

CHAPTER 4-11

ADAPTIVE STRATEGIES: VEGETATIVE DISPERSAL VECTORS

TABLE OF CONTENTS

Dispersal.....	4-11-2
Gravity	4-11-3
Wind Dispersal.....	4-11-3
Water Dispersal.....	4-11-4
Splash Cups.....	4-11-9
Animal Dispersal.....	4-11-10
Earthworms	4-11-10
Arthropods	4-11-12
Isopods.....	4-11-12
Mites	4-11-13
Insects	4-11-13
Weevil Gardens	4-11-14
Ants.....	4-11-14
Molluscs.....	4-11-15
Amphibians	4-11-16
Turtles	4-11-18
Birds.....	4-11-19
Mammals	4-11-23
Rodents	4-11-24
Flying Fox.....	4-11-27
Lessons from a Dog	4-11-28
Hoofed Mammals	4-11-30
Bears	4-11-34
Human Dispersal.....	4-11-34
Mystery Dispersal	4-11-38
Invasive Species	4-11-38
Summary	4-11-39
Acknowledgments.....	4-11-39
Literature Cited	4-11-39

CHAPTER 4-11

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Figure 1. *Pohlia annotina* with bulbils in leaf axils. Many species survive on dispersal of vegetative propagules. Photo by Dick Haaksma, with permission.

Dispersal

Laaka-Lindberg *et al.* (2003) stated that dispersal pattern of vegetative propagules (*e.g.* Figure 1) is affected both by the microtopography of the habitat (Kimmerer & Young 1996) and by the type and size of propagule (Söderström & Herben 1997). Kimmerer (1994) further demonstrated that two log-dwelling species [*Orthodicranum flagellare* (Figure 2) and *Tetraphis pellucida* (Figure 35)] differed in the dispersal ability of their propagules.

Conditions upon arrival can play a role in which species can become established following dispersal. Gradstein (2006) demonstrated this with the lowland cloud forest of French Guiana. Vegetative propagules there are protected from desiccation by the daytime fog, permitting good photosynthesis despite high temperatures. Asexual reproduction is significantly more common in the understory than in the canopy despite the greater

constraints on dispersability in the understory. The canopy seems to experience better dispersal by spores.



Figure 2. *Orthodicranum flagellare* with broken brood branches lying on top of the cushion. Most likely some of these have travelled with an animal that broke them off. Photo by Janice Glime.

Gravity

Whereas spores are light weight and therefore easily lofted away on a slight air current, vegetative structures are often much more bulky and heavy. Shed parts, unless caught in a gust that can even blow heavy maple fruits up into the air, are likely simply to fall to the ground. This seems to be a common means for structures like gemmae, deciduous perianths, and other bulky forms of brood bodies and fragments.

"Galloping mosses" have an intriguing movement, leaving behind a trail of changed rock (Figure 3). The actual method of movement and time required is unknown, but they seem to move rather slowly, staying long enough in one place to chemically change the surface of the rock. Hence, it appears that gravity plays at least a partial role, but water most likely also helps in the movement. Mosquin (2011) reported these slowly moving mosses from the Arctic, where the mosses *Sphagnum* and *Grimmia ovalis* (Figure 3), and *Racomitrium ericoides* (Figure 4) are known for this behavior. When they reach a crack, they may be stopped and remain there (Figure 5).



Figure 3. *Grimmia ovalis* "galloping." Photo by Wouter Bleeker, with permission.

Wind Dispersal

Imagine being a small fragment of a leaf or stem being blown by the wind. Lacking the protection of surrounding plants, desiccation is imminent. Bouncing on the ground or off trees or rocks could impose a significant blow to tissues that may be only one cell thick. Exposure to UV radiation is likely to be greater than in their normal niche. Nevertheless, using a weather balloon Studlar *et al.* (2007) showed that at least some species [*Sphagnum fallax* (Figure 6), *S. magellanicum* (Figure 7), *Atrichum angustatum* (Figure 8)] can survive these conditions and regenerate from fragments.



