CHAPTER 12-10
TERRESTRIAL INSECTS: HOLOMETABOLA – HYMENOPTERA

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Figure 1. Ant hill in Finland with leafy liverworts (***Barbilophozia hatcheri***, ***B. floerkei***, ***Tritomaria quinquedentata***, ***Lophozia ventricosa***) and the moss ***Pohlia nutans***. Photo by Des Callaghan, with permission.

HYMENOPTERA – Sawflies, Wasps, Bees, and Ants

Andrew *et al.* (2003) examined the variation in bryophyte fauna in Tasmania and New Zealand using different spatial scales along altitudinal gradients. Among these collections, they found six families of **Hymenoptera**. Although 77% of the faunal families were represented by 44 families, these 44 contributed only 10% of the total abundance.

This order is absent among bryophytes in the aquatic habitat, but in the terrestrial habitat, bees and ants find them useful in a variety of ways. As stated by Gerson (1969), some **Hymenoptera** feed on mosses. But others use them for nest materials, to house eggs, to provide water, and to provide cover. And of course some, including the sawflies, use them for pupation (Nägeli 1936).

Ants

Bryophytes, along with ants and grass, had a unique role for one Marine (Anonymous 1983). Trapped in a ravine in California for weeks, this marine subsisted on ants, moss, and grass! No wonder he lost 75 pounds before he found a way out!

The Phenomenal Ants

Ants are perhaps the most ordered insects on the planet. They work together to hunt and to build their trails and nests. In fact, they have been described as superorganisms because of their ability to work together as a unit (Oster & Wilson 1978). Ants are well endowed with defense, and depending on the species, they can bite, sting, or spray chemicals (Figure 2) such as formic acid (Wikipedia 2016). Their well-developed mandibles (Figure

3) serve for protection and prey capture. When an ant is killed, it emits a chemical that attracts ants from some distance, bringing an army to attack the intruder. Ants can also use chemical senses to identify dead colony members and remove them, and the workers are diligent in keeping the nest clean and free of bacteria. Their chemical signals, along with sounds and contact, permit them to communicate with each other. They also recognize their nest mates through the scent of hydrocarbon-laced secretions from their exoskeletons.

Figure 2. ***Formica aquilonia***, preparing to spray and adjusting the position of the abdomen with its legs. Photo by Brian Eversham, with permission.

Figure 3. ***Myrmica*** sp. mandibles, a genus with a number of bryophyte dwellers. Photo from <fir0002/flagstaffotos.com.au>, through Creative Commons.

Ants are common among bryophytes, especially in bogs. Those that frequent the bryophytes don't seem to have any special adaptations, but this has not really been explored systematically. Their body constrictions give them considerable flexibility compared to most other insects, permitting even large species to maneuver among the bryophytes. The bryophytes provide a temperature-buffered environment where many food organisms can be found. They also provide a suitable underground habitat for growing fungi, cultivated by the ants, and kept moist by the bryophytes that reduce moisture loss at the soil surface.

Where Ants Are Absent

Acacia ants, on the other hand, may actually avoid mosses. In Costa Rica, Angela Newton (Bryonet, 20 November 2006) found that ants under ant-acacias left the bryophytes mostly undisturbed, except for some obvious nibbling around the edges. The green patches of moss in the otherwise clear ant-acacia circles were quite healthy and more numerous than in the surrounding forest. The mosses seemed to benefit from the ants' gardening activities, whereby the ants removed the larger plants that could pose a competition threat.

Food Source?

We generally think of the ants with their large jaws and sharp bite as carnivores. But Plitt (1907) found moss capsules that were gnawed and spores removed. A patch of "***Webera sessilis***" (probably ***Diphyscium foliosum***, Figure 4) occurred immediately over an ant's nest. Both ***Myrmica ruginodis*** (Figure 39) and ***Formica picea*** (Figure 5) fed on the mosses and managed to gnaw a hole in nearly every capsule to obtain the spores. And beware – they were on the mosses in the collector's vasculum.

Figure 4. ***Diphyscium foliosum*** with capsules. Spores in these capsules serve as food for ***Myrmica ruginodis*** (Figure 39) and ***Formica picea*** (Figure 5). Photo by David T. Holyoak, with permission.

Figure 5. ***Formica picea*** on ***Sphagnum***. This ant species feeds on the spores of ***Diphyscium foliosum***. Photo by Barbara Thaler-Knoflach, with permission.

Loria and Herrnstadt (1980) found that in the Negev desert the harvester ant (***Messor***, Figure 6) ate capsules of ***Aloina aloides*** (Figure 7-Figure 8), ***Crossidium crassinerve*** (Figure 9), and ***Bryum bicolor*** (Figure 10) in winter when other food was not available. The ants climbed the seta of ***C. crassinerve***, chewed off the capsules, and carried them to their nests, forming a parade 15 m long. An average of 30 capsules per minute arrived at the nest! Longton (1984) considered this behavior to be opportunistic because capsules are not available every year in the desert climate. It is possible that this behavior is advantageous for the mosses as well – the ants are likely to place the capsules in places more suitable for spore maturation in this environment where such sites are rare. However, Loria and Herrnstadt (1980) emphasized that mosses do not seem to derive any advantage from this harvesting process.

Figure 6. ***Messor barbarus***, member of the genus that eats moss capsules in the Negev Desert. Photo by Valter Jacinto, through Creative Commons.

Figure 7. ***Messor*** on capsules of ***Bryum bicolor*** in Negev desert. Photo courtesy of Ilana Herrnstadt.

Figure 8. ***Aloina aloides*** with capsules. Capsules of this species serve as food for ***Messor*** in the Negev Desert. Photo by David Holyoak, with permission.

Figure 9. ***Crossidium crassinerve*** with capsules. Capsules of this species serve as food for ***Messor*** in the Negev Desert. Photo by Michael Lüth, with permission.

Figure 10. ***Bryum bicolor*** with capsules. Capsules of this species serve as food for ***Messor*** in the Negev Desert. Photo by Jonathan Sleath, with permission.

Bear feces are known to contain mosses, with one study reporting 50-90% mosses, primarily ***Pleurozium schreberi*** (Figure 30) (Dalen *et al*. 1996). But when the

feces contained 15% ***Brachythecium reflexum*** (Figure 11), Dalen and coworkers concluded that it was unlikely that the mosses were eaten by choice. Rather, they probably came along with its inhabiting food organisms – the ants.

Figure 11. ***Brachythecium reflexum***, a moss where ants can dwell and the moss seems to be eaten by bears along with the ants. Photo by Michael Lüth, with permission.

The Green Salamander, ***Aneides aeneus*** (Figure 12), is a well-known moss-dwelling insectivore. At Cooper's Rock in West Virginia, USA, the gut consisted of 53% ants, but also included moss fragments (Lee & Norden 1973). It is likely that this is another case of a moss inhabitant getting mosses along with its intended prey. Gunzburger (1999) likewise concluded that mosses in the gut of the Red Hills Salamander ***Phaeognathus hubrichti*** (Figure 13) got there in the process of eating moss inhabitants, including ants.

Figure 12. ***Aneides aeneus***, a moss-dwelling salamander that eats of lot of ants. Photo by Mike Graziano, with permission.

Figure 13. ***Phaeognathus hubrichti***, another moss dweller that eats ants among mosses and consumes part of the moss along with them. Photo by Danté B. Fenolio, with permission.

Anthills

Anthills range in size from those tiny volcanoes in the cracks in the sidewalk to massive structures that rival termite mounds (Figure 1). And some are simple entrances to a series of underground tunnels. In British chalk grasslands, King (1977) found that anthills have shorter vegetation, more rabbit dung, drier soil, smaller structural aggregates, lower bulk density, and more temperature extremes than the surrounding pasture. Several of these factors also lead to less moisture.

Eiseman and Charney (2010) report mosses on the abandoned anthill mounds of ***Formica exsectoides*** (Figure 14). Des Callaghan (Bryonet 3 August 2014) recently visited Finland and photographed a giant ant nest. The ants had cleared the nest of its tracheophytes, but, as he put it, they appear to have a fondness of leafy liverworts. Several species of liverworts [***Barbilophozia hatcheri*** (Figure 15), ***B. floerkei*** (Figure 16), ***Tritomaria quinquedentata*** (Figure 17), ***Lophozia ventricosa*** (Figure 18)] cover one of the mounds. In addition the mound served as substrate for the ubiquitous ***Pohlia nutans*** (Figure 19).

Figure 14. ***Formica exsectoides*** mound. Photo by Greg Schechter, through Creative Commons.

Figure 15. ***Barbilophozia hatcheri***, a colonizer on anthills of ***Formica exsectoides***. Photo by Michael Lüth, with permission.

Figure 16. ***Barbilophozia floerkei***, a colonizer on anthills of ***Formica exsectoides***. Photo by Hermann Schachner, through Creative Commons.

Figure 17. ***Tritomaria quinquedentata***, a colonizer on anthills of ***Formica exsectoides***. Photo by Malcolm Storey, through DiscoverLife.

Figure 18. ***Lophozia ventricosa***, a colonizer on anthills of ***Formica exsectoides***. Photo by Michael Lüth, with permission.

Figure 19. ***Pohlia nutans***, a colonizer on anthills of ***Formica exsectoides***. Photo by Michael Lüth, with permission.

Pekka Punttila (pers. comm.) explained the mound nests of the two species that may be inhabiting the mounds photographed by Des Callaghan (Figure 1). ***Formica lugubris*** (Figure 20) is **monogynous** (has only one queen in a mound). The longevity of this queen and her colony lasts typically only about 20 years. This loss opens the mound to invasion by other species or simply to die off if something happens to the queen. ***Formica aquilonia*** (Figure 21-Figure 23), on the other hand, is **polygynous**, meaning it has more than one queen in a mound. That strategy permits the species to maintain its nest for a long time. Furthermore, if many mounds are present, it is likely to be that of ***F. aquilonia***, a **polydomous** species. These mounds may reach dozens or even hundreds in an area. ***Formica lugubris*** typically builds single mounds.

Figure 20. ***Formica*** cf ***lugubris***, a monogynous species that builds single mounds. Photo by Richard Bartz, through Creative Commons.

Figure 21. ***Formica aquilonia*** mound. Photo by Villak, through Creative Commons.

Figure 22. ***Formica aquilonia*** on moss. Photo by Brian Eversham, with permission.

Figure 23. ***Formica aquilonia***, attacking its prey. Photo by Brian Eversham, with permission.

The monogynous species such as ***Formica lugubris*** (Figure 20) are able to disperse during their nuptial flight, temporarily parasitize other nests, and establish in young forests or older forest fragments (Punttila 1996). The polygynous species, including ***F. aquilonia*** (Figure 21-Figure 23), disperse primarily by "nest budding," permitting them to form large colonies of cooperative nests. These are found in older forests and larger old forest fragments.

