

CHAPTER 4-1

INVERTEBRATES: INTRODUCTION



Figure 1. *Marchantia polymorpha* that has been nibbled by an unknown organism. Note holes in the thallus. Photo by C. R. Stevenson.

The invertebrate Fauna

Einstein is credited with saying that the most incomprehensible fact about nature is that it is comprehensible (Miller 1992). The invertebrate community associated with bryophytes needs still to be comprehended.

Dendy (1895) coined the term **cryptozoic fauna** to describe "the assemblage of small terrestrial animals found swelling in darkness beneath stones, rotten logs, the bark of trees, and in other similar situations." Although not specifically mentioned, bryophytes surely belong among the "other similar situations," as evidenced by the browsed patches on the liverwort in Figure 1. A comparable term for such bryophyte dwellers in the aquatic realm is **meiofauna**, defined as "**benthic** (living on the bottom of a body of water) animals that can fit a mesh size of 1 mm and be retained on a mesh size of 42 μm " (Brave New Biosphere 1999). Although living among bryophytes directly contradicts being on the bottom, the bryophytes do occupy the bottom, and one might think of the habitat they create as simply an extension of that bottom.

The invertebrate fauna are likely to play an important role in nutrient cycling within the bryophyte community, thus facilitating return of detrital matter to ecosystem level nutrient cycling. Merrifield and Ingham (1998) suggested that the diversity of feeding strategies found in moss invertebrate communities provides evidence of within-bryophyte-community nutrient cycling. Studies by Davis (1981) seem to support this suggestion. He found that the moss turf community and the moss carpet community in the maritime Antarctic on Signy Island showed similar levels of productivity, trophic structure, and efficiencies of organic matter transfer, but they differed in Collembola (springtails) and Acari (mites) standing crops, turnover of mosses, and accumulation of dead organic matter. Both communities (turf of *Polytrichum alpestre* and *Chorisodontium aciphyllum* and carpet of *Calliergon sarmmentosum*, *Calliergidium austro-stramineum*, *Sanionia uncinata*, and *Cephaloziella varians* – a liverwort) had fauna of Protozoa, Rotifera, Tardigrada, Nematoda, Acari, and Collembola. Despite the diverse fauna, Davis found no evidence that the mosses would have been eaten. However, he based this on known feeding groups of the organisms and not on direct evidence. Nevertheless, it is likely that

detrital matter and predation were primary food pathways, permitting nutrient cycling.

Sampling

But determining the faunal composition and community structure of these microhabitats is not an easy task. The most obvious method of sampling invertebrates is sorting them from the bryophytes under the dissecting microscope. But this method is tedious, very time-consuming, and often misses the smaller organisms (personal experience!). The method of wringing and squeezing is much less tedious and faster, a method used by Morgan (1977), but certainly many get left behind, and attached organisms are likely to be preferentially left behind. To help in this time-consuming task, Paul Davison (pers. comm. 21 June 2006) modified the **Baermann funnel** (Figure 2) for extracting turbellarians (as well as nematodes, copepods, and tardigrades) from bryophytes. A piece of cheese cloth, muslin, or tissue paper is placed in a funnel to hold a sample (Tylka Nematology Lab 2005). This is usually supported by a piece of screening (Figure 2). Then water is run through the sample with rubber tubing clamped at the end of the funnel. After the sample sits overnight or longer, the water is released from the funnel and collected. The first few drops will have a concentration of nematodes, which are heavier than water.

Another method is use of the **Berlese funnel**, which does not have water, using a light and/or temperature gradient that separates mobile organisms such as arthropods and annelids, but that method leaves the non-mobile ones behind, and doesn't work for nematodes (ED-STEPP). If it is too hot, organisms die before they can drop.

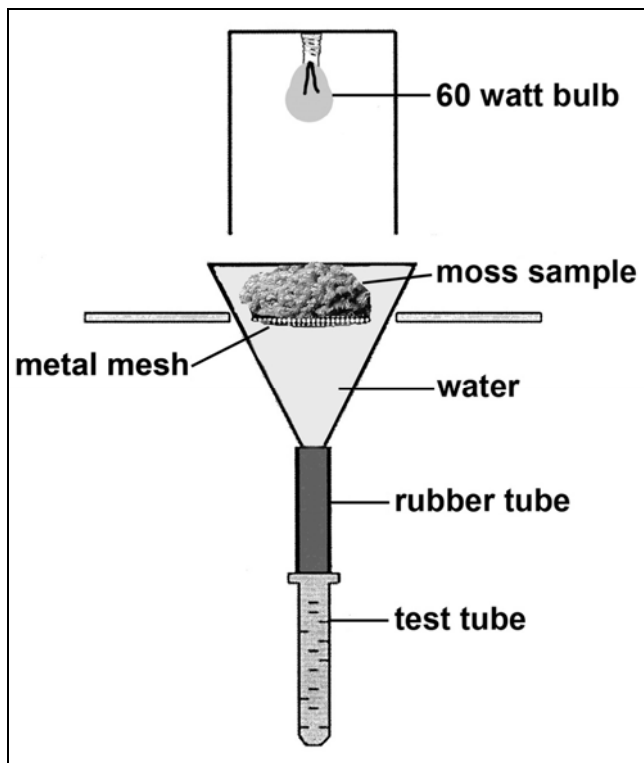


Figure 2. Baermann funnel using moss sample. Water can be replaced with air for non-aquatic organisms, thus making it similar to the Berlese funnel. Modified from Briones 2006.