Figure 4. *Racomitrium ericoides*, a moss that contributes to galloping mosses. Photo by Janice Glime



Figure 5. *Grimmia ovalis* trapped by cracks, with two clumps that managed to break loose, perhaps because of their larger size. Photo by Wouter Bleeker, with permission.



Figure 6. *Sphagnum fallax*, a species that seems capable of surviving wind dispersal. Photo by Michael Lüth, with permission.



Figure 7. *Sphagnum magellanicum*, a species that can regenerate from windborne leaf fragments. Photo by Michael Lüth, with permission.



Figure 8. *Atrichum angustatum*, a species that regenerates from leaf fragments. Photo by Bob Klips, with permission.

This demonstration gives credence to a number of studies that have inferred vegetative dispersal of bryophytes. And we have already seen viability in 12% of the fragments blown about on the snow in Canada by wind (Miller & Howe Ambrose 1976).

In the Antarctic, Skotnicki *et al.* (2000) found evidence of propagule dispersal from elsewhere, with the RAPD technique indicating short-distance dispersal by both wind and water and long-distance dispersal by wind across the ice caps. The genetic similarities of *Chorisodontium aciphyllum* (as *Sarconeurum glaciale*; Figure 9) from three locations on Ross Island, Antarctica, with those of Arrival Heights, Scott Base, and Crater Hill, a few km away suggest wind dispersal, a concept supported by the prevailing wind direction and absence of the species in areas in between.

Des Callaghan (Bryonet 11 May 2019) demonstrated the wind dispersal of *Plagiochila exigua* (Figure 10) in Britain. This rare oceanic plant produces only males, making spore dispersal impossible. But it has **caducous** (deciduous) leaves that are easily dispersed in the wind (Figure 11; see <<https://youtu.be/YCHhANT0dUM>>).



Figure 9. *Chorisodontium aciphyllum*, an Antarctic moss that is apparently dispersed by both wind and water. Photo by Jan-Peter Frahm, with permission.



Figure 10. *Plagiochila exigua* showing missing caducous leaves at right. Photo by Michael Luth, with permission.



Figure 11. *Plagiochila exigua* dispersing leaves. Photo by Des Callaghan, with permission.

Water Dispersal

Water aids in the dispersal of bryophytes in multiple ways. Aquatic mosses most likely depend primarily on water dispersal. Sexual organs can easily be damaged by abrasives in the water, as for example those in *Platyhypnidium riparioides* (Figure 12; Lewis 1973). These same abrasives can free leaves and branches that are possibly able to lodge on a substrate and regenerate. Conboy and Glime (1971) found similar abrasion in stream populations of *Fontinalis novae-angliae* (Figure 13).



Figure 12. *Platyhypnidium riparioides* in Europe, showing darkened and scoured leaves on lower parts of stems. Photo by Michael Lüth, with permission.



Figure 13. *Fontinalis novae-angliae* scoured by stream flow and suspended particles. Photo by Janice Glime.

Fontinalis species in streams are faced first with the problem of producing few sporophytes (Sayre 1945; pers. obs.), then of having spores lodge in a suitable place to stay put and begin new growth, whereas branches can easily get caught against rocks or snagged by submerged branches and roots, giving them an opportunity for new establishment (Figure 14; Sayre 1945; Welch 1948; Glime *et al.* 1979). Once these fragments get lodged against a rock or other suitable substrate, the contact stimulates the growth of rhizoids that eventually attach them to the substrate (Welch 1948; Glime *et al.* 1979; Figure 15-Figure 16). But this takes time, and experiments indicate that it requires at least nine weeks of impingement before the actual attachment (Figure 17; Glime *et al.* 1979). Temperature and flow rate influence the development of these rhizoids in *Fontinalis duriaei* (Figure 18) and *Hygroamblystegium fluviatile* (Figure 19), with flowing water conditions causing the mosses to produce more rhizoids than pool conditions (Glime 1980).



Figure 14. *Fontinalis novae-angliae* becoming established from a rhizome fragment in Fox Run, Grafton County, NH, USA. Photo by Janice Glime.



Figure 15. Rhizoids developing from stem wound tissue of *Fontinalis squamosa*. Note the spiral growth. These have not yet contacted a substrate. Photo by Janice Glime.

