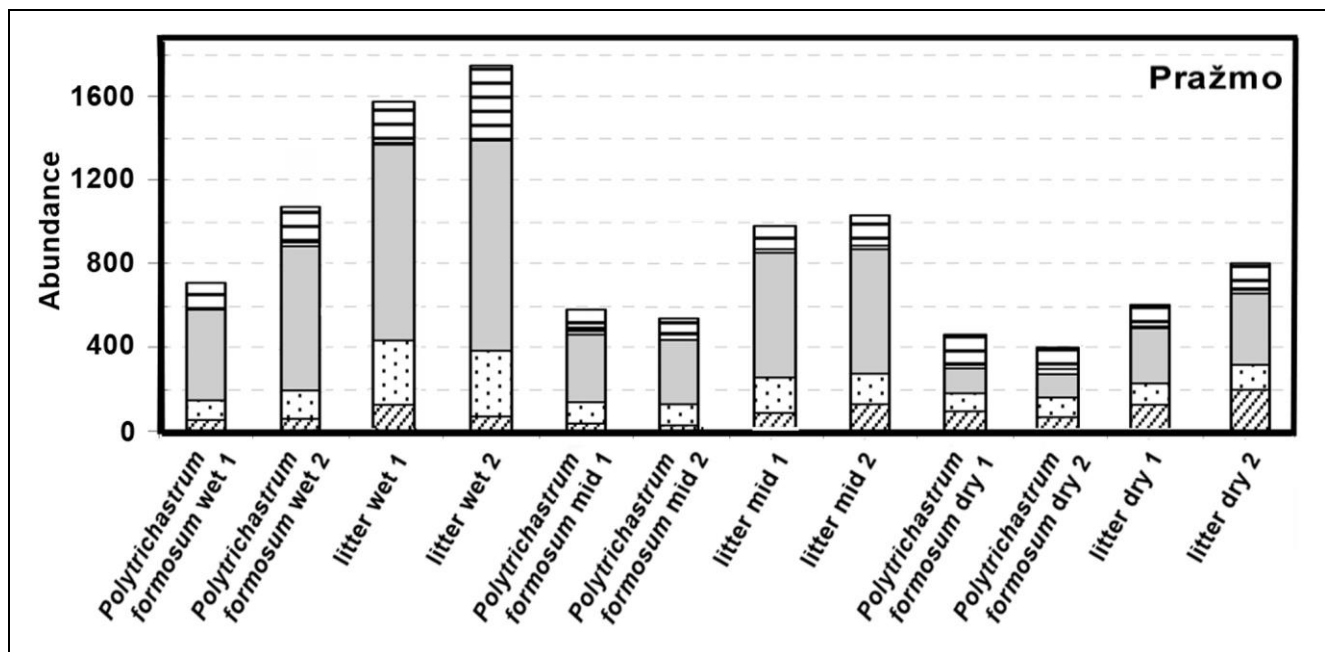


Figure 5. Abundance of arthropod taxonomic groups in pitfall traps at Pražmo in the mountains of the Czech Republic. Moisture categories are wet (high), middle, and dry (low). Redrawn from Drozd *et al.* 2009.

Epiphytes

The importance of bryophytes to the arthropod community is suggested by a positive correlation between bryophyte abundance and arthropod morphospecies in a study in Maine, USA (Miller *et al.* 2007). Epiphytes, especially in the tropics, are a habitat for a number of arthropod inhabitants (Nadkarni & Longino 1990). Nadkarni and Longino found that canopy "soils" in Costa Rica included Coleoptera, Collembola, Acari, insect larvae, ants, Amphipoda, and Isopoda. And disturbance that removes bryophytes typically results in a decrease in arthropods, at least temporarily.

Zytyńska *et al.* (2011) found that genetic variation in species of tropical trees could affect associated epiphytes and invertebrates. They found that greater genetic diversity

among the trees led to greater diversity among epiphyte and invertebrate communities. The very limited specificity of bryophytes for host trees suggests there may not be a strong influence on bryophyte diversity, but we must ask how much influence the genetic differences in the trees may have on the invertebrate communities living among those bryophytes. Peck and Moldenke (2010) found that there were no significant differences among arthropods between the two tree species they sampled, but rather arthropod communities related more to location of the mats.

Pettersson *et al.* (1995) found that the number of larger invertebrates, important food sources for birds, was greatest among arboreal lichens in the boreal forest of Sweden, compared to habitats in managed forests that lacked

abundant lichens. The predominant invertebrates were spiders (**Araneae**), **Lepidoptera**, and **Diptera** larvae. Thus, decline in bird populations have been linked to loss of food organisms that depend on lichens in that habitat. Similar studies for bryophytes (Nadkarni 1994), indicate that it is likely that loss of spiders from disturbed habitats that previously had more bryophytes might likewise be a cause for bird decline.

Secondary forests developed after deforestation are recolonized slowly by bryophytic epiphytes (Pettersson *et al.* 1995). Hence, the arthropods and other invertebrates are necessarily delayed in their arrival. Absence of suitable habitat nearby will further delay colonization of new growth. Pettersson *et al.* (1995) demonstrated that natural boreal forests (i.e., those without harvesting) supported five times as many invertebrates per tree branch as the mature secondary forests as well as a greater diversity. Spiders were among the dominant organisms. Non-migrating birds often depend on these invertebrates during the winter when small differences in food abundance can be critical to sustaining their lives. Furthermore, only the invertebrates larger than 2.5 mm form suitable prey for overwintering passerine birds, a size that was consistently higher in unlogged forest. Although most epiphytes in this case were lichens, bryophytes are likely to present a similar story.

Typical tropical sampling methods, including fogging, tend to miss many of the bryophyte-dwelling arthropods (Yanoviak *et al.* 2003). Nevertheless, tropical studies indicate the importance of epiphytic bryophytes as habitat for numerous arthropods (Yanoviak *et al.* 2007). In Monteverde, Costa Rica, secondary forests had thinner mats that were less structurally diverse than those in primary forests. Although species richness differed little between the two forest types, abundance of arthropods was significantly higher in the secondary forest, primarily because of the presence of ants. During the dry season (February – May), the number of taxa was lower, with arthropods becoming dormant or seeking places with greater moisture, including deep in mats. Nadkarni and Longino (1990) demonstrated the invertebrates that were dominant in the Costa Rican canopy as well as the forest floor: adult beetles (**Coleoptera**), **amphipods**, ants (**Hymenoptera**), springtails (**Collembola**), insect larvae, **isopods**, and mites (**Acari**). The ground fauna exhibited 2.6 times the density of that found in the canopy, but this does not diminish their importance for canopy-dwelling birds. Temperate bryophytic epiphytes can be suitable habitats for arthropods as well (Voegtlin 1982).

Forest Floor

It is likely that bryophytes, like litter, influence the kinds of spiders and other arthropods on the forest floor. Willett (2001) demonstrated in the Santa Cruz Mountains of California, USA, that forest floor spiders indicated such characters as old growth vs logged forest. Both diversity and abundance of spiders decreased with herb cover. Those spiders that live in association with moss mats are likely to decrease as well in disturbed (logged) forests, often due to a decrease in prey abundance.