Anthills create microhabitats of their own. This is evidenced by the moss ***Pseudoscleropodium purum*** (Figure 24). This species predominates on the north-facing sides of anthills constructed by ***Lasius flavus*** (Figure 25-Figure 26) (King 2003). King experimented with survivorship of the moss by rotating the anthills either 360° or 180°. Hence, half the anthills were now facing south. For those mosses facing south, over half the shoots turned white at the tips and up to 20 mm from the apex. Those rotated 360°, thus still facing north, remained green and healthy. Nevertheless, most of the mosses on the south side survived. Those on the north side grew faster and King concluded that it may be more difficult for the fragments to establish on the south side due to the longer periods that were dry and unfavorable for growth. Carl Farmer found anthills of this species in Scotland completely covered by mosses while the ants thrived inside.

Figure 24. ***Pseudoscleropodium purum***, a moss that lives on the north sides of anthills of ***Lasius flavus***. Photo by Michael Lüth, with permission.

Figure 25. ***Lasius flavus***, an ant that makes mounds where one can find ***Pseudoscleropodium purum*** on the north side of the mound. Photo by Anki Engström <www.krypinaturen.se>, with permission.

Figure 26. ***Lasius flavus*** tending aphids. Photo by Anki Engström <www.krypinaturen.se>, with permission.

In acidic grasslands, bryophytes may be confined to anthills. King (1981) found that the acrocarpous mosses ***Dicranum scoparium*** (Figure 27), ***Polytrichum juniperinum*** (Figure 28), and ***Polytrichum piliferum*** (Figure 29), all colonizers, were almost confined to the anthills in the Gower Peninsula of South Wales. King considered dispersal ability and ability to withstand burial to be primary factors to favor these mosses over surrounding tracheophyte plants, downplaying the importance of soil chemical and physical factors. ***Lasius flavus*** (Figure 25-Figure 26) builds mounds that are 15-20 cm high and 50-70 cm in diameter. In these acidic habitats, King found that ***Pleurozium schreberi*** (Figure 30), like ***Pseudoscleropodium purum***, is abundant on the north-facing sides of the mounds. On the other hand, ***Polytrichum juniperinum*** and ***Polytrichum piliferum*** are more frequent at the summit of the mound than at the periphery, but ***P. piliferum*** is more frequently on the south side, a location consistent with its habitation of more exposed, xeric habitats. ***Polytrichum juniperinum*** has its base 15 cm below the soil, suggesting that it grew up through the anthill as the anthill increased in size.

Figure 27. ***Dicranum scoparium***, a species that is common on anthills in South Wales. Photo by Janice Glime.

Figure 28. ***Polytrichum juniperinum***, a species that is common at the summit of anthills. Photo by Janice Glime.

Figure 29. ***Polytrichum piliferum***, a species that is frequent at the summit of anthills, but mostly on the south side. Photo by David Holyoak, with permission.

Figure 30. ***Pleurozium schreberi***, a moss that grows on north-facing slopes of anthills made by ***Lasius flavus***. Photo by Michael Lüth, with permission.

Des Callaghan (Bryonet 10 May 2017) has seen ***Buxbaumia viridis*** (Figure 31) living on the ant hills of the wood ant, ***Formica rufa*** (Figure 53-Figure 55). Many Bryonetters have reported what appears to be herbivory on this species of ***Buxbaumia***, but thus far there is no direct evidence that these are consumed by ants.

Figure 31. ***Buxbaumia viridis*** capsules, a species that can inhabit wood ant (***Formica rufa***) nests. Photo by Hermann Schachner, through Creative Commons.

For mosses in deciduous forests, anthills provide a substrate that rises above the forest floor. This permits the leaf litter to fall downward, keeping the anthill exposed and preventing burial of the bryophytes by leaf litter.

Ants as Gardeners

In several tropical areas, ants make ant gardens (Ule 1901; Blüthgen *et al.* 2001). These aerial gardens usually consist of plants, started as seeds by the ants, and used as a matrix in which soil is placed to construct a nest. But Ule reported only flowering plants in these ant gardens. In 1985, Frahm reported risk of life to collect a nest 15 cm in diameter with a yellow-green center surely of moss. The escapade began when he and Rob Gradstein chopped down the tree holding the nest, using machetes. But alas, the tree fell, only to land within the arms of another tree, with the nest still out of reach. Again, the second tree was cut in like manner, but it fell 10 meters deep into the river, thus drowning the ants in their nest! Not to be discouraged from their quest, the two bryologists then had to cross the river, as the tree was accessible only down a steep and rocky slope and to the other side of the valley. Attempts to raise the nest to the bridge with a rope destroyed most of it, but they were able to rescue the moss, determined as ***Brachymenium columbicum*** (Figure 32), a moss known also from Colombia and Ecuador, and now, for the first time, from Peru.

Figure 32. Ant garden, primarily of ***Brachymenium columbicum*** (and seedlings), from a tree in Peru. Photo by Jan-Peter Frahm, with permission.

Blüthgen *et al*. (2001) suggested the importance of these aerial ant gardens. Nutrients are scarce in the canopy. Some plants are adapted by producing **adventitious** roots (roots that arise from stems and other non-root axis points) that are able to grow and penetrate animal debris, bromeliad tanks, bryophytes, and plant cavities. But some lack the ability to take advantage of these nutrient sources. Among these some are able to form commensalistic associations. The association between ants and epiphytes is one such association. The ants carry seeds that they imbed in the garden. The ants then care for the garden by protecting it and providing a stable germination and establishment state. As noted by Frahm (1985), some of these gardens, as already noted, have bryophytes that can further help by maintaining moisture and trapping airborne dust and nutrients.

The leafy liverwort ***Nardia*** sp. (Figure 33) is a pioneer on volcanic ash, forming layered deposits up to 15 cm thick (Jongmans *et al*. 2001). These growths are able to adhere to vertical cliffs and to form bridges between volcanic boulders, facilitating the establishment of vascular plants. These carpets sometimes are invaded by ants and other insects that help to keep the liverworts clean and bring seeds and spores to continue the garden. In Costa Rica ants took up residence among the fronds of the hanging garden liverwort ***Nardia succulenta*** on the ash of volcano Arenal (Jongmans *et al*. 2001).

Figure 33. ***Nardia scalaris***. ***Nardia*** is a genus that forms bridges between volcanic boulders and is maintained by ants. Photo by Hermann Schachner, through Creative Commons.

Gibson (1993a, b) found that ants placed seeds of the cow wheat (***Melampyrum lineare***, Figure 34-Figure 36) more frequently under ***Polytrichum*** (Figure 28-Figure 29) than expected by chance, based on its relative cover (Figure 37). In the oak-pine forest of the New Jersey Pinelands, Gibson and Good (1987) found that the seeds of ***Melampyrum lineare*** were restricted to mossy patches. Ants gather these seeds and store them, later using the oily and nutrient-rich eliasome (Figure 36) as a food source without damaging the seed to which it is attached (Gibson 1993a, b). Litter and lichens were also used, but ***Polytrichum*** seemed to be highly selected. ***Dicranum*** (Figure 27) and ***Pleurozium*** (Figure 30), although more abundant than the ***Polytrichum***, attracted far fewer ants to store seeds. This behavior afforded the seeds a safe place where mice did not eat them and they retained sufficient moisture to survive. These seeds have low survival if they dry out and will die if they fall to the soil and remain exposed. If they remain in the capsules until evening, the mice will eat them.

Figure 34. ***Melampyrum lineare***, a hemiparasite whose seeds are dispersed by ants. These seeds are often deposited under mosses and lichens. Photo by Janice Glime.

Forest Ants

I have found little literature on forest floor bryophytes and their ant inhabitants. Ward (2000) reviewed some of these from leaf litter communities. Wilson and Hölldobler (2005) included bryophytes among the sites offering the desirable small spaces to ponerine ants on the forest floor. While these species are relatively abundant in the tropical and warm-temperate forests, they are scarce in the cool-temperate forests, deserts, and arid grasslands.

Myrmica rubra (Figure 38), ***M. ruginodis*** (Figure 39), and ***Formica lemani*** (Figure 40-Figure 41) are widespread among forest mosses (Stenhouse 2007). The latter nests in stumps. ***Myrmica rubra*** is the most moisture-loving of the ***Myrmica*** species, preferring moist, shady forests (Kupianskaya *et al.* 2000). It builds its nests in decaying stumps and logs, under mosses, and other moist locations. ***Myrmica ruginodis*** is the most abundant of the red ants in the North Vidzeme Biosphere Reserve, Latvia (Gluhovs 2013). Gluhovs determined that soil *p*H, bryophyte cover, and coarse woody debris did not have a significant effect on the ant communities in the forest.

Figure 35. ***Melampyrum lineare*** fruits. Photo by Keir Morse at <gobotany.newenglandwild.org>, with permission.

Figure 36. ***Melampyrum lineare*** moist seeds. Note the white eliasome. If the seeds drop to the ground they will dry out and turn black. Photo by Keir Morse at <gobotany.newenglandwild.org>, with permission.

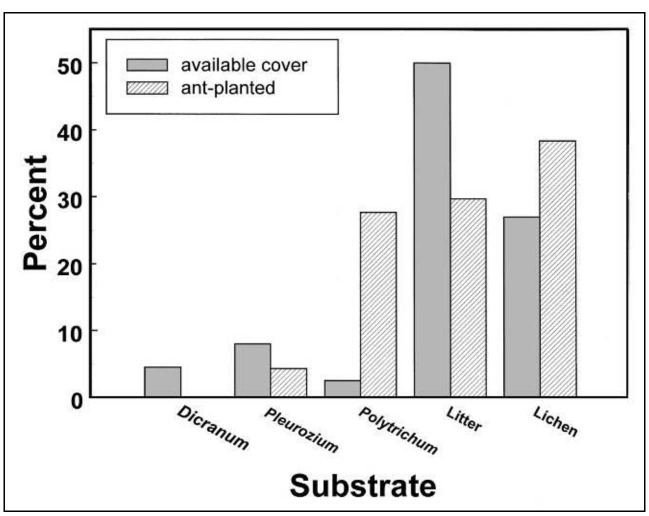

Figure 37. Percent frequency of ***Melampyrum lineare*** seeds stored by ants under various available substrates near Houghton, Michigan, USA. Modified from Gibson 1993a.

Figure 38. ***Myrmica rubra*** workers drinking from a water droplet on a leaf. Photo by Richard Becker at <www.bwars.com>, through open source permission.

Figure 39. ***Myrmica ruginodis*** worker carrying pupa. This species is common among forest mosses in Europe. Photo by Brian Eversham, with permission.