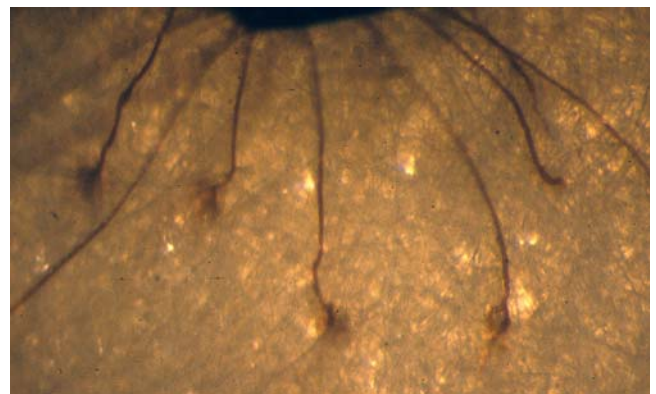


Figure 16. Rhizoids from wounded stem tissue of *Fontinalis squamosa*, showing the branched growth at their tips where they have contacted a substrate. In this case, the substrate is filter paper in contact with a glass test tube. Photo by Janice Glime.

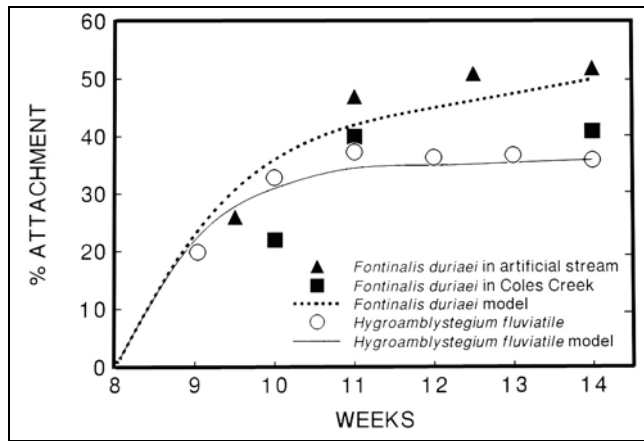


Figure 17. Comparison of times required and percentage of attachment for *Fontinalis duriaei* and *Hygroamblystegium fluviatile* in contact with rocks in an artificial stream (n=48) compared to rocks placed in Coles Creek, MI, with *F. duriaei* held in contact with netting. Based on Glime *et al.* 1979.

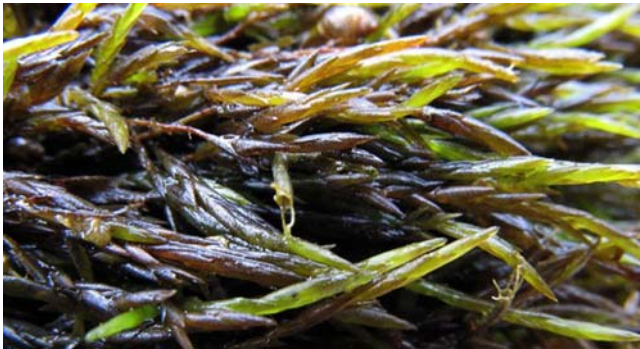


Figure 18. *Fontinalis duriaei* in Europe. Photo by Jan-Peter Frahm, with permission.



Figure 19. *Hygroamblystegium fluviatile* fragment in culture, showing dense rhizoids that formed, possibly in response to the substrate. Photo by Janice Glime.

In these early experiments, the moss fragments were held against the rocks with netting (Glime *et al.* 1979). But the field application of this concept was then tested by tagging 750 stems of *Fontinalis duriaei* (Figure 18) growing in Big Valley Creek, a forested stream in the Keweenaw Peninsula, Michigan, USA (Glime *et al.* 1979). Within the two years following tagging, many mosses could not be found again. But the proof of dispersal lies in two tagged mosses that were found in a different location. One of these was relocated downstream 60 weeks after the tagging date. The second was found nearly 100 m upstream! Possible upstream dispersal agents were fishermen and the black bear (*Ursus americanus*; Figure 20) that chased my graduate student; there was no evidence of beaver activity. And this moss was found attached in its new location only 9 weeks after it was tagged. In both cases, the mosses were attached by rhizoids and were

wrapped around fallen tree branches where they most likely were held in place by the flow of water. Several other fragments were found in new locations, but these lacked rhizoid attachments.