Rock Zonation

Bonnet *et al.* (1975) examined the ecology of 26 bryophyte-dwelling species of springtails (**Collembola**) and 45 species of mites (**Acari**, Figure 6). These

arthropods exhibited a population gradation from soil to aerial mosses. Likewise, there was a gradation from drier mosses on the south face of the forest rock to the deep soil communities on the north face. This study pointed to the importance of humidity and temperature in determining the distribution of these two arthropod groups.



Figure 6. Mite (**Acari**). Photo by Alan R. Walker, through Creative Commons.

Cryptogamic Crusts

The cryptogamic crust is a mix of lichens, algae, Cyanobacteria, and bryophytes that form a crust on dry soil. In prairies and semidesert lands they may occupy as much as 70% of the soil (Brantley & Shepherd 2004) and provide a means of conserving moisture, providing a suitable habitat for arthropods. In the piñon-juniper woodland of central New Mexico, mosses provided a better habitat (greater faunal abundance) than did lichens or mixed lichen crusts (Brantley & Shepherd 2004). Likewise, mosses housed the most taxa (29 species, then mixed lichens and mosses (27), then lichens (21). Fifteen taxa occurred on all three of these substrata, suggesting possible specificity, but with a greater degree of generalists than specialists among cryptogamic taxa. Shepherd *et al.* (2002) found that the fauna of crust mosses were active following winter precipitation, exhibiting significant increases in both richness and abundance. This period may introduce arthropods when other fauna are absent, thus having an important impact on soil nutrient cycling.

In the Little Desert National Park, northwest Victoria, Australia, the soil crusts (nine mosses and nine liverworts) housed only the phylum Arthropoda among the invertebrates (Milne *et al.* 2006). Diversity was low; diversity was greater in the wetter periods.

Streams

Bryophytes in streams greatly increase substrate available to arthropods (Suren 1988; Figure 7). Sometimes they house communities that mimic those of riffles, but in other cases they harbor very different communities. And the pH conditions can affect the faunal composition. In the River Liffey, Ireland, Frost (1942) compared 23 bryophyte samples each between an acid and alkaline stream and found that the numbers of organisms differed little between them (acid ca 282,000; alkaline ca 306,900 organisms), but the composition of the organisms differed. In a mountain

stream in Nara Prefecture in Japan, Tsuda and Nakagawa (1959) likewise found that communities of moss-covered rocks differed from those of bare rock.

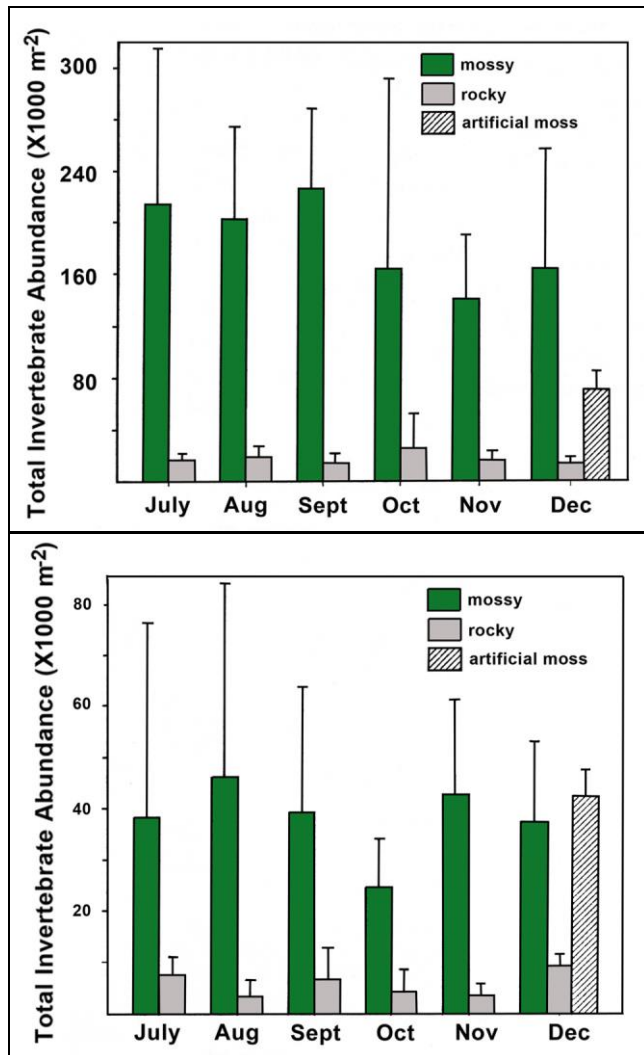


Figure 7. Comparison of invertebrate abundance in mossy habitats, rocky habitats, and artificial mosses made of nylon twine in two streams in New Zealand. Redrawn from Suren 1988.

In streams, bryophytes house not only numerous aquatic insects, but also amphipods like *Gammarus* (Figure 8, Figure 11) (Badcock 1949). And this invertebrate eats its own home. *Gammarus* lives among *Fissidens* (Figure 9) and eats its leaves (Minckley & Cole 1963).



Figure 8. *Gammarus* sp., a scud that is often found among aquatic bryophytes. Photo by Janice Glime.

Bryophytes in streams serve as a perennial refuge for many arthropods in a habitat where other plants usually disappear for the winter or are absent altogether because the flow rate is too rapid for them to survive at some times during the growing season. Such ephemeral plants prevent the establishment therein of such arthropods as *Asellus* (Figure 10) and *Gammarus* (Figure 11) (Fontaine & Nigh 1983), but the more permanent bryophytes often house these taxa.

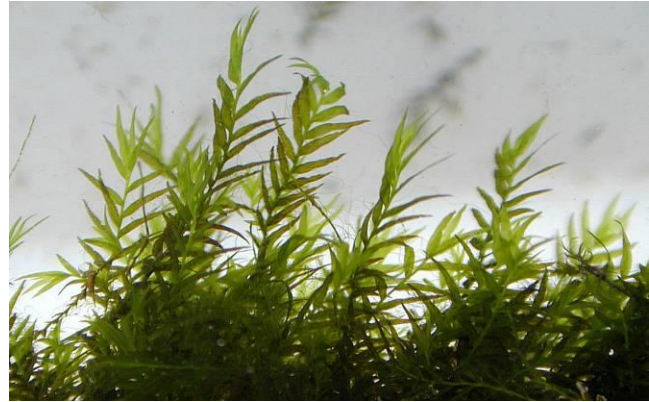


Figure 9. *Fissidens fontanus*, a moss that serves as both home and food for *Gammarus*. Photo by Michael Lüth, with permission.