Figure 40. ***Formica lemani*** queen on moss. Photo by Brian Eversham, with permission.

Figure 41. ***Formica lemani*** worker carrying pupa across moss. Photo by Brian Eversham, with permission.

In addition to ***Myrmica rubra***, it is likely that moisture is important to other species and may account for vertical distribution of species and location of nesting sites. Billings and Drew (1938) demonstrated that bryophytes created a microhabitat that held six times as much water as the bare bark of old-growth tulip trees (*Liriodendron tulipifera*) in Tennessee.

Myrmica lobifrons and ***Dolichoderus pustulatus*** are the dominant ants in bogs in New England, USA (Gotelli & Ellison 2002). In fact, ***M. lobifrons*** seems to specialize in bogs and other humid habitats.

In forest sites in the Czech Republic, the **Formicidae** were among the most abundant taxa in the biggest bryophyte samples (400 cm^2) (Božanić 2011). ***Lasius brunneus*** (Figure 42) was abundant among epiphytic mosses on trees with a diameter of 60-110 cm, especially on old oak trees.

Figure 42. ***Lasius brunneus*** adult, an inhabitant of old oak trees where it lives among epiphytic mosses. Photo by Stanislav Krejčík, through Creative Commons.

Božanić (2008) examined the aspects of forest mosses that made them suitable environments for invertebrates. He suggested that ants may live there or go to mosses to search for food or shelter or to lay eggs. The microclimate, especially in retaining moisture, provides a haven for forest dwellers. On the other hand, the invertebrates help the bryophytes by spreading spores. Using heat extraction with a Tullgren funnel, Božanić extracted invertebrates from 66 moss samples. The richest fauna of invertebrates, including **Formicidae**, occurred with the moss ***Brachythecium curtum*** (Figure 43). The most important factors for number of taxa were type of substrate, height above ground, and moss sample area. The species were affected by the type of substrate, height above ground, and tree diameter.

Figure 43. ***Brachythecium curtum***, a preferred moss for habitation by members of **Formicidae**. Photo by Janice Glime.

Božanić *et al*. (2013) investigated the factors that affected invertebrate communities among bryophytes in forests of the Czech Republic. The dominant bryophyte was ***Hypnum cupressiforme*** (Figure 44) and Božanić and coworkers reported on 13 invertebrate groups, encompassing 45 species. Of these classes, orders, and families, 4 species of **Formicidae** (ants) were present. Height above ground was an important parameter in describing the **Formicidae** communities. But unlike the epiphyte communities in Costa Rica described by Longino and Nadkarni (1990) discussed below, Božanić *et al*. found that the **Formicidae** preferred habitats on the ground or

close to it. It is likely that the epiphyte cover in the Czech Republic is much less developed and protective compared to that in the cloud forests of Costa Rica.

Figure 44. ***Hypnum cupressiforme***, a dominant bryophyte in forests of the Czech Republic and home to ants there. Photo by Michael Lüth, with permission.

Epiphyte Communities

As seen above, Blüthgen *et al*. (2001) have demonstrated one importance of ants as epiphyte gardeners. Yanoviak *et al*. (2007) likewise considered the epiphytic mats as important habitats. In Costa Rica, these mats were thinner and exhibited less structural diversity in secondary forests compared to undisturbed forests. But for ants, the diversity was significantly greater in the secondary forests, especially *Solenopsis* spp. (subterranean fire ants). During the dry season, arthropod diversity declined among the epiphytes.

Nadkarni and Longino (1990) used the Winkler sifting apparatus to extract arthropods from Costa Rican canopy soils. They found that ants were among the dominant invertebrate groups in these habitats. In fact, the ants were the only group that did not have higher densities on the ground than in the canopy.

Longino and Nadkarni (1990) demonstrated a vertical zonation of ants in these Costa Rican cloud forests. The genera were similar in the canopy (litter and humus that include mosses) to those among the ground litter, but represented a subset of those genera. But at the species level, the two habitats were distinct with rare overlap in species between the two. Surprisingly, their new find was on the ground, where ***Stenamma*** JTL-3 (see Figure 62) was nesting under moss mats.

Ant activity in the tropical forests seems to be greater in the canopy than on the ground. Yanoviak and Kaspari (2000) used bait defense to determine these differences. The bait indicated more defense in the canopy (60%) than in the litter (32%), independent of tree species and bait type. It also indicated higher activity in defending protein baits than carbohydrate baits. Furthermore, the litter and canopy had no species in common.

Epiphylls as Defenders

Not all bryophytes favor the ants. The leafcutter ant ***Atta cephalotes*** (Figure 45) is repelled by epiphylls, including bryophytes, on citrus leaves. Mueller and Wolf-Mueller (1991) removed the epiphylls from citrus leaves and found 2-3 times as much herbivore damage from ants comparee to leaves with epiphylls intact. These epiphylls consisted of leafy liverworts and crustose lichens. They suggested that the epiphylls increased the cutting effort, or that secondary compounds in the liverworts might have been major contributors to the antiherbivory (see Swain 1977). A further possibility is that the epiphylls inhibited the growth of the fungi that served as food for these ants.

Coley *et al*. (1993) looked at the relationship from a different perspective. They found that long-lived tracheophyte leaves have better defenses against herbivores and pathogens than those with deciduous leaves. They suggested that liverworts may provide protection of the leaves, citing the rich concentration of terpenoids in liverworts. It takes only two years to cover leaves with species that have rapid colonization rates.

Figure 45. ***Atta cephalotes***, a leaf cutter ant that is repelled by epiphylls such as leafy liverworts. Photo by Scott Bauer, through public domain.

Dispersal

The busy ants run all over their habitats and the tiny, widely spaced hairs on their bodies would seem to provide ideal locations for some sizes of dispersal units. Rudolphi (2009) set out to discover if such a hypothesis was indeed viable. He reasoned that both ants (***Lasius platythorax***, Figure 82) and mosses, ***Aulacomnium androgynum*** (Figure 46) in particular, occurred on the same dead wood in Swedish forests. Therefore, it is reasonable that the gemmae (Figure 47) of this moss might be transported by the ants. First he tested whether the gemmae would adhere to the ants. He put one tuft of moss in each of eight Petri dishes and released eight ants into each dish, repeating the experiment 8 times. Once the ants ran across the moss (at least 30 seconds), they were removed by letting them crawl into a bottle. Ants were frozen and examined for adherence of gemmae. As many as six gemmae did, in fact, adhere, with 1/3 of the ants having gemmae within less than two minutes of exposure. He found that while moisture on the moss did not influence time the ant spent on the moss (42 sec wet vs 48 sec dry), the adherence was five times as great on the dry mosses (mean 0.94) vs wet (mean 0.19).

Figure 46. ***Aulacomnium androgynum*** showing gemmae that adhere to ants that share the same dead wood. Photo by Michael Lüth, with permission.

Figure 47. ***Aulacomnium androgynum*** gemmae. Photo by Des Callaghan, with permission.

Rudolphi (2009) followed this with a second experiment to determine residence time of the gemmae on the ants. Using nine ants in each of five time periods (0, 1, 2, 4, 8 hours), he attached two gemmae to the dorsal abdomen and let the ants run around. Ants were then frozen and examined for gemmae. Each time interval experiment was again repeated 8 times. After two hours, ants averaged retention of one gemma. After eight hours, 24% of the ants still had at least one gemma attached, suggesting that ants could be an effective dispersal agent of these gemmae.

But why more dry propagules? Wet gemmae tend to stick together, making the dispersal unit larger and heavier, thus easier to dislodge. This greater success of dry gemmae is actually advantageous because the ants are more active when the weather is dry (Elchuk & Wiebe 2003). Now we just need to watch the ants to see if they traverse the mosses on the logs and if they drop the propagules in suitable sites for successful establishment. Surely both of these conditions are met at least some of the time.

Ants are able to make trails – trails that we can see and follow. They do this by cutting vegetation that slows them down, and that includes cutting bryophytes. This activity provides an opportunity for dispersal. Korpelainen *et al*. (2011) explored the importance of this role in the leafy liverwort ***Barbilophozia attenuata*** (Figure 48). Using microsatellite markers, they showed significant kinship relationships up to 8 m. After that the relationship coefficients approached 0, then decreased to negative correlations. At more than 25 m they again approached 0, indicating random distribution. They suggested that the large gemmae permit effective establishment more easily than do spores. Gemmae were favored over spores along the ant trails (and are more likely in other areas of disturbance). Nevertheless, the researchers concluded that ants do not have a large role as dispersal agents, and the physical structure of the ant trails likewise does not lead to greater dispersal. Rather, the trails provide colonization sites available to this liverwort.

Figure 48. ***Barbilophozia attenuata***, a liverwort with gemmae that are distributed by ants. Photo by Andrew Spink, with permission.

Spain (2012a) puzzled over a section of moss lawn where the mosses exhibited a trail (Figure 49). It ended at the base of a tree, ruling out a watering hose as the causal factor. Finally he observed the trail long enough to see carpenter ants (***Camponotus*** sp.; Figure 50) following the trail (Figure 49) in both directions, one after the other. The ants had apparently removed thousands of moss plants to make the trail, hence making travelling easier (Figure 52). They no longer needed to climb up and down across the stems (Figure 51). Although the trail was only 10 m long, by ant lengths it was equivalent of the length of more than 7 football fields traversed by a human. This trail had actually been cut to remove the obstructing branches. Spain suggests if you want to get rid of the ants, give the nests frequent disturbance, such as hosing them, or fill the entrance with disturbing powders such as cinnamon, diatomaceous earth, or cloves (Spain 2012b).

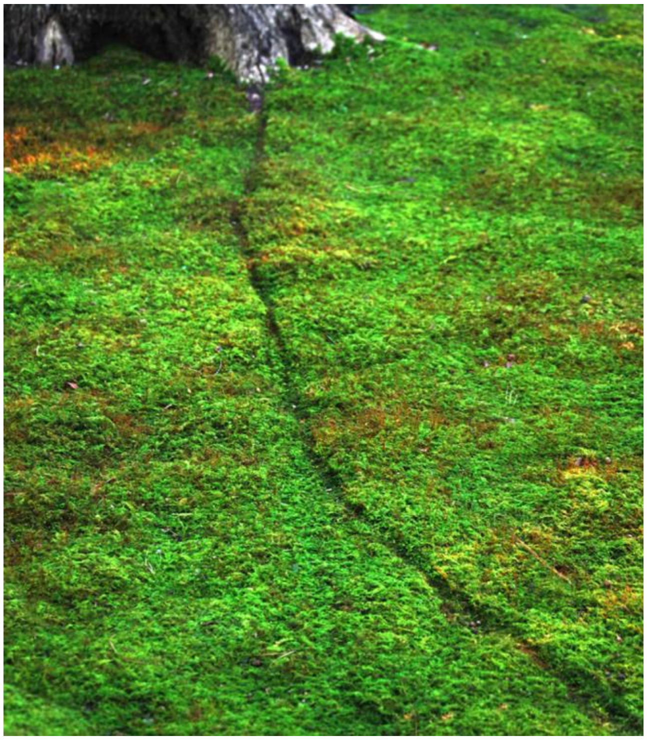

Figure 49. Moss-trail by made by carpenter ant. Photo from Moss and Stones Garden, with permission.