Figure 20. *Ursus americanus* catching salmon in Alaska stream. Dark patches of mosses can be seen by its feet, suggesting an opportunity for dispersal. Photo by J. Brew, through Creative Commons.

In experiments with *Fontinalis*, I have observed that stems with broken tips will often produce protonemata or several apical branches (Figure 21-Figure 22).



Figure 21. *Fontinalis hypnoides* broken shoot apex producing protonemata. Photo by Janice Glime.



Figure 22. *Fontinalis antipyretica* apical wound with new growth and rhizoids. Photo by Janice Glime.

In the winter, aquatic mosses can get frozen in the ice (Figure 23). When the ice breaks up, chunks may carry a number of fragments downstream where some may become impinged on suitable substrata.



Figure 23. Fragments of *Fontinalis dalecarlica* frozen in ice that has broken up in a New Hampshire, USA, headwater stream. Photo by Janice Glime.

Sayre (1945) demonstrated that connections of waterways could account for the dispersal of *Fontinalis* in a series of moraine ponds. Using Polymerase Chain Reaction (PCR) and involved amplification of DNA sequence with several ISSR primers, Korpelainen *et al.* (2004; 2013) found little variation in several bryophytes between lakes and concluded that *Fontinalis antipyretica* (Figure 22), *F. hypnoides* (Figure 21), and *Calliergon megalophyllum* (Figure 24) were dispersed by water between the lakes. This can occur by streams connecting lakes or by flooding that connects them. They did not rule out waterfowl, but found that the direction of flow and genetic patterns indicated that stream flow was a major contributor to the dispersal.



Figure 24. *Calliergon megalophyllum*, a species that is likely to be dispersed by water. Photo by Julita Kluša <daba.dziedava.lv>, with online permission.

Arts (1982) used circumstantial evidence to show that *Fissidens fontanus* (Figure 25-Figure 26) is dispersed by water. All the canals where he found them in Belgium and the Netherlands were fed by water from Maas and this source apparently dispersed them through the Albert Kanaal and the Zuid-Willemsvaart.



Figure 25. Canal with *Fissidens fontanus* growing on concrete (arrow). Photo by Michael Lüth, with permission.



Figure 26. *Fissidens fontanus* frond. Photo by Michael Lüth, with permission.

Fragments may be the most important means of dispersal in many aquatic bryophytes. For submersed species that produce submersed capsules, capsules are relatively rare and it is likely that most spores never lodge on a suitable substrate. As a result, some of these species are somewhat rare. *Dichelyma capillaceum* (Figure 27) is one such rare species in Europe (Hylander 1998). Only two populations are known with sporophytes. In Sweden it occurs along rivers, streams, and lakeshores – only in places that are inundated and then exposed annually. Hylander suggested that it was probably dispersed by fragments and more rarely through long-distance dispersal of spores.



Figure 27. *Dichelyma capillaceum* on a tree base in Europe where it gets flooded. Photo by Michael Lüth, with permission.

Antarctic researchers have used the RAPD technique to track populations and determine their genetic relatedness. For example, Dale *et al.* (1999) found *Hennediella heimii* (Figure 28) in Miers Valley, Antarctica, along melt streams within the valley, constituting a single large population, whereas it was distinct from populations in nearby valleys. RAPD indicates that *Chorisodontium aciphyllum* (Figure 9; as *Sarconeureum glaciale*) from three locations on Ross Island, Antarctica, appear to all be from one population and differ genetically from populations elsewhere (Skotnicki *et al.* 1999a). Dispersal was apparently in small, meltwater drainage streams. *Bryum argenteum* (Figure 29), likewise, has apparently been transported in the Antarctic by water (Skotnicki *et al.* 1999b).



Figure 28. *Hennediella heimii* with capsules, a moss that gets transported by melt streams in the Antarctic. Photo by David T. Holyoak, with permission.