Even in raging water of snowmelt, chambers within the bryophyte mat tend to be quiet (Dorier & Vaillant 1954; Kamler & Riedel 1960). This depends in part on the form and depth of the moss. The heavy flow often relegates the bryophytes to the downstream sides of rocks. The flow dynamics cause the water to arch over the bryophytes, creating the negligible flow within the moss mat (Kamler & Riedel 1960). These factors determine the quantity and composition of the fauna (Kamler & Riedel 1960).



Figure 10. *Asellus aquaticus*, a common inhabitant of aquatic bryophytes. Photo by Jacob LaCroix, with permission.

Referring to the stream bryophyte fauna, Suren (1992a) stated that "these invertebrates are traditionally neglected in stream surveys and their ecological roles poorly understood." He found that densities of meiofauna were greater than those in stream gravel habitats. Faunal communities among bryophytes were different from those in gravel. As in many other cases, the availability of periphyton as food seems to be an important factor in the distribution of these fauna (Glime & Clemons 1972;

Johnson 1978; Devantray 1987; Suren 1988, 1990; Suren & Winterbourn 1992b). But shelter from fast current among stems and in leaf axils is most likely important for many species (Suren 1992a; Suren & Winterbourn 1992a, b).



Figure 11. The scud *Gammarus* sp., sometimes an abundant inhabitant of aquatic bryophytes. Photo by Janice Glime.

Organic matter (FPOM and UFPM) fractions in bryophyte samples differ between shaded and unshaded sites (Suren 1992a, b; Suren & Winterbourn 1992b). At the unshaded site the food source was primarily periphyton, but at the shaded site it was primarily fine amorphous detritus (Figure 12). This greater detritus accumulation was largely due to the position of this portion of the stream below timberline (Suren 1992b).



Figure 12. *Hygroamblystegium fluviatile* showing detritus (grey areas) trapped among the branches. Photo by Michael Lüth, with permission.

There have been many discussions about the importance of bryophytes as a food source. Until relatively recently, ecologists considered bryophytes to be unfit food, hence rendering them unimportant in many ecosystem studies. More recent studies suggest that at least some organisms use them as food, but it is likely that their role as a substrate for epiphytic algae might be more important than their direct use, at least in aquatic systems. McWilliam-Hughes *et al.* (2009) examined the role of various components as carbon sources in two temperate rivers. Epilithic algae were primary food sources. They found that 98% of the scrapers (primarily insects) exhibited enriched $\delta^{13}\text{C}$ values relative to those of bryophytes, and that values in these two components were correlated. This relationship was not so obvious in slow-water habitats. In headwater streams, the brook moss *Fontinalis* (Figure 36)

was abundant. In low order streams (a first-order stream is a headwater stream), *Drepanocladus* (*sensu lato*?; Figure 13-Figure 14) was abundant. McWilliam-Hughes and coworkers suggested that when rivers had low productivity and were nutrient limited, scrapers compensated for the limited food availability by switching to "marginal" foods, including bryophytes. They based this suggestion on the scrapers in low-order streams that depended more on *Fontinalis* than did the scrapers in high-order streams depend on *Drepanocladus*.



Figure 13. *Warnstorfia fluitans* (formerly *Drepanocladus fluitans*). Photo by Michael Lüth, with permission.



Figure 14. Close-up of *Warnstorfia fluitans* (formerly *Drepanocladus fluitans*). Photo by Michael Lüth, with permission.

Linhart *et al.* (2002) support yet another means by which bryophytes support the food pyramid in streams. *Fontinalis antipyretica* on rock rip-rap in a channel of the Morava River, Czech Republic, trapped particulate matter that provided a food source for arthropods. Seasonal variation in the arthropod groups of **Hydrachnidia** (=Hydracarina – mites), **Cladocera** (Figure 15), **Copepoda**, and **Chironomidae** (midges) correlated significantly with trapped matter and specifically with organic matter. Linhart and coworkers concluded that aquatic bryophytes on rip-rap increase spatial diversity that supports considerably greater numbers of **meiofauna** (component of fauna of sea or lake bed comprising small, but not microscopic, animals; defined by size based on standard mesh width of sieves with 500-1000 μm as upper and 32-63 μm as lower limit; all animal life of any particular region or time) than the gravel bed.

Abundance of various types of arthropods varies widely among stream locations. Table 1 demonstrates a few of these differences from a wide range of studies. Unfortunately, the methods of reporting abundance vary as widely as the invertebrates, but relative numbers are useful. Those not reported often mean the investigators did not include them in the study.

Table 1. Comparison of arthropod abundance (exclusive of Insecta) in various locations around the world. NR = not reported.

	Sample Size	Hydracarina	Copepoda	Cladocera	Ostracoda	Amphipoda	Isopoda	Decapoda	Reference
Straffan, River Liffey, Ireland	200 g	147	329	0.4	4	6	2	0.3	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	114	45	0.4	0.3	0	0	0	Frost 1942
Cold Springbrook, Tennessee, USA	.1 m ²	+	NR	NR	NR	13.4	5.5	NR	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	880	582	180	175	NR	NR	NR	Vičková <i>et al.</i> 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	95	269	48	15	NR	NR	NR	Vičková <i>et al.</i> 2001-2002
Welsh Dee Tributary, Wales	~300 cm ²	1.7	6.8	0.1	0.4	NR	NR	NR	Hynes 1961
Mouse Stream, alpine, New Zealand	1 m ²	NR	15470	NR	NR	NR	NR	NR	Suren 1991a
Tim's Creek, alpine, New Zealand	1 m ²	NR	1120	NR	NR	NR	NR	NR	Suren 1991a
West Riding, Yorkshire, GB - loose moss	%	2.82	NR	NR	NR	0.8	NR	NR	Percival & Whitehead 1929
West Riding, Yorkshire, GB - thick moss	%	3.25	NR	NR	NR	1.35	NR	NR	Percival & Whitehead 1929
alpine unshaded stream, New Zealand	%	1.1	9	NR	2.8	NR	NR	NR	Suren 1991b
alpine shaded stream, New Zealand	%	5.9	1.5	NR	0.7	NR	NR	NR	Suren 1991b



Figure 15. **Cladoceran**, a member of the aquatic bryophyte fauna that feed on trapped organic matter. Photo by Yuuji Tsuki, with permission.

Heino and Korsu (2008) reminded us that there are few studies that address the species-area concept of stream bryophyte fauna (macroinvertebrates). Contrary to 2-d substrates, only one significant species-area relationship existed among the six that they tested.. They found two significant individuals-area relationships, but both were nevertheless weak. Rather, they found strong significant relationships between both species richness and the number of individuals with bryophyte biomass in all six sampling locations. Furthermore, disturbance by a bulldozer resulted in a stronger species-bryophyte biomass relationships. The species-area relationships on stones were weak. Heino and Korsu suggest that bryophyte biomass has a "pivotal role" both species richness and number of individuals among stream macroinvertebrates. They recommended experimental testing to determine the importance of passive sampling, provision of more food, more niche space, and flood disturbance refugia in these bryological-faunal relationships.