Fairchild *et al.* (1987) have taken advantage of the behavior of these invertebrates to develop an extraction method. By creating a vertical temperature and oxygen gradient in samples of *Sphagnum*, they were able to obtain an 85% efficiency. Merrifield and Ingham (1998) compared several methods of extracting invertebrates. In a study of *Stokesiella oregana* in the Oregon Coast Range, USA, Merrifield and Ingham first verified the extraction efficiency for nematodes and other invertebrates using the Baermann funnel. Invertebrates were first collected from the funnel apparatus, then more were collected from the mosses on subsequent days, and finally more were collected by squeezing and agitation of the moss. They found that more than 90% of the cumulative final counts of the nematodes *Monhystera* spp. and *Prionchulus muscorum* were extracted by the Baermann funnel technique by the fourth day of extraction. Tardigrade extraction was even more efficient, reaching 95% by day 4. Rotifers, however, were less than 50% extracted in the same time period, with only 42% by day 4 and 55% by day 7. Jennings (1979) had previously used this technique to extract invertebrates from mosses on Signy Island in the Antarctic.

Preservation of Specimens

Ecologists take note. Simply identifying and counting the faunal organisms and getting someone to identify the bryophytes isn't enough! Whereas you may be confident that your expert has identified everything correctly, it is likely that the expert is less confident and has provided you with the "best" determination possible with the material provided. But ecological specimens typically lack reproductive organs, are not well preserved, and may not even be the whole organism. Systematists always pay careful attention to keeping specimens and publishing their location. Ecologists and physiologists should also. Both the bryophytes and the fauna should be preserved and their locations in permanent, reputable herbaria and museums should be part of any publication based on the data. Furthermore, the specimens should be clearly labelled as voucher specimens, referencing the study.

Species concepts change; often physiological and ecological properties are not uniform among members of the earlier species concept. In the absence of a specimen, the data become useless. Yet, in 1950, Fosberg examined 270 ecological publications with discussions of species. Locations of preserved specimens were provided in only five of these publications! I decided to see if the situation had improved by using a much smaller sample size of three recent ecological journals and three recent bryological journals. In the 15 papers I examined from ecological journals, there was no mention of preserving or keeping specimens. In the three bryological journals, all 15 papers dealing with systematics or checklists provided the herbaria locations. However, even among this group of biologists who share the same journals, none of the six ecological papers in the same issues mentioned any preservation of specimens from the species included in the study. This practice of providing no preserved reference material defies the concept that scientific data must be verifiable.

I disagree with Fosberg (1950) when he pokes fun at stating the source of the nomenclature. Unlike his concept that this is presented to "verify" the identity of the organism, the source of nomenclature demonstrates the

species concept used and provides a link to a source where a description may be found. Thus, if one uses *Drepanocladus* from Crum 1973, we know that a broad concept of the genus is used and that *Sanionia*, *Warnstorfia*, or other genus might now apply instead.

Community Patterns

Kinchin (1992) reviewed the invertebrate fauna among bryophytes in the British Isles and provided us with a summary of the "moss" habitat. He found that acrocarpous cushions support a richer fauna than the more loosely packed pleurocarpous mosses, attributing this to the greater ability of acrocarpous cushions to hold water. He demonstrated this ability experimentally, showing that at 100% saturation a cushion of the acrocarpous *Bryum argenteum* held 277% of its "dry" weight in water. The pleurocarpous moss *Hypnum cupressiforme*, on the other hand, held 1496%. *Bryum argenteum* held 85% of its dry weight as soil trapped among the rhizoids, whereas *H. cupressiforme* has less than 1%. But perhaps most importantly, *B. argenteum* required 180 hours to reach steady dryness, whereas *H. cupressiforme* required only 132, and this was in a moss starting with more than 5X as much water! Slow drying, as you will soon see, is a prerequisite for survival in many of these faunal organisms. Supporting his argument, Kinchin found that the *B. argenteum* fauna was much richer than that of *H. cupressiforme*. Interestingly, he found that mosses such as *Tortula muralis* and *Grimmia pulvinata* with long hair points have particularly rich fauna, which might again result from a mechanism for slow drying.

The wonderful fauna of bryophytes led Gadsby (1926) to publish his paper, "Meanderings 'mong mosses." Even after a fire bryophytes such as *Funaria hygrometrica* (Figure 3) and *Ceratodon purpureus* (Figure 4) accumulate organic matter and dust, permitting invertebrates to colonize (Clément & Touffet 1981). Others are quick to colonize areas of harvested peat (Curry *et al.* 1989). Even glacial land in the Antarctic (Schwarz *et al.* 1993) and geothermal areas of Iceland (Elmarsdottir 2003) and Ireland (Fahy 1974) sport their own bryophyte invertebrate fauna, most likely facilitated by the ameliorating effect of the microclimate within the bryophyte clone. In the Antarctic, Sohlenius *et al.* (2004) found highest invertebrate densities where there were moss communities.