Figure 29. *Bryum argenteum*, a worldwide taxon that seems to be transported by water in the Antarctic. Photo by Dick Haaksma, with permission.

It appears that some species may respond adaptively to being submersed. *Leptobryum pyriforme* (Figure 30) produces rhizoidal gemmae (tubers; Figure 31) when the protonema grows in water (Schofield 1981), suggesting a possible secondary dispersal by water movement, or a way of surviving until the water recedes.



Figure 30. *Leptobryum pyriforme* with capsules. Michael Lüth, with permission.

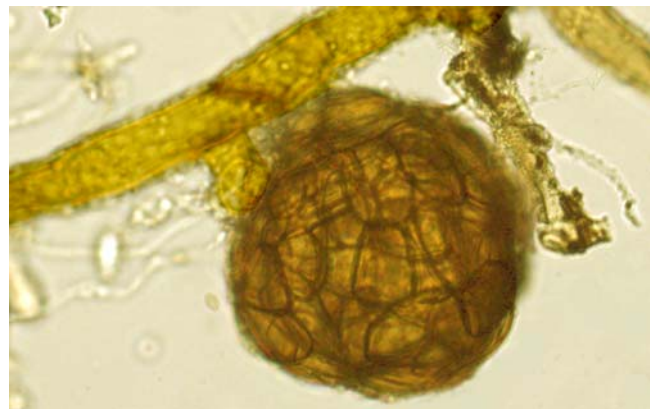


Figure 31. *Leptobryum pyriforme* rhizoidal tuber. Photo by Victoria Rozhina.

Water dispersal is a likely avenue for aquatic thallose liverworts. Patidar *et al.* (1986) studied effects of stream velocity on the floating liverwort *Riccia fluitans* (Figure 33-Figure 32). They found that a decrease in number of sporophytes was related to increase in water velocity, a likely consequence of reduced fertilization. Nevertheless, increased vegetative dispersal is likely in this species.

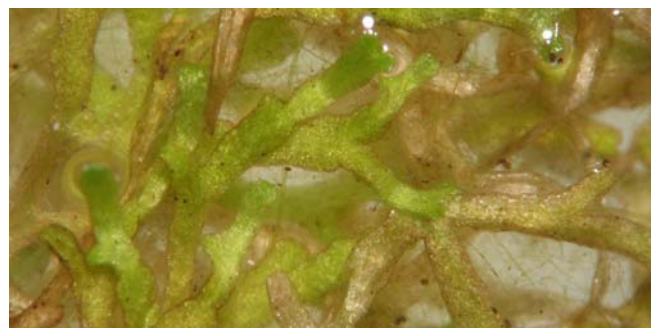


Figure 32. *Riccia fluitans* showing dead portions that will decay and break the clone apart. Photo by Kristian Peters, with permission.



Figure 33. *Riccia fluitans* stranded above water where it is also able to grow. Note the piece dangling from the colony at the bottom of the picture. This ramet can easily break away. Photo by Ralf Wagner at <<http://www.dr-ralf-wagner.de/>>, with permission.

Splash Cups

Water dispersal is not confined to plants living in or near water. Some bryophytes take advantage of splashing raindrops for their dispersal, providing cups or platforms from which asexual propagules can be splashed. The best-known method of dispersal is that of the **gemma cup** or **splash cup**, commonly taught in introductory botany courses. Although the splash cup and splash platform are somewhat frequent as a means of dispersing sperm, they are relatively rare as mechanisms of propagule dispersal. Several bryophytes have specialized cups where the gemmae are produced and from which they are subsequently dispersed by raindrops (Figure 34, Figure 35). The splash cup mechanism seems to be engineered to maximize the distance its contents can splash, thus forming an effective dispersal mechanism with the help of raindrops. The significance of its size and shape was apparently not recognized until Buller (1942) described its function in the bird's nest fungus, *Cyathus*. Brodie (1951) followed up on the observations of Buller and noted that splash cups commonly form 60-70° angles with the horizontal surface, the cups have a broad basal attachment, and the dispersed objects are lenticular. Gemmae of *Marchantia polymorpha* (Figure 34) can travel up to 120 cm when splashed from these cups, and Equihua (1987) suggests that this mechanism partly accounts for the worldwide distribution of this species. This ability to splash with water drops has made the species one of disdain for greenhouse owners who constantly find it invading their pots, spreading farther and farther from the original source through successive generations.