Figure 50. Carpenter ant (***Camponotus*** sp.) that made the moss trail. Photo from Moss and Stones Garden, with permission.

Figure 51. Here the busy ants appear to be dancing on a mound of moss, but its rough nature slows them down on their trail. Photo from Moss and Stones Garden, with permission.

Figure 52. Ant trail showing cut through mosses. Photo from Moss and Stones Garden, with permission.

Recognizing the importance of bryophyte fragments, Heiken *et al*. (2007) sampled nesting material from 25 ***Formica rufa*** (Figure 53-Figure 55) group nest mounds in five different forest types in Germany. In these nests they found numerous fragments of 20 bryophyte species occurring on almost all sampled mounds. Although both lichens and bryophytes occurred in the nests, 20 species represented bryophytes, whereas only 10 were lichens. The choices indicated some specificity. Those used were the abundant ones – no surprise there, but life form seemed to matter. Weft bryophytes accumulated on the mounds, but tall turfs seemed to be ignored. ***Hypnum cupressiforme*** (Figure 44) was the most abundant on the nests, appearing in 16 of the 25 samples and comprising 67.5% of the fragments detected. Other common flora were ***Pleurozium schreberi*** (Figure 30) and species of ***Brachythecium*** (Figure 63-Figure 64, Figure 43). Certain life forms (weft bryophytes, reindeer lichens) accumulate on mounds, while others (tall turfs, cup-type *Cladonia* spp.) discriminate, reflecting fragmentation features of the species.

Figure 53. ***Formica rufa*** nest in which bryophyte fragments are incorporated. Photo through public domain.

Figure 54. ***Formica rufa***, an ant that is known to use at least 20 species of mosses in its nests. Photo by Brian Eversham, with permission.

Figure 55. ***Formica rufa***, ready to bite or fire chemical weapons in its defense. Photo by Brian Eversham, with permission.

Some bryophytic nest contents were restricted by forest type (Heiken *et al*. 2007). ***Pohlia nutans*** (Figure 19) and ***Polytrichum piliferum*** (Figure 29) occurred in *Cladonio-Pinetum* nests; ***Pleurozium schreberi*** (Figure 30) in *Leucobryo-Pinetum*; ***Polytrichastrum formosum*** (Figure 56) and ***Rhytidiadelphus squarrosus*** (Figure 57) in spruce forests; ***Campylopus pyriformis*** (Figure 58) in low-mountain ranges; ***Plagiothecium*** spp. (Figure 59) in *Calamagrostio-Piceetum*.

Figure 56. ***Polytrichastrum formosum*** with frost. This species is found in ant nests in spruce forests. Photo by Aimon Niklasson, with permission.

Figure 57. ***Rhytidiadelphus squarrosus***, a species found in ant nests in spruce forests. Photo by Michael Lüth, with permission.

Figure 58. ***Campylopus pyriformis***, a moss used in ant nests in low mountain ranges. Photo by Michael Lüth, with permission.

Figure 59. ***Plagiothecium laetum***. Several species of this genus are ant nest components in the *Calamagrostio-Piceetum*. Photo by Michael Lüth, with permission.

Heiken *et al*. (2007) concluded that the ants were important dispersal agents by dropping fragments during transport and providing a colonization site on the mounds, especially those that were abandoned.

Anthills are not friendly bryophyte sites. The outer part of the nest dries faster than the forest floor (Heiken *et al*. (2007). Nests are frequently disturbed by ants, birds, and wild boar, suppressing the growth of the bryophytes. Heiken and coworkers determined that at least 25,000 fragments of bryophytes and lichens were carried to ant nests in one year. That is no guarantee they will grow.

Nesting

Ants build elaborate nests in trees or underground (Figure 60-Figure 61) (Wikipedia 2016). They typically maintain the nest at a temperature that is ideal for development of the larvae. They do this by choosing the location, materials, ventilation, and solar radiation. The worker and activity and metabolism help to contribute to heat control. In moist nests, microbial activity helps to control the temperature.

Figure 60. Ant nest under ***Dicranum scoparium***. Photo courtesy of Serhat Ursavas.

Figure 61. Ant nest under ***Dicranum scoparium*** showing closer view of the ants. Photo courtesy of Serhat Ursavas.

Longino (2005) examined nesting behavior of two species of the neotropical ***Stenamma*** (**Formicidae**; Figure 62). By comparing ants on soil banks, he found that they are absent from new (unvegetated) banks. They are very abundant on the banks at the intermediate stage that has only a sparse covering of small bryophytes. But when the mosses become abundant, the abundance of ants decreases greatly.

Ants use bryophytes to varying degrees to construct nests (Figure 63-Figure 65). Some nest under them (Figure 66). Some incorporate small bits of bryophytes in nest construction. And some use bryophytes almost exclusively. General collecting by Longino and Nadkarni (1990) in Monteverde and other highland sites in Costa Rica has revealed that ***Stenamma*** (Figure 62) makes nests under moss mats in the forest understory.

Figure 62. ***Stenamma brevicorne***, a species that lives under mosses, litter and similar protected sites, in this case carrying a grub. Photo by Galpert, through Creative Commons.

Figure 63. These ants have included ***Brachythecium*** (Figure 64) and ***Hypnum*** (Figure 65), among other things, in their nest. Photo by Janice Glime.

Figure 64. ***Brachythecium*** sp., a genus incorporated into ant nests. Photo by Janice Glime.

Figure 65. ***Hypnum imponens*** and ***H. jutlandicum***, mosses than can be incorporated into ant nests. Photo by Michael Lüth, with permission.

Figure 66. ***Polydesmus angustus*** nest under moss, Crowle Moors, UK. Photo by Brian Eversham, with permission.

The Neotropical frog ***Agalychnis saltator*** (**Hylidae**) makes nests and lays its eggs among mosses on lianas (vines) (Roberts 1994). Among the dangers to these eggs are cohabiting ants. As adults these frogs are able to escape quickly by parachuting.

My own experience is watching ants repair an ant nest mound made of ***Sphagnum*** during heavy winds (Figure 67-Figure 68). Bits were flying off the mound as fast as the ants could repair it. Ants are fairly common in bogs, and grabbing a handful of ***Sphagnum*** can result in an arm full of ants.

Figure 67. ***Formica*** on ***Sphagnum*** nest that makes this hummock in Michigan, USA. Photo by Janice Glime.

Figure 68. ***Formica*** on ***Sphagnum*** nest in Michigan, USA. These ants are busy repairing the nest as it is being blown apart by wind. Photo by Janice Glime.

Abandoned nests can become the site of moss invasions, as seen in Figure 69.

Figure 69. Ant hill with moss. Photo by Annette Schimming, with permission.

If you have ever trudged through a peatland with hummocks and hollows, you know how difficult walking can be. It is easy to twist your ankle on the uneven substrate. What you may not know is that ants can be

responsible for some of that rough terrain. They are clever engineers and in the peatlands they build elaborate nests, as you have just seen. But in natural hummocks formed by ***Sphagnum*** growth, ants can play a role in the changes in microtopography (Luken & Billings 1986). Due to their tunneling behavior, it appears that when the mosses die, hummock retrogression is accelerated by the tunnelling of the ants. In fact, some of these collapsed hummocks can eventually form hollows.

Ants, *Sphagnum* Collars, and Aphids

Robin Stevenson (Bryonet 17 June 2015) reported moss collars around the bases of pine (Figure 70-Figure 73) and birch (Figure 74) trees. "The lower part of the 'trunk' was covered in little bits of dried ***Sphagnum*** (Figure 78), and the whole plant was swarming with lots of ants. We didn't see the ants actually moving any of the ***Sphagnum***, but they did look as if they were coming up from *underneath* it. We got the impression that it was the ants who were responsible."

Figure 70. Ants, aphids, and ***Sphagnum*** sleeves on sapling in bog. Photo courtesy of Robin Stevenson.

Figure 71. Ants and basal sleeve of ***Lasius platythorax*** in bog. Photo courtesy of Robin Stevenson.

Figure 72. Ant (***Lasius platythorax***) ***Sphagnum*** sleeves on pine. Photo courtesy of Robin Stevenson.

Figure 73. Partial sleeve made by ***Lasius platythorax*** around branching point in Durham Bog. Photo courtesy of Robin Stevenson.

Figure 74. Birch sleeve of ***Sphagnum*** built by ***Lasius platythorax***. Photo courtesy of Robin Stevenson.

I have several hypotheses for the ***Sphagnum*** ant nests:

1. The ants are just beginning a nest and the pine serves as a central support column.
2. The nest has been mostly destroyed and the ants are repairing it.
3. The ***Sphagnum*** is tucked into the pine to maintain higher moisture for laying eggs. (I doubt that is the case.).
4. There is some commensal/symbiotic relationship going on, probably aphids, and the ants are improving conditions for aphids or other insects that will serve as food.

Stevenson returned to the site and found three more of these constructions (pers. comm. 22 June 2015). Not all were at the bases, but rather formed collars farther up the sampling trunk (Figure 75). The ants were scurrying about, on, and through, the moss collars (Figure 76). These collars were made of a variety of the materials available (Figure 77), but mostly of ***Sphagnum fallax*** (Figure 78) and ***Aulacomnium palustre*** (Figure 79-Figure 80), but also included leaves of ***Polytrichum commune*** (Figure 81), *Erica tetralix*, and *Calluna vulgaris*. Much of the composition was ***A. palustre*** tomentum (Figure 80). ***Sphagnum*** was tucked in among the leaves of the pine, well above the substrate (Figure 75).

Figure 75. Partial sleeve by ***Lasius platythorax*** at branching point on pine. This nest is at some distance from the tree base. Photo courtesy of Robin Stevenson.

Figure 76. ***Lasius platythorax*** in nest where they are running about. Photo courtesy of Robin Stevenson.

Figure 77. Sleeve material of ***Lasius platythorax*** collars that house aphids. Photo courtesy of Robin Stevenson.

Figure 78. ***Sphagnum fallax***, a moss used by ants to make collars housing aphids on saplings of pines and birches. Photo by Michael Lüth, with permission.

Figure 79. ***Aulacomnium palustre***, a common moss in ant-made moss collars in UK bogs. Photo courtesy of Robin Stevenson.