Peatlands

Be careful when you pull that handful of *Sphagnum* from the crimson mat in the peatland. It might bite! And

you might be crushing hundreds of lives – rotifers, ants, mites, spiders, and more, not to mention the numerous protozoa (Chacharonis 1956; de Graaf 1957; Heal 1962, 1964; Corbet 1973; Bninska *et al.* 1976; Bateman & Davis 1980; Clymo & Hayward 1982; Borcard 1986, 1993; Schönborn & Peschke 1990; Hingley 1993).

The bog provides a wide range of niches. The surface layer can experience a 30°C temperature variation in a single day, with humidity ranging 40-100% (Gerson 1969). But down in the layer of stems the temperature variation drops to only 5°C per day and the humidity is stable at 100%.

One *Sphagnum* site housed 145 species of invertebrates, whereas a nearby forested site housed only 65 (Schofield 1985). Chiba and Kato (1969) suggested that the testacean (protozoan) community in the Mt. Kurikoma district of Japan is related to the habitat of the bryophytes there.

Since *Sphagnum* is a habitat of large scale, it is not surprising that Biström and Pajunen (1989) found some of the larger invertebrates – the multipedes (animals with many feet, mostly used for millipedes, centipedes, and symphylans, but also sometimes applied to spiders and insects), including *Araneae* (mites; also Gerson 1972; Seyd 1988), *Pseudoscorpionida*, *Opiliones* (harvestmen), *Diplopoda* (millipedes), *Chilopoda* (centipedes), and *Symphyla* (blind, white multipedes; Figure 20) among both the *Sphagnum* and *Polytrichum commune* in the Finnish peatlands. *Sphagnum* and *Polytrichum commune* (Figure 16) habitats housed numerous spiders (1368 individuals/77 species), as well as *pseudoscorpions* (35/1) (Figure 17), *harvestmen* (157/5), *centipedes* (43/3) (Figure 18), *millipedes* (39/4) (Figure 19), and *Symphylans* (multipedes; 9/1) (Figure 20) (Biström & Pajunen 1989). It is interesting that despite high variability overall, *Sphagnum girgensohnii* (Figure 21) has its own characteristic species, with a high proportional similarity among samples, indicating that the faunal communities of this species are fairly consistent and suggesting the possibility of some characteristic favoring this species group (Biström & Pajunen 1989).



Figure 16. *Polytrichum commune*, a habitat for a wide range of arthropods. Photo by Michael Lüth, with permission.

Spiders can actually characterize the various biotopes within a peatland (Villepoux 1990). Lycosid spiders (wolf spiders) such as *Lycosa pullata* (Figure 22) and *Pirata piraticus* (Figure 23) seem to be common in peatlands (Nørgaard 1951), no doubt benefitting from the abundant invertebrates clambering about among the mosses. In poor pine fens, one can find the wolf spider *Pardosa maisa* in the *Sphagnum* layer (Itaemies & Jarva 1983). At the Massif Central, France, spiders in the *Sphagnum* bog were so diverse and common that they could be used to characterize the different biotopes making up the bog (Villepoux 1990). And not surprisingly, at least in Sweden, there is a rare spider wasp, *Anoplius caviventris* (Hymenoptera: Pompilidae), there to take advantage of the situation (Berglind 1993).



Figure 17. **Pseudoscorpion**, a group that often lives among mosses. Photo by Llnoba from Wikimedia Commons.



Figure 18. *Geophilus*, a centipede that is common among *Sphagnum* and *Polytrichum commune*. Photo by Fritz Geller-Grimm through Wikimedia Commons.



Figure 19. **Millipede** similar to those found among bryophytes. Photo by Dan L. Perlman through Creative Commons.



Figure 20. A symphylan (white millipede) that can inhabit mosses. This one is probably a species of *Scutigere*. Photo by Sonia Martinez through Wikimedia Commons.



Figure 21. *Sphagnum girgensohnii*, home to many kinds of arthropods that seem to have a high consistency among samples. Photo by Michael Lüth, with permission.



Figure 22. Wolf spider (**Lycosidae**), relative of *Lycosa pullata* that occurs in peatlands. Photo by Janice Glime.



Figure 23. *Pirata piraticus*, a lynosid spider that inhabits peatlands. Photo by Michael Hohner, with permission.

Arthropods can encounter difficulty in the base-poor environment of peatlands. Normally, calcite (CaCO_3) is used to harden the cuticle, but this compound is generally not available in the acid environment of the peatland. Norton and Behan-Pelletier (1991) found that the *Sphagnum*-dwelling mites *Eniochthonius minutissimus*, *Archoplophora rostralis*, and *Prototritia major* deposit whewellite, a form of calcium oxalate that may originate as precipitation from the fungal food eaten by the mites, using the whewellite as a cuticular hardening agent.

Removing invertebrates from *Sphagnum* can be a laborious task. While sifting may be viable for tiny beetles, it is impractical for many taxa. Providing a vertical gradient of temperature and O_2 (Fairchild *et al.* 1987) can drive the invertebrates to a common location at the top or bottom of the moss column for easy removal, suggesting to us that these organisms in the peatlands must balance the heat near the surface with the diminished oxygen but cooler temperatures further down in the *Sphagnum* mat.

Antarctic

Even the Antarctic and sub-Antarctic have their share of arthropod moss-dwellers (Goddard 1979; West 1984; Block 1985). Booth and Usher (1986) examined the life history of mites living among moss turfs. They (Booth & Usher 1984) found that *Polytrichum* (s.l.?) cover was somewhat important, but percentage water content was consistently important, a factor discussed already for other invertebrates. Calcium and potassium were likewise important in the arthropod distribution. It is also likely that the warmer temperatures in the bryophytes encouraged arthropod colonization (Gerson 1969). Gerson (1969) suggested that, particularly in the Antarctic, the moss-arthropod associations were the result of modifications of the soil. The mites sometimes feed on mosses as well.

The bryophyte habitat is very important for diversity of Antarctic arthropods (Gerson 1969; Block 1985; Kennedy

1994), although diversity can be somewhat low (Block 1985). Mats of *Polytrichum-Dicranum* harbor more arthropods than do *Pohlia* mats. They are less wet and cold in summer had have more open texture. *Ceratodon purpureus* (Figure 24) and *Distichium capillaceum* (Figure 25) have larger numbers of microarthropods compared to communities of *Andreaea* (Figure 26). Kennedy suggests that the paucity of invertebrates in *Andreaea* may relate to its lack of convolutions or internal spaces compared to the other aforementioned species.



Figure 24. *Ceratodon purpureus*. Photo by Michael Lüth, with permission.



Figure 25. *Distichium capillaceum* showing chambering at base where arthropods can hide. Photo by Michael Lüth, with permission.



Figure 26. *Andreaea rupestris*, a compact moss possessing less chambering than that found among *Distichium capillaceum* stems. Photo by Michael Lüth, with permission.