Figure 3. *Funaria hygrometrica*, a common colonizer after fires that collects organic matter, permitting invertebrates to colonize. Photo by Michael Lüth.



Figure 4. *Ceratodon purpureus*, a common colonizer after fire, accumulates organic matter, permitting invertebrate fauna to develop. Photo by Michael Lüth.

Jones *et al.* (1994) described mosses as ecosystem engineers that provide living spaces by providing a suitable physical structure. Although *Sphagnum* is the most cosmopolitan engineer, bryophytes create habitats for invertebrates in many ecosystems. Sayre and Brunson (1971) compared the moss inhabitants in a variety of habitats to determine what faunal taxa were most common (Figure 5).

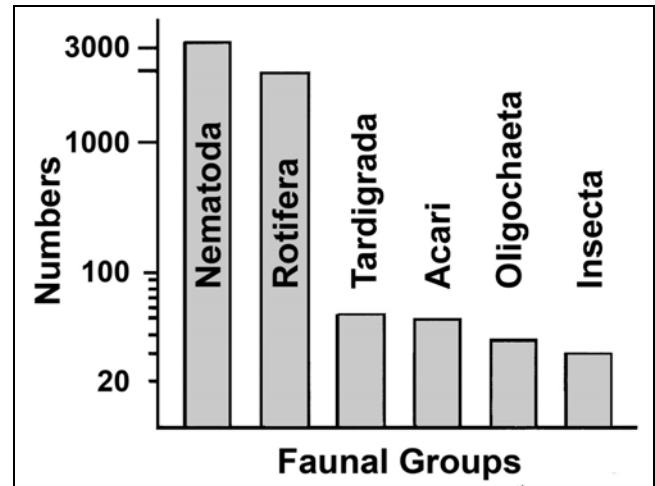


Figure 5. Mean population numbers of faunal groups from 3 2.5-cm diameter cores per moss sample, plotted on a logarithmic scale. Samples represent a variety of habitats from 26 locations in Maryland and Virginia, USA. Redrawn from Sayre & Brunson 1971.

Bryophyte habitats generally influence the faunal community structure based on their moisture availability. Five classes can be recognized (Hofmann 1987; Hofmann & Eichelberg 1987):

- I Submerged mosses
- II Mosses that are permanently moist
- III Mosses that are only rarely dry
- IV Mosses that are frequently dry
- V Exposed mosses that are often dry for long periods

Kinchin (1992) considered the faunal inhabitants to grade from unspecialized among the submerged mosses to more specialized, drought-resistant or drought-tolerant toward the dry end. Nevertheless, some habitats, while appearing suitable, are not colonized by any species.

When only aquatic vs terrestrial are considered, we find a difference in groups dominating the bryophytes. In terrestrial habitats, arthropods dominate (Kinchin 1992). Nevertheless, few arthropods spend their entire life cycle among mosses (Kinchin 1990a). The aquatic fauna, Kinchin (1992) contends, is dominated by nematodes, tardigrades, and rotifers. It is not clear if he includes the peatlands in this aquatic grouping, but certainly I have examined the preserved fauna of stream bryophytes, where I have found insects to be the dominant organisms (Glime 1994).

Aquatic habitats generally house the largest and probably the most diverse fauna. Amos (1999) described the torrent among the *Fontinalis* branches (Figure 6) in a poetic fashion: "All was quiet at the bottom of the torrent moss world, despite the storm of rushing water overhead." Here one could find zones of algae – diatoms, desmids, and filamentous species. Inhabitants included round and segmented worms, rotifers, gastrotrichs, water fleas, copepods, scuds, and a variety of larval insects as well as adults of tiny species. The mountain midge larva anchors there with suction cups that are even better than those of the squid and octopus. Yet Kinchin (1990b, 1992) paints a different picture of the waterfalls in Ein Gedi Nature Reserve, Israel, where the fauna is relatively poor.



Figure 6. *Fontinalis antipyretica* houses a wide range of invertebrates in streams and lakes. Photo by Michael Lüth.

In aquatic habitats, bryophytes are particularly important in contributing to faunal diversity (Priddle & Dartnall 1978; Suren & Winterbourn 1992a). In the Antarctic, these faunal groups are dominated by Protozoa, Rotifera, Nematoda, Turbellaria, Tardigrada, Oligochaeta, and Acari (Ingole & Parulekar 1990). In alpine streams of New Zealand, bryophytes provide shelter with reduced flow (Suren 1991b) and catchment for algae and detritus, thus creating a habitat with both shelter and food (Suren 1992), and in some cases materials for constructing larval cases (Suren 1987). Among 23 invertebrate taxa, 14 were found with bryophyte fragments in their gut, but their presence in the gut was only common in several of the aquatic insects (Suren & Winterbourn 1991). Bryophytes contained more indigestible compounds than did other plants, making them less nutritious. Rather, it appears that detritus and periphyton were the primary food sources (Suren & Winterbourn 1992b).

The bryophyte faunal communities were greater in streams above the treeline (Suren 1993). Greater invertebrate density occurred within bryophyte communities with periphyton than those with detritus (Suren 1993). Bryophyte communities were dominated by aquatic insects and Nematoda, oribatid mites, Hydracarina, Copepoda, and Ostracoda (Suren 1988). When artificial mosses were used in place of real ones, similar invertebrate communities developed, but some, *e.g.* Nematoda, Acarina, Tardigrada, Ostracoda, seemed to suffer from loss of the food supply (Suren 1991a).