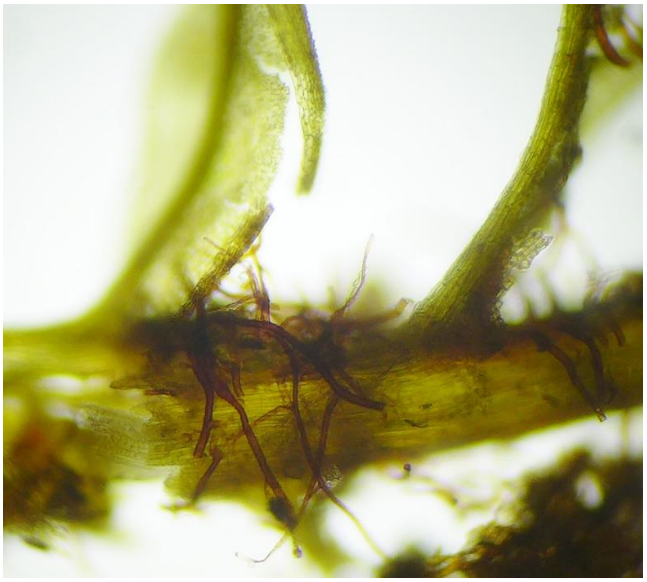

Figure 80. ***Aulacomnium palustre*** showing tomentum from ant nest at Durham Bog. Photo courtesy of Robin Stevenson.

Figure 81. ***Polytrichum commune*** fragments from nest of ***Lasius platythorax***. Photo courtesy of Robin Stevenson.

So let's return to the moss collars to shed more light on these hypotheses. On another return visit, Stevenson had a "good look to see what the ants were up to: lots of scurrying about, and a few interactions with aphids – of which there didn't seem to be too many. However... when I broke a bit of sleeve off, there were a lot of aphids all huddled together underneath. So, it looks as if the ants are herding them under the cover of the sleeve – or might they shelter there of their own volition? Herding sounds more likely – but how does that work? I'd have thought that pine bark was a bit tough, even for an aphid's mouth parts, and they would have been better off up among the leaves?"

The ants were ultimately identified as ***Lasius platythorax*** (Figure 82-Figure 83) (Wells 2015). The aphids provide **honeydew** (Figure 84-Figure 85) for the ants, and the ants, in turn, police the stems with the nests (Figure 83, Figure 86), warding off a number of kinds of predators. Interestingly, the aphids are species-specific. That is, the birch aphids are ***Symydobius oblongus***, whereas those on the pine are ***Cinara pini*** (Figure 84-Figure 86).

Figure 82. ***Lasius platythorax***, an ant that makes moss sleeves around saplings in bogs to cultivate aphids. Photo by April Nobile, through Creative Commons.

Figure 83. Ants (***Lasius platythorax***) and free aphids (***Cinara pini***) on pine stem at Durham Bog, UK. Photo courtesy of Robin Stevenson.

Figure 84. ***Cinara pini*** with honeydew drop at anus. This one is on ***Pinus sylvestris***. Photo from <Influentialpoints.com>, through Creative Commons.

Figure 85. Ant feeding on aphid honeydew. Photo by Jmalik, through Wikipedia Commons.

Bauer-Dubau (2000) found that ***Cinara pini*** (Figure 84-Figure 86) produces more offspring when attended by ants. In Germany, the aphids on several pine species are heavily attended by the ant ***Lasius fuliginosus*** (Figure 87). The density of ants increased from 10-20 to 26-48 ants per colony in one generation. Without the ants, the aphid anus becomes covered with honeydew and the colony disperses.

Beattie (1985) reviewed ant service to aphids. That review demonstrated that the ants provide not only protection, but also sanitation and transportation, decrease their development time, and increase the colony growth rate, survivorship, and fecundity (Kennedy & Stroyan 1959; El-Ziady 1960; Banks 1962; Way 1963; Banks & Macauley 1967; Bristow 1982). Furthermore, the ants reduce parasitism by wasps (27.4-98.4% reduction) by preventing the egg-bearing female parasites from landing on the aphids and ovipositing there (Bartlett 1961). Disturbance by ants resulted in 27.4% to 98.4% reduction in parasitism, depending on the parasite species. Ants even place aphids in areas that give them better access to the phloem that provides their food source (Banks 1962; Way 1963). The ants build shelters that protect them from rain and enemies, using soil, vegetation, and other materials (Andrews 1929; Levieux 1967; Duviard 1969; Duviard & Segeren 1974).

Figure 86. The aphid ***Cinara pini*** being attended by the wood ant ***Formica rufa*** on ***Pinus sylvestris*** at Flatropers Wood. Photo from <influentialpoints.com>, through Creative Commons.

Figure 87. ***Lasius fuliginosus***, a species that attends the aphid ***Cinara pini*** on pines in Germany. Photo by Ab H Baas, with permission for non-commercial use.

Ants are known for feats of strength and strong societal behavior. In one recent study in Israel, Gelblum *et al*. (2015) describe their seemingly undirected behavior while carrying a Cheerio. The ants doing the carrying can't see what is ahead and often get off course. But navigator ants (scouts) occasionally enter the scene and direct the Cheerio carriers back on course. The communication between the scout and the carrier ants seems to be through the changed direction felt through the Cheerio. It would be interesting to observe whether similar carriers and scout leaders exist in the movements of mosses to make the mounds observed in bogs and fens or the collars around birch trees.

Bogs and Fens

One must be careful when reaching deep into a moss hummock to collect the moss because a swarm of ants may soon be on its way up one's arm! I have experienced this in several locations in North America. Rosengren (1969) and Collingwood (1979) relate the commonness of ants among ***Sphagnum*** turfs in Central Europe, where such ants as ***Formica uralensis*** (Figure 88) likewise carve nests (Figure 89) out of the peat (Stankiewicz *et al*. 2005) and hibernate under mosses in winter (Collingwood 1979) . This species is restricted mostly to ***Sphagnum*** habitats. Matthey (1971) reported that both ***Myrmica ruginodis*** (Figure 39) and ***Formica picea*** (Figure 5) make nests in ***Sphagnum***. As mentioned above, I have observed nests made of ***Sphagnum*** (Figure 90), but I was unable to identify the species. Blank Shaw found a similar nest in Maine (Figure 91).

Figure 88. ***Formica uralensis***, an ant that nests in ***Sphagnum*** in Europe. Photo by Ruth Ahlburg, with permission.

Figure 89. Nest of ***Formica uralensis***, made of ***Sphagnum***. Photo by Ruth Ahlburg, with permission.

Figure 90. These ants are busy repairing their nest in this ***Sphagnum*** hummock on a windy day in Michigan's Upper Peninsula. Photo by Janice Glime.

Figure 91. Ant nest made of ***Sphagnum rubellum*** in Maine. Photo by Blanka Shaw, with permission.

Šteffek and Wiezik (2008) reported 11 species of ants in a peat bog at Hrabušice, N Slovakia. ***Myrmica scabrinodis*** (Figure 92) is dominant there in patches with the highest humidity. They build their colonies among the thick mosses. In Switzerland, the inhabiting ***Myrmica ruginodis*** (Figure 39) and ***Formica picea*** (Figure 5) form nests among the ***Sphagnum*** (Matthey 1971).

Figure 92. ***Myrmica scabrinodis***, a dominant ant in peat bogs of northern Slovakia. Photo by Tim Faasen, with permission.

Certainly many insects are housed in mosses, but one of the most distinctive nests is the smooth dome built by ants in a fen. I watched these industrious creatures groom

their mound of ***Sphagnum*** continuously on a windy day, weaving each loose fragment of moss back into the construction (Glime, personal observation). They could barely move against the wind and often were moved backward by its force.

Lesica and Kannowski (1998) reported that the ants ***Formica podzolica*** (Figure 93), ***Myrmica fracticornis*** (Figure 94), and ***M. incompleta*** (Figure 95) are common in large rich fen complexes of Montana, USA. All three of these species build nests there. ***Formica podzolica*** nests are much larger than nests of the two species of ***Myrmica*** and occur in the hummock-hollow complex. The nests are about the size of a hummock, and likewise have elevated levels of K, PO_4^-, Mg, and Na similar to those of hummocks. Lesica and Kannowski (1998) suggested that the hummocks were actually abandoned ant mounds. Even here, the ***Formica podzolica*** gains most of its nutrition by tending the aphids that feed on the shrubs. And the shrubs are provided a rich habitat for establishment when they germinate in the mounds. Because of this germination relationship, the ants become ecosystem engineers that permanently change the structure and composition of the rich fen vegetation. But there is a feedback mechanism in which the ants benefit from the increase in host plants for the aphids.

Figure 93. ***Formica podzolica*** adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Tracy Barbaro, through Creative Commons.

Figure 94. ***Myrmica fracticornis*** adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Dan Kjar <www.discoverlife.org>, through Creative Commons.

Figure 95. ***Myrmica incompleta*** adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Tom Murray, through Creative Commons.

In a Norway mire, Collingwood (1976) found even greater diversity. Using pit-fall traps, Collingwood recorded 18 species in 13 mires habitats at Eidskog. Among these, ***Formica forsslundi*** and ***F. transkaucasica*** are ture mire species. Among the most abundant species were ***Myrmica scabrinodis***, ***M. ruginodis***, ***F. transkaucasica***, and ***Leptothorax acervorum***.

Ants can influence the distribution of other invertebrates in peatlands. Antonovic *et al*. (2012) suggested that the higher diversity of terrestrial isopods could in part be the result of predator pressure by ***Myrmica*** ants (and lycosid spiders).

Bees

Bees are disappearing in alarming numbers, so anything new we can learn about them may be important in saving them. It may surprise you to learn that a number of bees use mosses for various purposes.

Guy Brassard (Bryonet 31 March 2016) reported that bees on Ellesmere Island in the Canadian High Arctic use bryophytes in their nests! He identified more than 50 species of mosses and about 8 species of liverworts among the 47 nests, with an average of 6-7 species per nest. Some of the moss species were present in more than 25 nests and some in very few nests, suggesting that the bees are selective about the bryophytes chosen.

Annie Martin (Bryonet 31 March 2016) reported observations of honey bees, wasps, and butterflies gathering on mosses at her Mossery. They would sit for up to half an hour instead of just a quick stop. A beekeeper explained that worker bees gather water and take it back to the hive or nest. Given the choice between a puddle or larger water body compared to moss colonies, the bees seem to prefer the moss option! There didn't seem to be any species preference.

And if you are a moss gardener, beware. Martin also has found yellow jackets, carpenter bees, wasps, ants, and termites making their homes in giant ***Polytrichum commune*** (Figure 81) colonies.