Altitude

On four mountains in New Zealand, Andrew *et al.* (2003) found that although diversity varied with altitude, there was no trend along the altitudinal gradient. For example, Otira had the highest diversity among both invertebrates and bryophytes at low altitudes, whereas Kaikoura had its highest invertebrate diversity coupled with the lowest bryophyte diversity at the highest altitudes. However, on Mt. Field, Andrew and Rodgers (1999) found a mid-altitudinal peak in abundance of invertebrates living among bryophytes. On Mt. Rufus they found an altitudinal abundance gradient but no differences in species richness with altitude. They determined that scale variation was a greater contributor to richness than altitude on Tasmanian mountains.

Temperature Protection for Arthropods

Bryophyte mounds and turfs provide an insulating layer that is important for a number of organisms. Some insects, like the Mecopterans *Boreus westwoodi* (Figure 27) and *B. hyemalis* in southeast Norway, are active on the snow in the winter (Hagvar 2001). These insects lay their eggs among mosses in **subnivean** (under snow) air space, thus protecting the larvae from exposure. **Collembola** (springtails) are likewise winter active and are common both on the surface and in the moss mats (Hagvar 2001).



Figure 27. *Boreus westwoodi* on mosses. Photo by Barbara Thaler-Knoflach, with permission.

In peatlands, *Sphagnum* hummocks may maintain a nearly constant temperature just below freezing (-2.5 to -8.5°C) while the air temperature drops to as low as -20°C (Longton 1979a). Nevertheless, in the cold Antarctic, Booth and Usher (1984) found that the cover of *Polytrichum* was usually less important than percentage water content and calcium content for the inhabiting arthropods.

In summer, bryophytes in some locations provide a cool haven from the summer heat (Gold *et al.* 2001). Under the moss-dominated crusts in the Olympic Mountains of Washington, USA, soil surface and near-surface temperatures are 5-8°C cooler at midday than in bare soil. Lichens cool the soil surface even more, by 10-11°C. *Sphagnum*, on the other hand, can reach temperatures as much as 10°C above ambient (Longton

1979a), forcing its inhabitants to move further down into the mat. And in the boreal forest at Pinawa, Canada, temperatures in *Bryum argenteum* (Figure 28) reached as high as 55°C! (Longton 1979b). It is likely that dark pigments contribute to the warming of bryophyte habitats, even under light snow cover.

Disturbance

Disturbance of bryophyte habitats creates islands that may limit faunal dispersion. Using experiments, Lawton (1999) found that bryophyte islands support all the predictions for isolated micro-arthropod communities. That is, Lawton found that fragmentation would lead to species extinctions, corridors will reduce extinctions, and abundance will decrease in those species that survive.

Hoyle and Gilbert (2004) examined the effects of fragmentation on the microarthropod microcosms in a temperate ecosystem. Earlier evidence had suggested that the species richness and abundance are maintained if moss patches are connected by corridors. While this may be true, Hoyle and Gilbert found that species richness (including microarthropods) actually varies little between landscapes of various sizes and connectivity with other moss landscapes. Furthermore, there seemed to be no differences in responses between predators and non-predators. However, they suggested that corridors might be more important in more extreme environments, such as the Antarctic.



Figure 28. *Bryum argenteum*. Photo by Michael Lüth, with permission.

But not all small patches are doomed to extinction of their arthropod fauna. As exhibited by many studies on Antarctic mosses (discussed in a later chapter), new fauna will arrive. This is typically achieved by passive transport (**aerobiology**) for both the bryophytes and their microfauna (Mandrioli & Ariatti 2001). And the smaller arthropods might just hitch a ride on bryophyte fragments.

Role of Life Form

Kinchin (1992) found that acrocarpous cushions house a richer fauna than the more open pleurocarpous mosses. This suggests that moisture-holding capacity of the habitat is an important attribute. For example, at 100% relative humidity, the acrocarpous *Bryum argenteum* had a water

content equaling 277% of its dry weight. This contrasted with the pleurocarpous *Hypnum cupressiforme*, which held 1496% of its weight as water. Whereas *B. argenteum* held 85% of its dry weight as soil among its rhizoids, *Hypnum cupressiforme* held less than 1%. This soil difference could have contributed to the differences in fauna, but it is more likely that rate of water loss played a more important role. *Hypnum cupressiforme* reached steady dryness in 132 hours, whereas *B. argenteum* required 180 hours, despite starting at a much lower moisture content. Further support for the moisture hypothesis is provided by *Tortula muralis* and *Grimmia pulvinata*. These mosses have long hair points, most likely contributing to slow drying, and are inhabited by an especially rich fauna. But greater protection from UV light and heat of the sun could also play a role in accounting for the greater number of species within acrocarpous cushions.

Chemical Refuge

More recently, researchers have investigated the role of bryophytes as a chemically defended refuge. Because the bryophytes are well defended by secondary compounds, larger generalist feeders do not consume them. This results in an avoidance of the bryophytes so that they likewise do not consume the smaller invertebrates that live among them. Parker *et al.* (2007) demonstrated that crayfish (*Procambarus spiculifer*, Figure 29) and Canada geese (*Branta canadensis*, Figure 30) selectively consumed *Podostemum ceratophyllum* (riverweed, a tracheophyte; Figure 31) in preference over the brook moss *Fontinalis novae-angliae* (Figure 36), despite the fact that the moss made up 89% of the total plant biomass. Extracts of the moss demonstrated the presence of a **C18acetylenic acid**, octadeca-9,12-dien-6-ynoic acid, that discouraged feeding by crayfish. Experiments with pellets demonstrated that it was not plant structure that determined which plant was eaten. On the other hand, the moss supported a community of macroinvertebrates twice the size of that on riverweed. By being unpalatable to large carnivores, the moss could provide a refuge for smaller animals, especially arthropods.



Figure 29. *Procambarus spiculifer*, a crayfish that won't eat *Fontinalis novae-angliae*. Photo by Josh Geyer through Creative Commons.

The deterrents, as in this case, may not be general deterrents. While crayfish rejected it, the amphipod *Crangonyx gracilis* (Figure 32) and isopod *Asellus aquaticus* (Figure 33) consumed the moss but not the riverweed. Such chemical defenses thus create enemy-free space for these smaller invertebrates and can influence the community structure.



Figure 30. Canada geese (*Branta canadensis*), a species that avoids eating invertebrates from among *Fontinalis antipyretica*. Photo by Janice Glime.



Figure 31. *Podostemum ceratophyllum* (riverweed), a flowering plant that looks like an overgrown liverwort when it does not have flowers, and that is not avoided by Canada geese as a source for invertebrate food. Photo by Alan Cressler, with permission.



Figure 32. *Crangonyx gracilis* (amphipod). Photo from Discover Life through Creative Commons.



Figure 33. *Asellus aquaticus* (isopod). Photo by Morten D. Hansen, with permission.

The study by Parker *et al.* (2007) supported a further advantage of the bryophyte habitat (Figure 34 & Figure 35). The geese were often swept downstream by the rapid water where the bryophytes grew. The smaller invertebrates, however, were able to navigate safely within the protection of the moss, taking advantage of the reduced flow there.