Linhart *et al.* (2002) examined the fauna of *Fontinalis antipyretica* (Figure 6) growing on rocks used to stabilize a side channel of the Morava River in the Czech Republic. The moss-dwelling meiofauna numbered a mean of $253,917 \pm 178,335$ (\pm SD) per 10 g dry weight of moss and $7,160,461 \pm 5,029,047$ per 1 m² of the bottom area during October 1999–November 2000. Bdelloidea (rotifers) formed the dominant group (76%), followed by Monogononta (rotifers) (11.23%), Nematoda (6.38%), Chironomidae (midges) (4.08%), and Oligochaeta (worms) (1.06%). Linhart and coworkers (2002) considered that fine particulate matter trapped by the mosses would serve as both a habitat and a food source. They found that about 4% of the trapped matter was coarse matter (500–1000 μ m), 14% medium (10–500 μ m), and 82% fine (30–300 μ m). Only 10% of the trapped matter is organic. The size and content of the trapped matter were significantly correlated ($P < 0.05$) with densities of Oligochaeta (segmented worms), Hydrachnidia (mites), Cladocera, Copepoda, and Chironomidae. They reported that the bryophyte habitat houses considerably greater numbers of meiofauna compared to the stream gravel bed. Table 1 compares the numbers of moss-dwelling organisms in streams.

In desert cryptogamic crusts, bryophytes seem to be important to the soil fauna (Brantley & Shepherd 2004). Among these invertebrates are arachnids, mites, nematodes, springtails, tardigrades, and other small arthropods. Mixed lichen and moss patches supported 27 taxa at sites in New Mexico, whereas mosses had 29 taxa. Abundance and diversity were higher in winter than in summer, most likely due to a lower water stress. Even the moss *Tortula desertorum* may have its own invertebrate community (Kaplin & Ovezova 1986; Ovezova 1989).

In Vaccinium heaths, the moss litter is difficult to break down (Frak & Ponge 2002). The invertebrate fauna process the litter, convert it to animal feces, and transform the soil to mor.

In the Antarctic, the structure of the mosses (*Calliargon sarmentosum*, *Drepanocladus* sp.) provides a complex community where epiphytic algae and invertebrates form a higher diversity than the surrounding algal community (Priddle & Dartnall 1978). For example, *Calliargon* provides the site of most abundant algae in leaf axils. Six stem zones result from deterioration of basal portions. Benthic invertebrates move actively among these mosses. Six species of rotifers are common in the middle stem zones where there is the greatest abundance of epiphytes. Of these, two colonize the bare underside of leaves whereas four live mostly in leaf axils. Wind-induced mixing in the summer provides transportation for at least some of the epiphytes from the shallow portions of the lake. Rotifers settle there as larvae.



Figure 7. *Calliergon sarmentosum*, a common component of the moss-invertebrate community in the Antarctic. Photo by Michael Lüth.

The invertebrate representation can be more limited in the Antarctic than in many other parts of the world. Schwarz *et al.* (1993) found that the moss-dominated flushes near the Canada Glacier supported a community where Protozoa, rotifers, worms, and tardigrades dominated, with all but the Protozoa occurring at 5-10.83 mm depth in the moss. Following melt, more of the organisms were found in the upper 5 mm of the moss habitat. Mites occurred in lesser quantities and Collembola were nearly absent. On the other hand, a catenulid flatworm in that habitat was a rare find; microturbellarians are quite rare in Antarctica.

Table 1. Comparison of numbers of invertebrate organisms in moss collections from streams. **NR** means not reported.

	Sample Size	Hydrozoa	Platyhelminthes	Nematoda	Annelida	Rotifera	Gastrotricha	Tardigrada	Non-Insect Arthropoda	Insecta	MOLLUSCA	Reference
Straffan, River Liffey, Ireland	200 g	NR	0.1	56.0	48.0	NR	NR	NR	489	12755	0.7	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	NR	0.1	38.0	36.0	NR	NR	NR	160	12051	+	Frost 1942
Cold Springbrook, Tennessee, USA	0.1 m ²	NR	1.1	NR	NR	NR	NR	NR	18.9	255	NR	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	34	319	18305	1355	54561	1347	736	1817	46426	NR	Vičková <i>et al.</i> 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	0.0	37	16198	3602	222084	189	277	427	11229	NR	Vičková <i>et al.</i> 2001-2002
Welsh Dee Tributary, Wales	~300 cm ²	NR	0.5	1.8	11.5	NR	NR	NR			NR	Hynes 1961
Mouse Stream, alpine, New Zealand	1 m ²	NR	NR	87430	NR	NR	NR	5640			NR	Suren 1991a
Tim's Creek, alpine, New Zealand	1 m ²	NR	NR	6810	NR	NR	NR	0			NR	Suren 1991a
West Riding, Yorkshire, GB - loose moss	%	NR	NR	NR	4.6	0.0	NR	NR	4.6	90	0.4	Percival & Whitehead 1929
West Riding, Yorkshire, GB - thick moss	%	NR	NR	NR	0.0	0.0	NR	NR	4.7	63	4.1	Percival & Whitehead 1929
alpine unshaded stream, New Zealand	% top 10	NR	NR	22.1	NR	NR	NR	2.4	12.9	61		Suren 1991b
alpine shaded stream, New Zealand	% top 10	NR	NR	12.5	NR	NR	NR	0.0	8.1	74		Suren 1991b