Apidae – Honey Bees, Bumblebees, Carder Bees, *etc.*

Honey Bee

The small red dwarf honey bee, ***Apis*** (***Micrapis***) ***florea*** (**Apidae**; Figure 96-Figure 98) has a mysterious habit of collecting "something" from mosses. Sunil Chaturvedi observed this species probing the pots with mosses, whereas they were not doing this in nearby pots of similar moisture but no mosses (Bryonet 26 February 2011). Daniel McConnell, a US Forest Service botanist, reported seeing this behavior for many years (probably with a different honey bee species), and observed that it seemed to be much more common on calcareous mosses (Bryonet 27 February 2011). Wolfgang Hofbauer (Bryonet 28 February 2011) stated that "bees love to take in water at open moist places. For this purpose moss cushions seem to be very suitable. In spring beekeepers even offer them moistened moss cushions near their beehives."

Figure 96. ***Apis florea*** adult, a species that collects something, probably water, from bryophytes. Photo by John Ascher <www.discoverlife.org>, through Creative Commons.

Figure 97. ***Apis*** (***Micrapis***) ***florea*** on moss, apparently getting water, but perhaps not. Photo by Sunil Chaturvedi, with permission.

In their blogspot, the Hive Honey Shop recommends providing bees with water in summer (Beekeeping 2013). They warn not to use fresh water because the bees will not touch it. Rather, they prefer mature mineral-rich water. Provide them with a number of places where they can land to get water without drowning. They suggest putting moss around the edges or in the water dish not only for safe footing, but also to filter the water and prepare it for drinking (Figure 98).

Figure 98. Close-up of ***Apis*** (***Micrapis***) ***florea*** on ***Pohlia***, apparently getting water, or is it simply attracted by UV reflectance by the bulbils of the ***Pohlia***? Photo by Sunil Chaturvedi, with permission.

But what draws the bees to the mosses? Sunil Chaturvedi suggested that the mosses may bring more bees to the area because of UV reflectance, hence increasing pollination of crop plants. These observations recalled to my mind the interesting observations of Gisela Nordhorn-Richter that demonstrated UV reflectance of ***Pohlia*** **bulbils** (Figure 99). Could it be that the bees are attracted to some bryophytes by UV waves, seen by bees but not by humans? Jon Shaw (pers. comm.) noted that the mosses observed by Sunil Chaturvedi appeared to be ***Pohlia*** with abundant **bulbils** (Figure 99). In any case, the mosses seem to be important sources of seasoned water for the bees.

Figure 99. ***Pohlia bulbifera*** bulbils. These fluoresce under ultraviolet light and could possibly attract bees. Photo by Des Callaghan, with permission.

Annie Martin (2015) reports that honey bees rest on the mosses in her moss garden, simply sitting quietly for a period of time. These bees drink the water on the leaves of the mosses. Beekeepers have suggested that the bees prefer moss water, possibly because of antibiotics in the water (Adventures in Natural Beekeeping 2017). This needs to be verified.

Grdović and Sabovljević (2008) also observed bees visiting bryophytes in beehive yards. They suggested that the bryophytes influence the humidity, maintaining a milder microclimate for the flowering plants and enabling those plants to remain moist longer and grow better. The same moisture provides a water source for the bees.

Figure 100. Honey bee (***Apis*** so.) on ***Sphagnum*** cf. ***palustre***, where it is able to get a drink of water and rehydrate. Photo courtesy of J. Paul Moore.

One could pose several hypotheses for this bee activity on mosses. Tom Thekathyil stated that bees and wasps often "imbibe water" from the surfaces of mosses and suggested that the mosses may have tiny pools of free water that are not available on the bare soil. This is a reasonable hypothesis, given the tiny capillary spaces on mosses that typically hold water longer than the soil surface. The straw-like mouth parts (Figure 101) of the honey bees would permit them to extract water from these tiny droplets.

Figure 101. Honey bee proboscis. Photo from <www.MzePhotos.com>, through Creative Commons.

Another hypothesis is that the water quality might be different on the mosses. On calcareous soil, high concentrations of carbonates might deter the bees, whereas the capillary water of the mosses could be altered by the cation exchange on the moss surface, or by the addition of oxygen from photosynthesis. This suggestion is supported by the observations at the Hive Honey Shop (Beekeeping 2013).

Water certainly seems to be a likely motivator. Bashir Yusuf Abubakar, Bryonet 28 February 2011, pointed out that water is a prime requirement of bees in culture such that they are always available in moistened areas. One can even find them surrounding a dripping tap. The water retention capacity of mosses varies between mosses and could account for differences in visitation frequencies.

The bee mouthparts facilitate the use of tiny drops of water such as those on bryophytes. The proboscis (Figure 101) uses capillary action and suction to draw a fine stream of liquid to the mouth (Krenn *et al*. 2005).

Bumblebees

Guy Brassard (Bryonet 1 June 2010) identified bryophytes from 47 bumblebee nests, primarily ***Bombus polaris*** (Figure 102) and ***Bombus hyperboreus*** (Figure 103) on northern Ellesmere Island, in the Canadian High Arctic (Richards 1973). The use of mosses helps to insulate the nests, permitting these two bees to survive farther north than other bumble bees (Heinrich 2004). But then, ***B. hyperboreus*** is a parasite on ***B. polaris***. Hence, the behavior of ***B. polaris*** determines the temperature control for both species.

Bombus polaris sometimes takes advantage of the activities of rodents, building their own nests in lemming and other burrows, but these locations are too cold. Instead, most build their nests in meadows and marginal pools on flat areas, in depressions, and beside small hummocks of mosses or other vegetation. Entrances typically faced the sun during the daily temperature peak. and rearranging the mosses to suit their needs (Richards 1973). The female pulls the moss with her mandibles and forelegs, pushing it under her body with her mid- and hind legs to the desired position. The queens and assisting workers continue to rearrange the bryophytes as the colony expands. Guy Brassard (pers comm. 1 April 2016) reported to me that an individual nest typically had 2-14 species of bryophytes and an average of about 6 or 7 species per nest. These comprised at least 56 species of mosses and 6 species of liverworts overall (see Richards 1970). Only one of the nests lacked any bryophytes. Bryophytes were typically intermixed with dried sedge leaves to cover the nest and create a thick, tight surface of insulation. The most frequent bryophyte species were all common in the region. The following were the most often found (with total number of nests out of 47): ***Campylium arcticum*** (33) (Figure 107); ***Orthothecium chryseum*** (29) (Figure 109); ***Drepanocladus revolvens*** (28) (Figure 108); ***Distichium capillaceum*** (21) (Figure 105); ***Ditrichum flexicaule*** (19) (Figure 106); also *Bryum* sp. (38 – tiny unidentifiable scraps) (Figure 10). The three pleurocarpous species were usually dominant or abundant; the others were often very minor components.

Figure 102. ***Bombus polaris***, a species that uses mosses in its nest. Photo by J. C. Schou, with permission.

Figure 103. ***Bombus hyperboreus*** adult, a species that uses mosses in its nest. Photo by Marko Mutanen, through Creative Commons.

Figure 104. **Apoidea** nest uncovered from mosses, showing bees in the nest. Photo by Panoramedia, through Creative Commons.

Figure 105. ***Distichium capillaceum***, one of the species used in bee nests. Photo by Michael Lüth, with permission.

Figure 106. ***Ditrichum flexicaule***, one of the species used in bee nests. Photo by Michael Lüth, with permission.

Figure 107. ***Campylium arcticum***, one of the species used in bee nests. Photo by Michael Lüth, with permission.

Figure 108. ***Drepanocladus revolvens***, one of the species used in bee nests. Photo by Kristian Peters, with permission.

Figure 109. ***Orthothecium chryseum***, nesting material for bees. Photo by Michael Lüth, with perission.

Bumblebees (***Bombus***; Figure 110) can use abandoned mouse nests in areas with tussock grass or moss (Saunders 2015). Goulson (2010) found that suitable sites for nesting provided insulating materials for the nest. Such materials include mosses, feathers, hair, and grass. Harvey (2015) echoed this advice for rearing bees, including the need for attracting mice and voles to create nesting sites. In fact, Sladen (2014) reported that a carder bee may build its own nest when moss is abundant instead of occupying abandoned nests of small animals.

Figure 110. ***Bombus*** sp. adult, a genus that uses abandoned mouse nests that often contain mosses. Photo by Yann, through Creative Commons.

Fussell and Corbet (1992) found that nesting sites differed significantly among color groups of British bumblebees. These involved position of the nest relative to ground level, time of day at which direct sunlight reached the nest, and nature of the immediate environment of the nest.

Bumblebee visits to bryophytes may be facultative (Grdović & Sabovljević 2008). These researchers did find that a relationship of the bees with the bryophytes was supported statistically, suggesting that humidity and a milder microclimate supported the relationship.

Even bumblebees that do not build nests of mosses may find them useful for overwintering. ***Bombus lucorum*** (white-tailed bumblebee; Figure 111), ***B. lapidarius*** (Figure 112), and ***B. hortorum*** (garden bumblebee; Figure 113) spend their winter in mosses (Alford 1969). ***Bombus pratorum*** (early bumblebee; Figure 114) uses mosses facultatively – overwintering sometimes in moss, sometimes underground.

Figure 111. ***Bombus lucorum*** adult, a bee that overwinters among mosses. Photo by James K. Lindsey, with permission.

Figure 112. ***Bombus lapidarius*** adult, a bee that overwinters among mosses. Photo by Beate & Heinz Beyerlein, through Creative Commons.

Figure 113. ***Bombus hortorum*** adult on protonemata on soil. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 114. ***Bombus pratorum*** adult sometimes overwinters in mosses and sometime underground. Photo by Aiwok, through Creative Commons.

Carder Bees

Carder bees include the moss carder bee, ***Bombus muscorum*** (Figure 115). These bees are so-named because they cleanse/comb the mosses before inserting them into the nest construction (Smith 1876). They typically build the nest entirely of moss, working it with their feet into a compact mass that resists the weather (Cuthbert 1895). If mosses are abundant, the nest may be made entirely of mosses, but if mosses are scarce, they may build nests with no mosses. The nest is comprised of a series of cells connected by coarse brown wax (Cuthbert 1895).

Figure 115. ***Bombus muscorum*** adult, a species that uses mosses to build its nest. Photo by J. C. Schou <www.biopix.com>, through Creative Commons.

Rennie (1857) describes the nest-building of ***Bombus muscorum*** (Figure 115) as a series of backward pushes. The bees establish a line of up to 6 bees to transport the moss from the source to the nest. The last bee in the file grabs some moss with her mandibles, disentangling it and carding it with her forelegs into a small bundle. She pushes this bundle under her body to the next bee, who passes it to the next with the same under body move, and so forth.