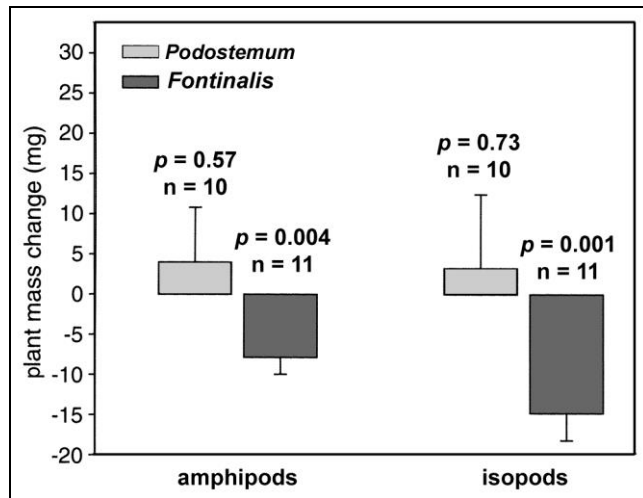


Figure 34. Mean loss or gain (\pm SE) of plant mass in the moss *Fontinalis novae-angliae* vs tracheophyte *Podostemum ceratophyllum* due to grazing by amphipods (*Crangonyx gracilis*) and isopods (*Asellus aquaticus*). Probability level indicates whether change in biomass is significantly different from zero when the two plant species were offered individually to amphipods and isopods. Redrawn from Parker *et al.* 2007.

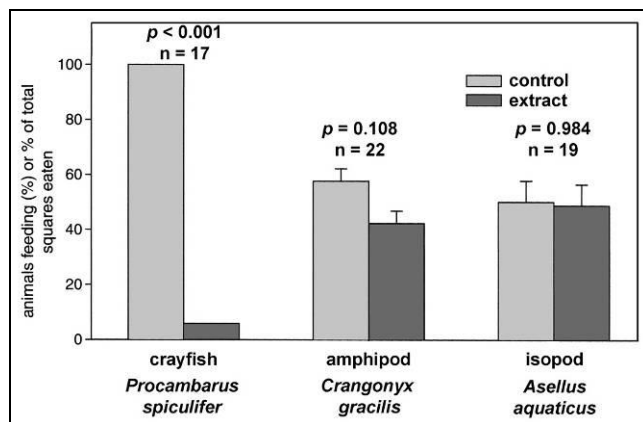


Figure 35. Comparison of feeding by geese on control pellets (freeze-dried, powdered broccoli & lettuce) vs pellets enhanced with crude extracts of the brook moss *Fontinalis novae-angliae*. Squares refer to number of window screen squares from which pellets were eaten. Redrawn from Parker *et al.* 2007.

Food Value

Despite traditional thinking, terrestrial bryophytes can serve as food for some arthropods (Lawrey 1987). Catching them in the act can be difficult as many of these herbivores are nocturnal (Hribljan 2009). A common pattern of eating seems to be to strip all but the border and costa (Wyatt & Stoneburner 1989, Davidson *et al.* 1990), not unlike insects that skeletonize tree leaves.

Contrary to many statements in the literature about poor nutritional value of mosses (*e.g.* Pakarinen & Vitt 1974; Suren & Winterbourn 1991), Parker *et al.* (2007)

found that *Fontinalis novae-angliae* (Figure 36) had the highest dry mass, ash-free dry mass, and protein content among the available plants in their study stream at Chattahoochee River National Recreation Area near Atlanta, Georgia, USA.

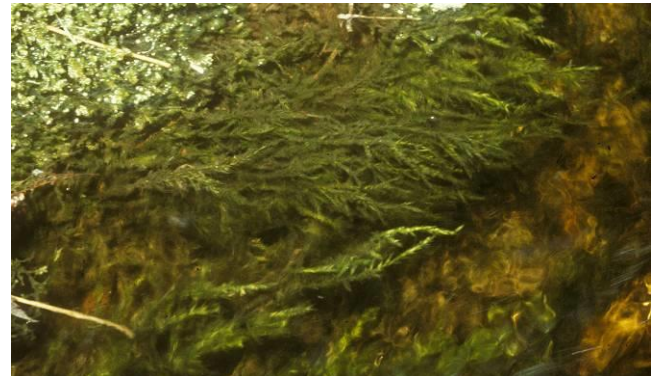


Figure 36. *Fontinalis novae-angliae*. Photo by Janice Glime.

It is not just aquatic mosses that provide nutrition. Lawrey (1987) provided us with a review of moss and lichen nutritional value for arthropods. He contends that the nutritional composition is similar to that of the tracheophytes, containing the same sugars (Lawrey 1987), but with the addition of some unknown ones in at least some mosses (Maass & Craigie 1964). The caloric content is likewise similar to that of higher plants (Bliss 1962; Forman 1968; Pakarinen & Vitt 1974; Rastorfer 1976). Elemental concentrations are similar (and vary among species), with only potassium and magnesium being at lower levels than in tracheophytes (Prins 1981). Spores have the highest lipid concentrations, resulting in their consumption by some arthropods such as ants (Plitt 1907) and other animals.

Thus, we must ask why there is so little evidence of consumption of bryophytes by arthropods. Lawrey (1987) suggests several explanations. Low digestibility has been suggested several times, in part based on the high ratio of cell wall to cell contents. Furthermore, liverworts are well known for their secondary compounds (Adam & Becker 1994; Adio & König 2005; Veljić *et al.* 2008), and recent studies likewise indicate that other bryophytes, including mosses, are highly endowed with antifeedant secondary compounds as well (Davidson 1988; Mueller & Wolf-Mueller 1991; Frahm & Kirchoff 2002; Asakawa 2005). But it is not just the high ratio of cell walls or the antifeedants that make the bryophytes less digestible. They have lower concentrations of easily digested soluble carbohydrates and hemicelluloses than do tree leaves, and, supporting the cell wall to contents ratio hypothesis, they have higher concentrations of structural components such as cellulose and lignin-like polyphenolic compounds that are not easily digested than do their tracheophyte counterparts (Table 2) (Skre *et al.* 1975; Lawrey 1987).

Lawrey actually compared these components in the moss *Polytrichastrum* (=Polytrichum) *ohioense* (Figure 37-Figure 39) with those of a conifer and angiosperm. My concern with using this study as a basis for understanding bryophyte herbivory is that Polytrichaceae has a more highly structured body plan than most bryophytes and I

suspect its content of lignin-like polyphenolic compounds is greater than that of many kinds of moss. Furthermore, the cuticle, at least in *Polytrichum commune* (Figure 40), seems likewise to be more developed than that of many other moss taxa (Proctor 1979), so it may not be representative of the edibility of mosses.

Table 2. Comparison of percentage of structural components of tree leaves and of plants of the moss *Polytrichastrum* (= *Polytrichum*) *ohioense*. From Lawrey 1987.