Lobules as Habitat

As discussed in the chapters on micro-organisms and rotifers, the water-holding lobules of some leafy liverworts may house a variety of invertebrates. In fact, these invertebrates seem in some cases to be attracted to the plants and readily enter the lobules (Hess *et al.* 2005). In *Pleurozia purpurea* (Figure 8-Figure 9), the fauna include Ciliata, Rhizopoda (protozoans), turbellarians, worms, rotifers, tardigrades, and copepods. A detailed discussion of the "trapping" mechanism of the lobules is in Chapter 2-6. Whether these invertebrates are truly trapped and consumed by the liverworts remains unknown. Decaying organisms provide food for other members of the community and provide a proximal source of nutrients for the liverwort leaves. These organisms form a unique faunal community where organisms live, consume, and die.



Figure 8. The leafy liverwort *Pleurozia purpurea*, showing the protective nature of the curved leaves. The lobules are underneath. Photo by Sebastian Hess.



Figure 9. **Left:** Worm, probably an oligochaete, from the lobule of the leafy liverwort *Pleurozia purpurea*. **Right:** Lobule of the liverwort, *Pleurozia purpurea*. Photos by Sebastian Hess.

Food Webs

The aquatic food web is quite complex and will be discussed in the chapter on aquatic insects, since they are major players in that realm. Much less is known about the terrestrial food webs in bryophyte microcosms. Sayre and Brunson (1971) pointed out that these ecosystems have the same four basic food units as larger ecosystems described by Odum (1963): abiotic, producer, consumer, and decomposer. In fact, there are often secondary consumers and even some tertiary consumers.

The **abiotic** portion of the habitat includes dust and other particles gained from the atmosphere, organic leachates from the mosses (and host trees for epiphytes), decaying moss parts, and the remains of dead inhabitants. The water film enveloping the bryophytes is essential to their survival in active states, but like the mosses, most of the organisms living here are capable of dormancy when the water dries up.

The mosses themselves are **producers**, but they often also have algae on them (yes, even those on trees) and may have lichens associated with them.

The **consumer** component has not been investigated often. We know that tardigrades are often specifically adapted to sucking the contents from bryophyte cells and may be the primary consumers (Pennak 1953; LeGros 1958). However, many tardigrades are also carnivores; Sayre and Brunson (1971) suggest that most of those in their study were secondary consumers, *i.e.* predators/carnivores. Higgins (1959) suggested that rotifers were a food source for tardigrades. As one of the two most abundant invertebrates in the samples of Sayre and Brunson (1971), these rotifers would provide a good source of food. Tardigrades also feed on nematodes (Sayre 1969).

As in other habitats, fungi and bacteria break down the debris that accumulates among the mosses. The bacteria and the by-products of their decomposition provide food for nematodes, rotifers, and oligochaetes (Sayre & Brunson 1971). Hence, one could hypothesize a simple food web (Figure 10).

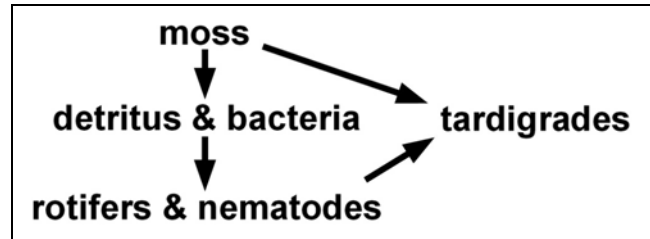


Figure 10. Theoretical food web involving mosses and lower invertebrates. Mollusks, insects, and other arthropods could form secondary and tertiary consumers in this web.

Frost (1942) considered the mosses in some habitats to be a fallback substrate. She thought that those organisms that reach large numbers on other kinds of plants could colonize the moss when the other plants became overcrowded. This would increase the importance of the mosses in the food web.

Pollution

Mosses are well known for their ability to monitor and indicate pollution. But it appears that their fauna may also be important indicators of the assault by heavy metals and other air pollutants (Steiner 1994a, b, c). Zullini and Peretti (1986) found that lead pollution affects nematodes living among mosses. Species richness declines and communities become more uniform as pollution levels rise, especially for the oribatid mites (Steiner 1995a). Moss communities of nematodes, rotifers, and tardigrades change composition in response to SO₂ fumigation (Steiner 1995b). Both nematodes and tardigrades were greatly reduced in numbers by the highest SO₂ levels (0.225 ppm), particularly the nematodes *Chiloplectus cf. andrassyi* and *Paratripyla intermedia*. Nevertheless, the tardigrade *Macrobiotus persimilis* actually increased with increasing SO₂ levels. Population numbers of these three organisms can serve as suitable indicators of pollution.

Although the arthropods in aquatic systems have often been used as indicators, in terrestrial moss communities they seem to be less sensitive to pollution than nematodes and tardigrades (Steiner 1995b).