The nest has a long, arched passageway that is formed by a variety of mosses, wide enough to permit free passage for the bees (Smith 1876). The final nest has a dome of 10-15 cm above the ground (Rennie 1857). Wax from the bees forms the ceiling, repelling rain and preventing high winds from carrying away the nest. During the day, the top of the dome may be opened more than 2.5 cm, apparently to ventilate the nest. It is not used for entry, and it is closed again at night. Instead, there is an entrance passage at the bottom of the nest that is about 30 cm long and 1.2 cm wide. The larvae spin cells. When the grubs are ready to emerge, it is the older bees that chew off the cover to free them. One of these spheres may house 3-30 eggs. Rennie found that the adults were of a color similar to the moss they used.

Bombus muscorum (Figure 115) carders collect mosses and dry grass, constructing the nests on or just under the ground (Wikipedia 2015a). The mosses and grass are used to cover the nest. Once the nest is completed, the bee aggressively protects it, attacking intruders by biting and stinging them simultaneously.

The carder bees differ from other members of ***Bombus*** that nest underground (Carvell 2002). The partially above ground nesting by carder bees seems to necessitate the grass-moss habitat to maintain warmth. Nevertheless, there is a negative relationship between number of carder bees and depth of moss. On the other hand, Jukes (2008) reported that ***Bombus muscorum*** (Figure 115) in Sussex made its nest in deep moss in exposed places.

Iles (2010) listed the carder bees ***Bombus humilis*** (Figure 116), ***B. sylvarum*** (Figure 117), and ***B. muscorum*** (Figure 115) as species that require tall grassland with "plenty of leaf litter or moss" to use as nesting material. ***Bombus pascuorum*** (Figure 118) appears to be more flexible, as indicated by its many habitats. Similarly, ***Bombus ruderarius*** (Figure 119) builds its nest at the surface or just below, using grass and mosses, and likewise often utilizing an abandoned mouse or vole nest (Benton 2008).

Figure 116. ***Bombus humilis*** adult, a species that uses mosses to build its nest. Photo by Tim Faasen, with permission.

Figure 117. ***Bombus sylvarum*** adult, a species that uses mosses to build its nest. Photo by James K. Lindsey, with permission.

Figure 118. ***Bombus pascuorum*** adult, a species that uses mosses in its nests, but that occupies a variety of habitats. Photo through Creative Commons.

Figure 119. ***Bombus ruderarius*** adult, a species that nests under mosses and grasses. Photo by James K. Lindsey, with permission.

The common carder bee, ***Bombus pascuorum*** (Figure 118), is widespread in Europe, living in meadows, waste ground, ditches, embankments, roads, gardens, parks, and forests (Wikipedia 2015b). Like the moss carder bee ***B. muscorum***, this species also collects mosses and grasses, constructing a small, hollow sphere. Walls of this sphere are bonded with wax and sealed off. Inside they form a large bowl (5 mm diameter) of brown wax filled with pollen. They deposit 5-15 eggs, then close the cell. They fill a second chamber (20 mm high) with nectar to provide a food reserve for days when weather is not suitable for foraging. Larvae hatch in 3-5 days, then spend only a week to mature as they feed on the food reserves.

Braconidae – Parasitic Wasps

In New Zealand, a new genus, ***Shireplitis***, was described as mostly in moss, litter, or tussock grasslands (Fernández-Triana *et al*. 2013). ***Parolitis wesmaeli***, also **Braconidae**, from Europe, is a parasitic wasp that uses larvae of ***Scoparia basistrigalis*** (**Pyralidae**) and ***Bryotropha umbrosella*** (**Gelechiidae**) (both **Lepidoptera**) as hosts. Larvae of both of these hosts feed from their silken tube or tent, grazing on mosses and grasses. Four of the ***Shireplitis*** species (*e.g.* Figure 120) were themselves collected from mosses and may likewise live on moss-eating **Lepidoptera**. Fernández-Triana *et al*. considered the robust body and legs with shortened antennae of these **Braconidae** to be adaptive for moving among "litter" while searching for hosts. See Chapter 12-14 for further discussion of the Lepidoptera hosts.

Figure 120. ***Shireplitis bilboi*** adult, an inhabitant of ***Sphagnum*** and grasses. Photo through Creative Commons.

Cynipidae and Mimicry

Some members of the **Cynipidae** take advantage of mosses in a different way. ***Diplolepis rosae*** (Figure 121) causes a gall formation that resembles a moss to house its eggs and larvae (Callan 1940).

Figure 121. ***Diplolepis rosae*** gall, a mimic of real mosses. Photo by Björn Appel, through Creative Commons.

Diprionidae – Conifer Sawflies

Jarmo Holopainen (pers. comm. 16 September 2011) found that in experiments pupae of pine sawflies (***Neodiprion sertifer*** – **Diprionidae**; Figure 122-Figure 125) had a higher emergence rate when kept in ***Sphagnum*** peat. He suggested that the antibiotic properties of peat helped to increase wasp survivorship.

Figure 122. ***Neodiprion sertifer*** female and male adults, a species that has a higher emergence rate when kept among ***Sphagnum***. Photo by Jarmo Holopainen, with permission.

Figure 123. ***Neodiprion sertifer*** larva and eggs, a species that survives better when cultured in ***Sphagnum***. Photo by Jarmo Holopainen, with permission.

Figure 124. ***Neodiprion sertifer*** larvae, a species that survives better when cultured in ***Sphagnum***. Photo by Jarmo Holopainen, with permission.

Ichneumonidae

Among the **Ichneumonidae**, twelve genera are able to overwinter as adults (Duffield & Nordin 1970). These take advantage of the insulating properties of logs, rocks, and mosses to endure the extreme conditions of winter. Those that overwinter accumulate glycerol and sorbitol when subjected to cold temperatures of winter. Dana <Abundantnature.com> tells of lifting a clump of moss from a rock and discovering not one, but two, species of ***Ichneumon*** hibernating there as adults (Figure 126-Figure 128).

Figure 125. ***Neodiprion sertifer*** pupa, a species that has higher emergence rates when cultured in ***Sphagnum***. Photo by Jarmo Holopainen, with permission.

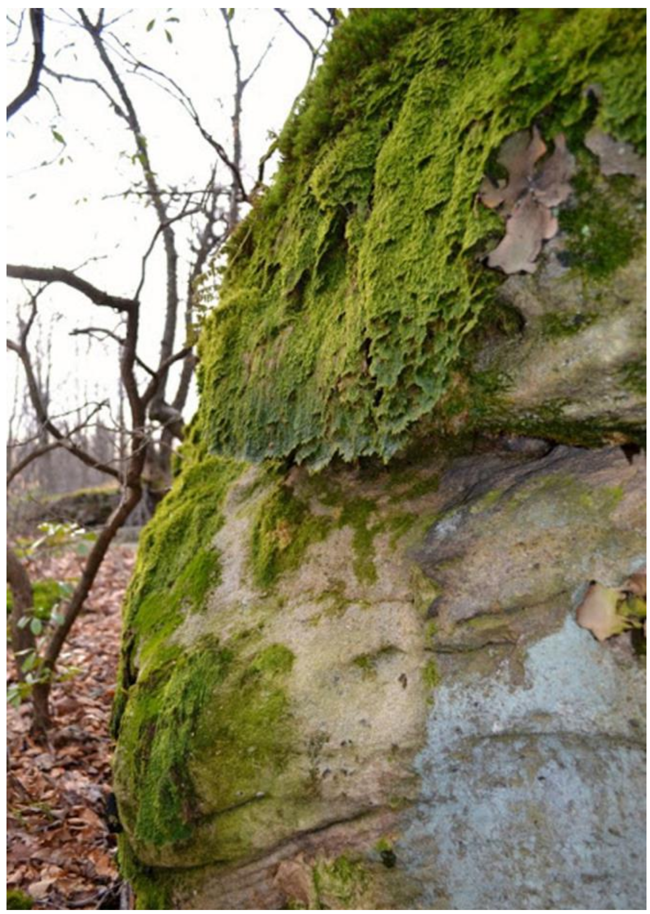

Figure 126. Habitat of ***Ichneumon*** *cf* ***mendax*** hibernating adults. Photo by Dana <Abundantnature.com>, with permission.

Figure 127. ***Ichneumon*** *cf* ***mendax*** and a second species, hibernating adults under mosses. Photo by Dana <Abundantnature.com>, with permission.

Figure 128. ***Ichneumon*** *cf* ***mendax*** hibernating adult that has been disturbed. Photo by Dana <Abundantnature.com>, with permission.

Lungu-Constantineanu and Constantineau (2014) found the importance of mosses as hibernation sites for at least 10 species of **Ichneumonidae** in the Bârnova Forest Massif, Romania. They found six types of hibernation sites, two of which required mosses. Ten of these sites were between the cracks of bark covered by moss. Others were in dense carpets of mosses on stones. They found that pollution reduced the moss cover, resulting in the disappearance of large ichneumonid clumps with dozens of hibernating individuals. Instead, the hibernating ichneumonids were mostly isolated individuals. The mosses that contributed to the large number of habitats for ichneumonid hibernation between cracks of bark of old but living trees were ***Anomodon attenuatus*** (Figure 130-Figure 131), ***A. viticulosus*** (Figure 132-Figure 133), ***Brachythecium salebrosum*** (Figure 134), ***Hypnum cupressiforme*** (Figure 44), ***Platygyrium repens*** (Figure 135), and ***Porella platyphylla*** (Figure 136). These ichneumonids under mosses in the cracks in tree bark were ***Apaeleticus mesostictus***, ***Deloglyptus pictus***, ***Diadromus troglodites*** (Figure 137), ***Herpestomus brunnicornis*** (Figure 138), ***Heterischnus truncator***, (Figure 139), ***Ichneumon balteatus*** (Figure 140), ***Ichneumon simulans*** (Figure 141), ***Rhadinodonta flaviger*** (Figure 142), and ***Tycherus cephalotes*** (=***Phaeogenes cephalotes***). Only one species of ichneumonid (***Cinxaelotus erythrogaster***) hibernated on the rocks, where ***Mnium stellare*** (Figure 143) covered them.

Figure 129. ***Ichneumon stramentor*** adult on moss, a species that hibernates as an adult under mosses. Photo by Ladislav Tábi, with permission.

Figure 130. ***Anomodon attenuatus*** on tree base, covering cracks in the bark where ichneumonid adults overwinter. Photo by Bob Klips, with permission.

Figure 131. ***Anomodon attenuatus***, a moss that provides insulation for ichneumonids overwintering in cracks and under bark. Photo by Michael Lüth, with permission.

Figure 132. ***Anomodon viticulosus*** covering cracks in bark where ichneumonids overwinter. Photo by Michael Lüth, with permission.