Litter type	soluble carb	hemi-cellulose	cellulose	"lignin"	ash
<i>Pinus resinosa</i> leaves	35.41	13.44	19.37	23.56	3.68
angiosperm tree leaves	43.89	11.59	20.43	11.04	6.97
<i>Polytrichastrum ohioense</i>	16.51	14.07	24.37	12.90	4.24



Figure 37. *Polytrichastrum ohioense*. Photo by Bob Klips, with permission.



Figure 38. Leaf cross section of *Polytrichastrum ohioense*, showing the complex structure of the leaf. Photo by Amelia Merced through Duke University Herbarium, with permission.



Figure 39. *Polytrichastrum ohioense*. Photo by Morgan L. Vis and Kathy Aleric.



Figure 40. *Polytrichum commune* showing waxy surface. Photo by James K. Lindsey, with permission.

Not only are the polyphenolic compounds difficult to digest, but they typically have antibiotic activity (e.g. Madsen & Pates 1952; Pates & Madsen 1955; Ramaut 1959; McCleary *et al.* 1960; Wolters 1964; McCleary & Walkington 1966; Gupta & Singh 1971; Banerjee & Sen 1979; Asakawa 1990, 2007; Basile *et al.* 1995; Verhoeven & Liefveld 1997; Frahm & Kirchoff 2002). Lawrey (1987) suggests that these antibiotics could affect both palatability and digestion for the arthropods. Since the microflora of the gut aids digestion in a number of arthropods (not many have been examined carefully), antibiotics could kill these important digestive components, to the detriment of the host. Hence, not only would the bryophytes be difficult to digest, but so would other food eaten with them.

But bryophytes can serve as food sources for arthropods indirectly. Their many invertebrate inhabitants (Yanoviak *et al.* 2003, 2006) provide food for birds, especially in the tropics (Nadkarni & Matelson 1989). In discussing the role of lichens in boreal forests, Pettersson *et al.* (1995) suggested that this habitat could be critical for passerine birds in winter, citing the loss of spiders and insects in managed forests compared to natural forests. It is likely that bryophyte communities in many forests serve as a similar refuge of importance during seasons of limited access to arthropods as food.

Bryophytes most likely play a major role in the locations and activity of soil organisms, hence facilitating movement of nutrients through that ecosystem, although little definitive study seems to exist. Organisms such as pillbugs migrate downward in the daytime and back up at night, feeding on the mosses, then returning downward where their feces ultimately rest (Hribljan 2009). This results in cycling of nutrients from one location to another, undoubtedly causing these recycled nutrients to reach the soil more easily. It is likely that insects and other invertebrates actually retreat into the soil to escape predation, desiccation, and UV light, then venture upward into moss mats at night to forage. In some cases, mosses may be essential as part of the habitat. They therefore contribute, through these migrant invertebrates, to aeration, nutrient movement, biodiversity, and water movement in the soil. While this role is an intriguing notion for soil properties and nutrients, its importance needs to be tested.

Collection and Extraction Techniques

When I first tried to publish my doctoral work on insects associated with stream mosses, I listed numbers like 12,064 Chironomidae per gram of moss. The reviewer wanted to know how I had developed these numbers because I "obviously had not counted them." But I did!

The variety of invertebrates makes a single technique impractical – and biased. The 6 or more legs of arthropods easily get caught on the stems and leaves. Mine were necessarily preserved because I would have a collecting day and come back with 30-40 collections of mosses that needed to have arthropods removed. I had no way to provide the cold, oxygenated water they required to stay alive, and many of them would disintegrate quickly once dead. In fact, many insects release enzymes when their cells die that cause the cells to break down quickly, a process known as **autolysis**.

Collection

One problem one must face during collection is the loss of organisms during the collection. Borcard (1986) used a cylindrical sampler mounted on a hand drill to make a core of *Sphagnum* for collecting mites. These samples were not deformed or compressed and thus provided uniform samples suitable for statistical comparisons.

For epiphyte dwellers, particularly in the tropics, insecticide fogging (**Pyrethrin** insecticide) is commonly used for arthropods (Yanoviak *et al.* 2003), but this method is often not effective for arthropods that hide in crevices, tree holes, humus pockets, and epiphytes, including bryophytes. Instead, most of the bryophyte inhabitants are trapped within the mats. The smaller of these arthropods are the least likely to be knocked down by fogging. Mites, in particular, are missed when the fogging method is used for sampling.

Loss of organisms could be especially problematic in streams where the escapees are quickly washed downstream. On the other hand, these stream bryophyte-dwelling organisms are adapted to clinging to the bryophytes against the drag of stream flow, so it appears that few escape. I tested this occasionally during my own research by putting a collection net downstream as I used hand grabs to sample. Few organisms, compared to the large number present, actually escaped, so I abandoned the downstream nets.

Suren (1993) was more cautious in his mountain stream sampling. He placed a **Surber sampler** (area = 10x10 cm, 100 µm mesh) (Figure 41) around the bryophyte clump to be sampled. A Surber sampler has a square frame that must be placed on the bottom of the stream, and a net extends downstream from that, usually about 50 cm or more. Suren used a razor blade to dislodge the bryophytes, but one could use a knife or scalpel. I used my hands – fortunately, I have strong fingernails. Its disadvantage is that it is often difficult to make the entire frame touch the substrate, and the stream may be too deep to reach from substrate to surface, hence permitting some organisms to float away and others to escape along the bottom. It is, perhaps, better than a simple hand grab, except that one can clasp the hand around the mosses, seemingly preventing many escapes.



Figure 41. Surber sampler, showing the investigator removing a rock from the sampling area. The opening of the net faces upstream and the net catches organisms dislodged during sampling. Photo by Ray Drenner, with permission.

A modification of Suren's method is to use a screen with handles. This device usually has a wooden support or pole on each end with the mesh extended between them. The base is placed as snugly as possible against the stream substrate and bryophytes are dislodged to flow into the screen. The ones I have used are made of metal window screening, giving them rigidity, but perhaps one with a fine cloth mesh would work, permitting a closer fit around rocks in the streambed and capturing smaller organisms. The big disadvantage of the window screening is that the mesh size is large enough for mites and others of the smallest organisms to go right through the mesh, creating a sampling bias toward larger organisms. Furthermore, for collecting bryophyte communities, both the screening and fine cloth mesh samplers would require two people, one to hold the device and one to dislodge the moss.

Extraction

There are extraction techniques that are usable to get estimates of various groups if you are willing to live with their biases. The Winkler technique is still useful (Nadkarni & Longino 1990), but relies on the movement of the arthropods away from heat or light, thus creating a bias against less mobile organisms. Trägårdh (1929) recognized the limitations of this method to small soil invertebrates such as mites that are sensitive to evaporation. He found that if the moss dries too quickly they are likely to die before they can escape the heat. Instead, he chose to use a warm water funnel such as that used by chemists to filter colloidal matter. He covered this with sieves of different mesh sizes, depending on the material to be sampled.