Harvesting Dangers

It would be irresponsible to include this and the succeeding chapters without reminding the readers of the dangers lurking in harvested mosses. Such mosses, like their living counterparts, harbor numerous invertebrates (Peck *et al.* 1996), many that can become dormant for extended periods of time.

Muir (2004) reported 81 million pounds per year, the equivalent of about 10,500 semi-trucks, harvested in the Pacific Northwest. This massive harvest on logs can take 10-23 years to recover (Peck 2006). Most likely a greater recovery time is needed for epiphytes.

Using a Berlese funnel for extraction, Peck and Moldenke (1999) identified 125 invertebrate taxa from 200 moss mats. Greater overall numbers were present at shrub bases than at tips. However, this pattern did not exist for all organism groups (Peck & Moldenke 1999). Coleoptera (beetles) and Thysanoptera (thrips) exhibited greater numbers per gram at the base, as did detritivores in general, but spiders and predators in general were actually lower in numbers at the bases. Turtle-mites characterized

basal samples (*Ceratoppia* sp., *Hermannia*, and *Phthiracarus* sp.), whereas microspiders (Micryphantidae) and springtails (*Sminthurus*) were typical of tips.

Moss harvesting therefore creates two problems. At first it creates the possibility of endangering specific inhabitants that thrive only among bryophytes. Secondly, transport of harvested mosses will undoubtedly also transport the invertebrate fauna, providing the possibility for these creatures to invade areas where they did not exist before, most likely altering their new ecosystem, often to the detriment of the native fauna and flora. Details of harvesting will be discussed in a different volume.

Summary

The invertebrate fauna living among bryophytes can be variously categorized as **cryptozoic fauna** (hidden animals), **meiofauna** (retained on a mesh size of 42 µm, and **benthic** (living on the bottom of a body of water). The non-arthropod fauna include primarily nematodes, rotifers, tardigrades, and annelids, generally in that order of abundance. Their diverse feeding strategies engage them in nutrient cycling.

Sampling can be difficult and often requires extraction by hand or use of a **Baermann or Berlese funnel**. Whenever possible, specimens should be preserved in a recognized museum and that location published along with any studies involving them.

In aquatic habitats, the bryophytes provide a safe site away from torrents and large predators, where invertebrates are known to number as much as 25,400 per g dry weight of *Fontinalis*. Detrital matter trapped by the moss is a ready food source. In prairies and desert regions, bryophytes may provide the most important suitable habitat. In the Antarctic, epiphytic algae provide food for the meiofauna.

Most of the organisms do not eat bryophytes and depend on adhering detritus and bacteria for food (rotifers & nematodes). Tardigrades, however, may also eat bryophytes.

Because of their ability to respond to heavy metals and other pollutants, the invertebrates provide a suitable group to monitor air pollution, along with their bryophyte habitat.

On one hand, harvesting of bryophytes can remove endangered invertebrate species, and on the other may distribute species to new areas where they may become invasive or disruptive to new ecosystems.

Acknowledgments

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Literature Cited

Amos, W. H. 1999. Life in the Torrent – the moss *Fontinalis* and its tiny inhabitants. Microscopy UK, Accessed on 16 April 2008 at <<http://www.microscopy-uk.org.uk/mag/indexmag.html?http://www.microscopy-uk.org.uk/mag/artsep99/bamoss.html>>.