Figure 133. ***Anomodon viticulosus***, overwintering home for adult ichneumonids in cracks in bark. Photo by Michael Lüth, with permission.

Figure 134. ***Brachythecium salebrosum*** covering broken bark where ichneumonids overwinter. Photo by Michael Lüth, with permission.

Figure 135. ***Platygyrium repens*** on bark, covering cracks where ichneumonid adults overwinter. Photo by Dick Haaksma, with permission.

Figure 136. ***Porella platyphylla*** on bark, overwintering home for adult ichneumonids in cracks in bark. Photo by Michael Lüth, with permission.

Figure 137. ***Diadromus troglodytes*** adult, a species that hibernates in cracks in bark under mosses. Photo by James K. Lindsey, with permission.

Figure 138. ***Herpestomus brunnicornis*** adult, a species that hibernates in cracks in bark under mosses. Photo by Marko Mutanen, through Creative Commons.

Figure 139. ***Heterischnus truncator*** adult, a species that lives in cracks in tree bark under mosses. Photo by Jonas Lutz, through Creative Commons.

Figure 140. ***Ichneumon balteatus*** adult, a species that hibernates in cracks in bark under mosses. Photo by Stefan Schmidt, through Creative Commons.

Figure 141. ***Ichneumon simulans*** adult, a species that hibernates under mosses in cracks in bark. Photo by James K. Lindsey, with permission.

Figure 142. ***Rhadinodonta flaviger*** adult, a species that hibernates in cracks in bark under mosses. Photo by Stefan Schmidt, through Creative Commons.

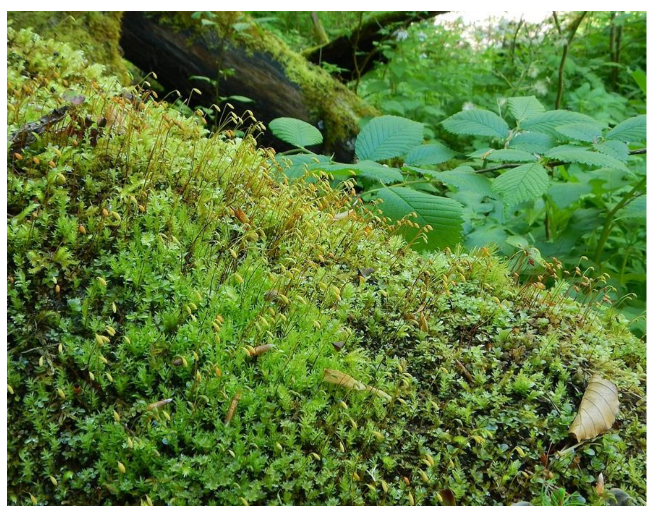

Figure 143. ***Mnium stellare*** on rock outcrop, providing an overwintering habitat for ***Cinxaelotus erythrogaster***. Photo by Michael Lüth, with permission.

But overwintering is not the only use they make of mosses. Sarah Lloyd caught one in the act of ovipositing among mosses (Figure 144).

Figure 144. Ichneumonid wasp ovipositing on moss. Photo courtesy of Sarah Lloyd.

Pompilidae

Bees and wasps do not seem to be usual active inhabitants of bryophytes, but the rare spider wasp, ***Anoplius caviventris*** (**Pompilidae**; Figure 145) in Sweden lives in a ***Sphagnum*** habitat (Berglind 1993). In Sweden, this species was found in 1991 and 1993 in a reed swamp (*Phragmites communis*) where it was living on mosses, primarily ***Sphagnum*** in three different mires.

Figure 145. ***Anoplius caviventris*** adult, a ***Sphagnum*** dweller in Sweden. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Scelionidae

It appears that among the **Hymenoptera**, the ants are the only ones with well-developed relationships in peatlands. However, Austin (1988) did find a new genus of wasps in the **Scelionidae** to be associated with mosses in New Zealand. Austin (1988) described this new genus, based on ***Neobaeus novazealandensis***. Austin found that collection data indicate this species lives on moss-covered ground, with 80% of the specimens collected by putting mosses in Berlese funnels. This species differs from ***Baeus*** in having a micropterous (short-winged) male. Austin suggested that wings would hinder movement in this mossy habitat.

Sphecidae

O'Brien (1987) observed ***Tachysphex aethiops*** (**Sphecidae**; Figure 146) digging at the bases of clumps of moss on sand. They inspected the burrow entrances throughout the day at various times. Females of this species typically nest in mossy sand slopes where they use pre-existing burrows made by other kinds of insects. One female intermittently removed sand from a burrow, raking the sand onto the nest mound after carrying several loads out of the nest.

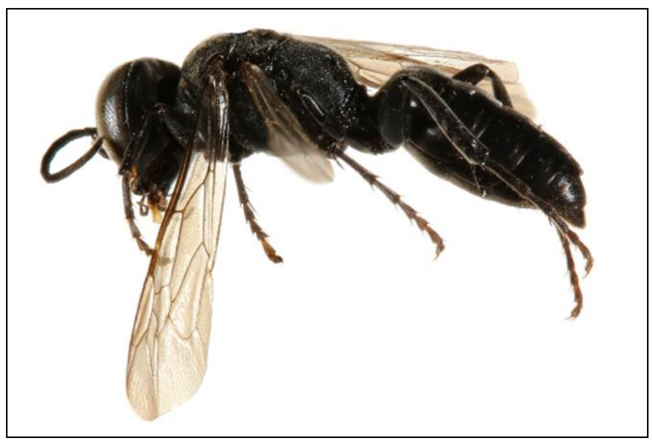

Figure 146. ***Tachysphex aethiops*** adult, a species that nests in mossy sand slopes. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Vespidae – Wasps

The yellow jackets [***Vespula*** (Figure 147) and ***Dolichovespula*** (Figure 148); **Vespidae**] are best known for their papery aerial nests (Figure 149). But they also can inhabit mosses such as ***Polytrichum*** (Figure 28-Figure 29) with at least 15-20 cm of soil attached, where they constantly go in and out (Annie Martin, pers. comm. 6 October 2013).

Figure 147. ***Vespula germanica*** worker, a species that sometimes lives under mosses. Photo by James K. Lindsey, with permission.

Figure 148. ***Dolichovespula arenaria*** adult, member of a genus that sometimes lives under mosses. Photo by Gilles Gonthie,r through Creative Commons.

Figure 149. ***Vespula vulgaris*** nest showing the interior intricacies of this papery nest. Photo by Richerman, through Creative Commons.

A Calyptra Mimic

This story lacks a critical detail – the name of the wasp. But it is too interesting to omit, and perhaps someone can shed light on the wasp involved.

Györffy (1952) tells of checking out the twin capsules on the seta of ***Polytrichum strictum*** (Figure 150). Upon closer examination, he found that these were not Siamese twins, but rather a capsule with its calyptra and a wasp cocoon, both perched on a single seta. In one of his favorite haunts in Austria, Györffy had seen these "twin capsules" among the "billions" of plants of this moss species in the harvested peat bogs. In this exploration, what he found was that the second twin was a lemon yellow cocoon closely adjacent to the calyptra, and from these cocoons deep black larvae hatched. Mimicry of a calyptra by Hymenoptera – or any other invertebrate – seems to be reported only here. Györffy concluded that such mimicry protected the larvae from cocoon-eating birds as they would prefer to do their "gymnastics" on tree branches.

Figure 150. ***Polytrichum strictum*** capsules with calyptrae – a structure mimicked by the egg cocoon of a wasp. The insect shown here appears to be an orthopteran – also somewhat resembling the covered capsules. Photo by Michael Lüth, with permission.

Summary

Ants have flexible bodies that permit the to maneuver among the bryophytes. The ants are able to chew and move the bryophytes, permitting them to build trails through the bryophytes, making their foraging easier. They defend themselves with strong mandibles, stings, and chemical sprays. They keep their nests clean. Some remove the tracheophytes around their nests, thus creating space where bryophytes can grow.

Bryophytes provide insulation that maintains a buffered temperature and moisture. For some ants such as ***Messor***, bryophytes also provide food, especially the capsules, but some are also known to eat the leafy plants. bryophytes also provide a suitable habitat for some of their predators such as salamanders. Even bears may forage in the bryophytes for ants. As the ants move about, spores, fragments, and gemmae may be trapped between the body hairs and get transported to a new location.

Some bryophytes are prone to growing on ant hills, possibly taking advantage of the higher concentration of nutrients or being raised above the forest floor where

they can avoid burial by leaf litter. They also avoid competition. Some take advantage of the north-facing slope to reduce desiccation.

A number of ant species use bryophytes in building nests. ***Sphagnum*** in particular is used, in some cases to make a nest for aphids that provide honeydew for the ants. Ants may be responsible for the hummocks in some peatlands. Some ants create arboreal gardens, using mosses and planting seeds among them. Others place seeds under mosses on the ground, providing them with a suitable protected germination site.

Bryophytes in the environment provide sites for finding drops of water and seeking cover. Others use them for finding food or laying eggs. Epiphylls on leaves, especially in tropical forests, may produce compounds that discourage herbivory on the leaves.

Honeybees appear to use bryophytes for obtaining water from that resting on the bryophytes. Beekeepers often place bryophytes near hives to provide watering sites, but species such as ***Pohlia*** spp. may attract more bees by reflecting UV light.

Bumblebees use bryophytes in their nests. Some species overwinter under the bryophytes. Carder bees build elaborate nests, partly above ground, lined with bryophytes.

Some species of the parasitic wasps in **Braconidae** are consistently associated with mosses because their lepidopteran hosts live there. One member of the **Cynipidae** mimics mosses with the galls it makes. For some **Hymenoptera**, the peat helps survival, possibly through antibiotic properties. A number of **Ichneumonidae** overwinter in and under mosses and some may oviposit there. Some members of **Pompilidae** live in ***Sphagnum*** habitats. The scelionid ***Neobaeus novazealandensis*** lives on moss-covered ground. Even the wasps sometimes nest under mosses such as ***Polytrichum***.

Acknowledgments

Christian Berg helped me obtain permission to use the photograph of *Formica uralensis*. Des Callaghan and Pekka Puntilla provided me with the lead image for the chapter and the story of the *Formica* ants that make the mounds. Thank you to Robin Stevenson for sharing his story about ants and *Sphagnum* on pine and birch saplings. Sunil Chaturvedi shared his story about bees visiting mosses and provided me with photographs. I am most grateful to Gerhard Winter for translating the article by ván Györffy on calyptra mimicking wasp cocoons. Thank you to Annie Martin for helping me get a picture of a honey bee on a moss and to Paul Moore for providing it. Thank you to José L. Fernández-Triana for pointing out an error and checking my presentation of his work on *Shireplitis* and *Paroplitis*.

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