Andrew and Rodgers (1999) used multiple extraction techniques to sample small invertebrates living among bryophytes in Tasmania. They used Tullgren Funnels and sugar flotation (Pask & Costa 1971), but also tried a new method using kerosene phase separation (Andrew & Rodgers 1999). They determined that the phase separation freed more total individuals and more **Acari** (mites) and **Collembola** (springtails) in particular. The technique works because the kerosene attaches to the cuticles of insects, causing the insects to float. Their procedure is to "pickle" the insects and their moss housing for two weeks in 95% ethanol. This mix is then put into a

test tube, filling it to 3/4 full. This is topped off with 1 cm of kerosene and shaken vigorously until the solutions are fully mixed. After the mix settles for 10-15 minutes, the tube is rolled to release trapped bubbles from the sides and bottom. The insects and other arthropods collect on the interface between the alcohol and kerosene. The kerosene must be removed with a pipette, then the remaining kerosene plus interface can be removed. To get the arthropods from the sides of the test tube, they washed the sides with 95% ethanol and repipetted to collect the arthropods. The entire process should be repeated to increase the efficiency (about 16% more). A fume hood should be used to examine the organisms safely. Brantley and Shepherd (2004) used heptane flotation to avoid the desiccation problems caused by alcohol and other flotation media.

Taxonomic Difficulties

Bryologists are very familiar with the difficulties of making determinations in the field. The myriad of arthropod species creates even greater taxonomic problems, particularly when dealing with the tiny organisms living among bryophytes. It is rare to find a person with taxonomic expertise in both groups (spanning two kingdoms!), and within the huge group of arthropods, scientists typically are experts in only one class or for insects, only one order. In 1996, Walter *et al.* estimated that the 45,000 species described represented only 5% of the number of species actually **extant**. Among those 95% of undescribed, unnamed species, the bryophyte dwellers may represent an even higher percentage of undescribed members. Instead, crop and other economic pests are usually the first taxa to be investigated.

Such taxonomic challenges explain in large part the lack of detailed information about the faunal arthropod communities among bryophytes. Facing this challenge, Oliver and Beattie (1993) suggested another method that would permit an assessment of biodiversity without requiring taxonomic expertise, large expenditures of time, or high cost. They compared the estimates of species richness (number of species) made by both experts and technicians. The technicians were trained for only a few hours so that they could separate organisms into **recognizable taxon units (RTUs)**.

Using the same sampling methods, the specialists for each taxonomic group of spiders, ants, polychaetes, and mosses identified and separated the taxa to species (Oliver & Beattie 1993). Interestingly, for the three animal groups the experts determined there to be 147 taxa, whereas the technicians separated their organisms into 165 groups. Among the ants and spiders, the technicians had an error rate of 13% or less. When 13 undergraduate students repeated the procedure, the average error was only 14.4%. Some of the differences arose from splitting or lumping by the experts – taxonomic concepts that will continue to plague the ecologists trying to describe ecosystems and communicate their findings. It seems that the results for mosses were more difficult to interpret. The results in numbers had greater similarity between experts and technicians, but splitting and lumping of taxa made the comparisons more difficult.

Such methods as that of Oliver and Beattie (1993) are useful for rapid assessment of biodiversity, but they do not

tell us about community shifts. When comparing two ecosystems, the composition of the species may tell us more than the numbers of species. Further problems arise due to differences in sexes and juvenile vs adult life forms, perhaps accounting for some of the greater diversity reported by the technicians. We have thus far no reason to expect that these age and sex-related within-species morphological differences are habitat related, and they do have significance in assessing functional groups. On the other hand, as we will see for amphibian taxa, various color morphs of adults can indeed relate to habitat and niche differences. Technicians are not likely to be aware of these variations, and even the experts disagree over whether to consider some of them to be different species.

Summary

Bryophytes form a habitat for many kinds of arthropods. They serve this function well by providing moisture, cover, protection from UV exposure, temperature modification, and a habitat for smaller invertebrates that serve as food. Even the soil habitat is enhanced when covered by bryophytes. They provide a refuge under some conditions and are suitable egg-laying sites for some arthropods, but are unsuitable for habitation at others. In winter they provide insulation and protection. In their role as a habitat or a refuge, they can greatly enhance species richness. This amplifies the food source for predators such as birds.

Despite the presence of secondary compounds (antifeedants, antibiotics) in many bryophytes, some still serve as food and are able to contribute protein and dry mass. Smaller organisms living there serve as food items, and the fauna serve as nutrient cyclers, moving nutrients back toward the soil.

The arthropods often form gradations of communities from soil to treetops, with mosses being present in each of those habitat zones. These ranges reflect differences in temperature, light, and humidity preferences. Disturbance of the epiphytic communities can impact food sources for non-migrating birds, especially in winter.

In dry habitats such as prairies, mosses in cryptogamic crusts provide a refuge from the sun and desiccation. These arthropods in turn contribute to soil nutrient cycling.

In streams bryophytes provide a safe site against predators that don't like the taste of the bryophytes, but these bryophytes are also a safe site against the rapid flow of streams and rivers. Furthermore, they provide this habitat during winter when tracheophytes disappear from the streams. They furthermore increase surface area that collects periphyton and detritus, suitable food sources for many arthropods, a role most likely much more important than the role of the bryophyte itself as a food source.

Sphagnum sites are particularly rich in species, sometimes having double the number of species found in forested areas. Lycosids are common. Spiders have unique niches within the peatlands and often characterize biotopes there. Nevertheless, the low pH and need for basic compounds to harden the cuticle make the peatlands inhospitable for many taxa.

In the Antarctic, water content in and under bryophyte cover is important, but in some cases the bryophytes are important for providing suitable temperatures. This can be especially important for overwintering of eggs and larvae, as well as some adults. Nevertheless, higher altitudes in New Zealand do not seem to influence species richness.

Bryophytes in many habitats can provide refuge from the heat of summer, but upper layers of mosses such as *Sphagnum* or *Bryum argenteum* can reach temperatures 10°C or more above ambient. A further protection by bryophytes is the chemical defense that discourages larger predators and protects the microarthropods hiding among the bryophytes.

Disturbance and fragmentation seems to have little effect on the microarthropod fauna remaining in the bryophyte islands. Recolonization can occur by passive transport.

Acrocarpous cushions can house more arthropods than pleurocarpous mosses, perhaps due to greater moisture-holding capacity in the former. But cushions also hold much more soil. And cushions generally afford more protection from UV light and heat of the sun.

Secondary compounds that prevent herbivory may also defend the small inhabitants living among the bryophytes. Crayfish and Canada Geese tend to avoid feeding on bryophyte inhabitants.

Collecting and extracting is somewhat problematic because not all arthropods can be collected and extracted by the same techniques. Collection includes fogging, hand grabs, Surber samplers, and kick nets. One can accomplish extraction with a Tullgren funnel, sugar flotation, or kerosene phase separation, as well as hand picking. Once the arthropods are extracted, the difficult task of identification begins. For purposes of assessing diversity, morphotypes will suffice, but for comparing actual community composition, species names are important.

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