- Brantley, S. L. and Shepherd, U. L. 2004. Effect of cryptobiotic crust type on microarthropod assemblages in piñon-juniper woodland in central New Mexico. *Western North American Naturalist* 64: 155-165.
- Brave New Biosphere. 1999. The Why Files. Glossary. University of Wisconsin. Accessed on 7 January 2008 at <<http://whyfiles.org/022critters/meiofauna.html>>.
- Briones, M. J. I. 2006. Enchytraeidae. In: Lal, R. (ed.). *Encyclopedia of Soil Science*, 2nd ed., Vol. 1. CRC Press, pp. 514-518.
- Clément, B. and Touffet, J. 1981. Vegetation dynamics in Brittany heathlands after fire. *Vegetatio* 46: 157-166.
- Crum, H. 1973. Mosses of the Great Lakes Forest. *Contrib. Univ. Mich. Herb.* 10: 1-404.
- Curry, J. P., Boyle, K. E., and Farrell, E. P. 1989. The invertebrate fauna of reclaimed cutaway peat in central Ireland and its influence on soil fertility and plant growth. *Agric. Ecosyst. Environ.* 27: 217-225.
- Davis, R. C. 1981. Structure and function of two Antarctic terrestrial moss communities. *Ecol. Monogr.* 51: 125-143.
- Dendy, A. 1895. The cryptozoic fauna of Australasia. Report of the sixth meeting of the Australasian Association. *Adv. Sci.* 6: 99-119.
- ED-STEELP. Constructing a Berlese Funnel for Collecting Soil Invertebrates. Accessed on 6 May 2009 at <<http://pnwsteeep.wsu.edu/edsteeep/SoilInvertebrates/Berlese.doc>>.
- Elmarsdottir, A., Ingimarsdottir, M., Hansen, I., Olafsson, J. S., and Olafsson, E. 2003. Vegetation and invertebrates in three geothermal areas in Iceland. *International Geothermal Conference, Reykjavik*, Sept. 2003, 12: 49-55.
- Fahy, E. 1974. Fauna and flora of a thermal spring at Innfield (Enfield), Co. Meath. *Irish Nat. J.* 18: 9-12.
- Fairchild, W. L., O'Neill, M. C. A., and Rosenberg, D. M. 1987. Quantitative evaluation of the behavioral extraction of aquatic invertebrates from samples of *Sphagnum* moss. *J. N. Amer. Benthol. Soc.* 6: 281-287.
- Fosberg, F. R. 1950. Remarks on the factual basis of ecology. *Ecology* 31: 653-654.
- Frak, E. and Ponge, J. F. 2002. The influence of altitude on the distribution of subterranean organs and humus components in *Vaccinium myrtillus* carpets. *J. Veg. Sci.* 13: 17-26.
- Francez, A.-J. and Devaux, J. 1985. Repartition des rotifères dans deux lacs-tourbières du Massif Central (France). [Distribution of rotifers in two peat bogs in the Massif Central (France)]. *Hydrobiologia* 128: 265-276.
- Frost, W. E. 1942. River Liffey survey IV. The fauna of submerged "mosses" in an acid and an alkaline water. *Proc. Royal Irish Acad. Ser. B* 13: 293-369.
- Gadsby, E. J. 1926. Meanderings 'mong mosses. *Bryologist* 29: 43-44.
- Glime, J. M. 1994. Bryophytes as homes for stream insects. *Hikobia* 11: 483-497.
- Hess, S., Frahm, J.-P., and Theisen, I. 2005. Evidence of zoophagy in a second liverwort species, *Pleurozia purpurea*. *Bryologist* 108: 212-218.
- Higgins, R. P. 1959. Life history of *Macrobotus islandicus* Richters with notes on other tardigrades from Colorado. *Trans. Amer. Microsc. Soc.* 78: 135-254.
- Hofmann, I. 1987. Habitat preference of the most frequent moss-living Tardigrada in the area of Giessen (Hessen). In: Bertolani, R. (ed.). *Selected Symposia and Monographs U.Z.I.*, 1, Mucchi, Modena, pp. 211-216.