Gemmae in the splash cups of the moss *Tetraphis pellucida* (Figure 35) and the liverworts *Lunularia cruciata* (Figure 36-Figure 37) and *Marchantia polymorpha* (Figure 34) are lenticular. It seems to be a common feature for the splashing to carry the contents about 60 cm in *L. cruciata* and *M. polymorpha* (Brodie 1951), but in *T. pellucida*, they seem only to go about 10 cm (Kimmerer 1991). Brodie (1951) considered *T.*

pellucida too frail to benefit from raindrops striking its apex, finding that the plants bent under the weight.

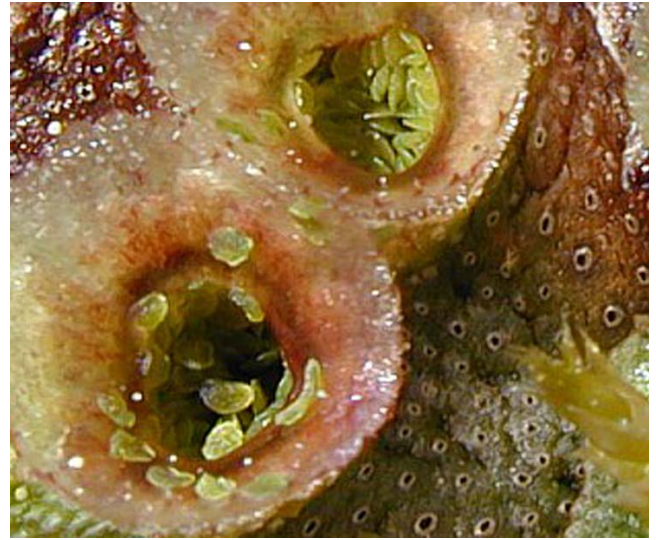


Figure 34. Lens-shaped gemmae of *Marchantia polymorpha*. Photo by Michael Lüth, with permission.



Figure 35. Gemma cups of the moss *Tetraphis pellucida*. Photo by Michael Lüth, with permission.



Figure 36. Gemmae in half-moon-shaped pouches of *Lunularia cruciata*. Photo by David T. Holyoak, with permission.



Figure 37. Pouch of *Lunularia cruciata* showing lenticular gemmae. Photo by Martin Hutten, with permission.

Stieha *et al.* (in prep.) quantified the production and dispersal of gemmae in the clonal thallose liverwort *Marchantia inflexa* (Figure 38). They found that these asexual propagules could move great distances during even a light rain, with some most likely leaving the parent clonal population. Further dispersal can occur in a stair-step fashion over time, providing long-distance dispersal. In this species, survival of female gemmae is greater than that of male gemmae.



Figure 38. *Marchantia inflexa*. Photo by Scott Zona, through Wikimedia Commons.

Animal Dispersal

The dispersal of vegetative parts by animals may be an important mode of travel, at least occasionally. Various insects use fragments of mosses and lichens to build "houses" that they carry on their backs.

Even mammals may eat (perhaps not intentionally) bryophytes, as indicated by ^{14}C studies on animal remains of late Pleistocene large herbivorous mammals (Ukrainseva 1979). But we have no evidence that these bryophyte fragments remain viable after passing through the mammalian digestive tract.

Earthworms

Dispersal in the guts of earthworms (During *et al.* 1987; van Tooren & During 1988) can surely at times beat the 10 cm record for splashing in *Tetraphis pellucida*

(Figure 35) reported by Kimmerer (1991); these and other invertebrates that eat bryophytes will deposit fragments in new locations. These could be distances of centimeters to hundreds of meters. Not only earthworms, but moles, voles, and ants have underground activities that can bring diaspores from their dormant state below ground to a position of activity above ground. Van Tooren and During (1988) found that eight species of bryophytes from the Netherlands appeared frequently in castings (Figure 39) from the earthworms *Allolobophora caliginosa*, *A. chlorotica* (Figure 40), and *Lumbricus terrestris* (Figure 41).