- Hofmann, I. and Eichelberg, D. 1987. Faunistisch-oekologische Untersuchungen zur Habitat-praeferenz moosbewohnender Tardigraden. [Ecological investigations of the habitat preference of moss-inhabiting tardigrades.]. Zool. Beitr. 31(1): 61-76.
- Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57: 344-388.
- Ingole, B. S. and Parulekar, A. H. 1990. Limnology of Priyadarshani Lake, Schirmacher Oasis, Antarctica. Polar Rec. 26(156): 13-17.
- Jennings, P. G. 1979. the Signy Island terrestrial reference sites. X. Population dynamics of Tardigrada and Rotifera. Brit. Antarct. Surv. Bull. 47: 89-105.
- Jones, C. G., Lawton, J. H., and Shachak, M. 1994. Organisms as ecosystem engineers. Oikos 69: 373-386.
- Kinchin, I. M. 1990a. The moss fauna 3: Arthropods. J. Biol. Ed. 24: 93-100.
- Kinchin, I. M. 1990b. Observations on the structure of *Ramazottius* (with a checklist of British Eutardigrada). Microscopy 36: 475-482.
- Kinchin, I. M. 1992. An introduction to the invertebrate microfauna associated with mosses and lichens with observations from maritime lichens on the west coast of the British Isles. Microscopy 36: 721-731.
- LeGros, A. E. 1958. How to begin the study of tardigrades. Countryside 18: 322-330.
- Linhart, J., Vlčková, Š., and Uvíra, V. 2002. Bryophytes as a special mesohabitat for meiofauna in a rip-rapped channel. River Res. Appls. 18: 321-330.
- Merrifield, K. and Ingham, R. E. 1998. Nematodes and other aquatic invertebrates in *Eurhynchium oregonum* (Sull.) Jaeg., from Mary's Peak, Oregon Coast Range. Bryologist 101: 505-511.
- Miller, J. 1992. Trouble in mind. Sci. Amer. September 1992: 180.
- Morgan, C. 1977. Population dynamics of two species of Tardigrada, *Macrobotus hufelandii* (Schultze) and *Echiniscus (Echiniscus) testudo* (Doyère), in roof moss from Swansea. J. Anim. Ecol. 46: 263-279.
- Muir, P. S. 2004. An Assessment of Commercial "Moss" Harvesting from Forested Lands in the Pacific Northwestern and Appalachian Regions of the United States: How Much Moss is Harvested and Sold Domestically and Internationally and Which Species are Involved? U. S. Fish and Wildlife Service and U. S. Geological Survey, Corvallis, 80 pp.
- Odum, E. P. 1963. Ecology. Holt, Rinehart, and Winston Inc., N. Y., 152 pp.
- Ovezova, A. Kh. 1989. Peculiarities of summer population of *Tortula desertorum* invertebrates in eastern Karakum. Akad. Nauk Turkmenskoi, Ser. Biol. Nauk 1989(5): 19-23.
- Peck, J. E. 2006. Regrowth of understory epiphytic bryophytes 10 years after simulated commercial moss harvest. Can. J. Forest Res. 36: 1749-1757.
- Peck, J. E. and Moldenke, A. 1999. Describing and estimating the abundance of microinvertebrates in commercially harvestable moss. Report to the Eugene District Bureau of Land Management, Eugene, OR.
- Peck, J. E., McCune, B., and Moldenke, A. 1996. Epiphytes, invertebrates, and hosts associated with the commercial moss harvest, northwestern Oregon, U. S. A. Amer. J. Bot. suppl. Abstracts 83(6): 17.
- Pennak, R. W. 1953. Fresh Water Invertebrates of the United States. Ronald Press, New York.
- Percival, E. and Whitehead, H. 1929. A quantitative study of the fauna of some types of stream-bed. J. Ecol. 17: 283-314.
- Priddle, J. and Dartnall, H. J. G. 1978. The biology of an Antarctic aquatic moss community. Freshwat. Biol. 8: 469-480.
- Sayre, R. M. 1969. A method for culturing a predacious tardigrade on the nematode *Panagrellus redivivus*. Trans. Amer. Microsc. Soc. 88: 266-274.
- Sayre, R. M. and Brunson, L. K. 1971. Microfauna of moss habitats. Amer. Biol. Teacher Feb. 1971: 100-102, 105.
- Schwarz, A.-M. J., Green, J. D., Green, T. G. A., and Seppelt, R. D. 1993. Invertebrates associated with moss communities at Canada Glacier, southern Victoria Land, Antarctica. Polar Biol. 13: 157-162.
- Sohlenius, B., Boström, S., and Jönsson, K. I. 2004. Occurrence of nematodes, tardigrades and rotifers on ice-free areas in East Antarctica. Pedobiologia 48: 395-408.
- Steiner, W. A. 1994a. The influence of air pollution on moss-dwelling animals: 1. Methodology and composition of flora and fauna. Rev. Suisse Zool. 101: 533-556.
- Steiner, W. A. 1994b. The influence of air pollution on moss-dwelling animals: 2. Aquatic fauna with emphasis on Nematoda and Tardigrada. Rev. Suisse Zool. 101: 699-724.
- Steiner, W. A. 1994c. The influence of air pollution on moss-dwelling animals: 4. Seasonal and long-term fluctuations of rotifer, nematode and tardigrade populations. Rev. Suisse Zool. 101: 1017-1031.
- Steiner, W. A. 1995a. Influence of air pollution on moss-dwelling animals: 3. Terrestrial fauna, with emphasis on Oribatida and Collembola. Acarologia (Paris) 36(2): 149-173.
- Steiner, W. A. 1995b. The influence of air pollution on moss-dwelling animals: 5. Fumigation experiments with SO₂ and exposure experiments. Rev. Suisse Zool. 102(1): 13-40.
- Stern, M. S. and Stern, D. H. 1969. A limnological study of a Tennessee cold springbrook. Amer. Midl. Nat. 82: 62-82.
- Suren, A. M. 1987. The ecological role of bryophytes in high alpine streams of New Zealand. In: Sladecek, V. (ed.). Proceedings of the Conference (23) Congress in New Zealand, Hamilton, New Zealand, 8 Feb 1987.
- Suren, A. M. 1988. Ecological role of bryophytes in high alpine streams of New Zealand. Internat. Ver. Theor. Angew. Limnol. 23: 1412-1416.
- Suren, A. M. 1991a. Assessment of artificial bryophytes for invertebrate sampling in two New Zealand alpine streams. N. Z. J. Marine Freshwat. Res. 25: 101-112.
- Suren, A. M. 1991b. Bryophytes as invertebrate habitat in two New Zealand alpine streams. Freshwat. Biol. 26: 399-418.
- Suren, A. M. 1992. Enhancement of invertebrate food resources by bryophytes in New Zealand alpine headwater streams. N. Z. J. Marine Freshwat. Res. 26: 229-239.
- Suren, A. M. 1993. Bryophytes and associated invertebrates in first-order alpine streams of Arthur's Pass, New Zealand. N. Z. J. Marine Freshwat. Res. 27: 479-494.
- Suren, A. M. and Winterbourn, M. J. 1991. Consumption of aquatic bryophytes by alpine stream invertebrates in New Zealand. N. Zeal. J. Marine Freshwat. Res. 25: 331-343.
- Suren, A. M. and Winterbourn, M. J. 1992a. Bryophytes as invertebrate habitat in two New Zealand alpine streams. Freshwat. Biol. 26: 327-339.
- Suren, A. M. and Winterbourn, M. J. 1992b. The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. Freshwat. Biol. 17: 327-339.

- Tylka Nematology Lab. 2005. Extracting Nematodes from Soil with a Baermann Funnel. Accessed on 6 May 2009 at <<http://www.plantpath.iastate.edu/dept/labs/tylka/node/108>>.
- Vlčková, S., Linhart, J., and Uvíra, V. 2002. Permanent and temporary meiofauna of an aquatic moss *Fontinalis antipyretica* Hedw. Acta Univers. Palack. Olom. Biol. 39-40: 131-140.
- Zullini, A. and Peretti, E. 1986. Lead pollution and moss-inhabiting nematodes of an industrial area. Water Air Soil Pollut. 27: 403-410.