Figure 39. Earthworm castings on moss. Photo by Ken Gergle at Moss and Stone Gardens, with permission.



Figure 40. *Allolobophora chlorotica*, an earthworm that can transport bryophytes in its feces. Photo by Jacopo Werther, through Wikimedia Commons.



Figure 41. *Lumbricus terrestris* on mosses, a species known to ingest mosses and re-deposit them, still viable, in their feces. Photo by Michael Linnenbach, through GNU Free Documentation.

Since the light travels at most only a few centimeters into the soil, these diaspores remain dormant until some disturbance brings them to the surface and light. The species that survived the enzymes, crushing, and scarification of the earthworm guts, then grew to be identified, were *Bryum klinggraeffii* (Figure 42), *Dicranella schreberiana* (Figure 43), *Ephemerum recurvifolium* (Figure 44), *Pottia* spp., *Pottia lanceolata* (Figure 45), and *Weissia* spp. (Figure 46) (van Tooren & During 1988). *Bryum rubens* (Figure 47), common in the castings, never produces capsules in the area and presumably survived as rhizoidal tubers. Most of the other taxa probably also survived as vegetative diaspores except for *Pottia* sp. and *Weissia* sp., which probably originated from spores. Among these, tubers of *Bryum klinggraeffii* (Figure 42), *Bryum rubens* (Figure 47), and *Dicranella schreberiana* (Figure 43) successfully germinated, but in general, there was high mortality among tubers and other vegetative structures. Van Tooren and During suggested that spore survival was higher than vegetative diaspore survival in earthworm guts, but they did not have quantitative measures of this.



Figure 44. *Ephemerum recurvifolium*, a species whose vegetative diaspores survive earthworm guts. Photo by Tomas Hallingbäck, with permission.



Figure 42. *Bryum klinggraeffii*, a species that survives earthworm guts. Photo by Des Callaghan, with permission.



Figure 45. *Pottia lanceolata*, a species that survives earthworm gut, probably as vegetative diaspores. Photo by Michael Lüth, with permission.



Figure 43. *Dicranella schreberiana*, a species dispersed in earthworm castings in Europe. Photo by Michael Lüth, with permission.



Figure 46. *Weissia fallax*, member of a genus known from earthworm castings in Europe. Photo by Michael Lüth, with permission.



Figure 47. *Bryum rubens* showing rhizoidal tubers, a possible means of surviving earthworm guts. Photo by Jan-Peter Frahm, with permission.

Arthropods

Isopods

I suspect that isopods (pillbugs, sowbugs, wood lice, roly pollies) play a greater role in bryophyte dynamics than we understand. They make good experimental animals, and in our experiments, we have learned that both aquatic and terrestrial isopods readily eat some bryophytes (Figure 48-Figure 52), but avoid others, depositing their feces elsewhere. Some fragments can break off during the feeding and others are likely to be broken by their movements. We have not, however, observed any fragments being carried on their bodies and viability of mosses in their feces needs to be tested.



Figure 48. *Porcellio scaber* (isopod) eating *Pleurozium schreberi*. Photo by John Hribljan, with permission.



Figure 49. *Porcellio scaber* escaping from *Rhytidiadelphus triquetrus* that has been disturbed. Photo by John Hribljan, with permission.

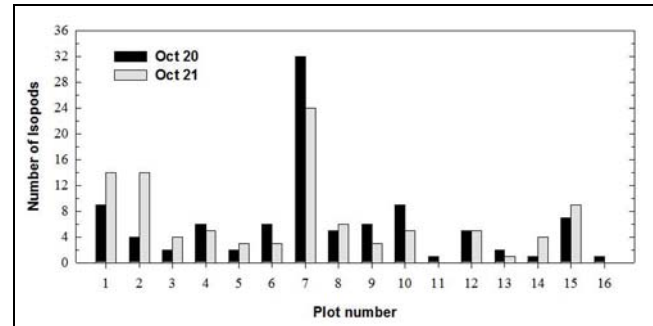


Figure 50. Comparison of abundance of *Porcellio scaber* in moss plots in the Keweenaw Peninsula of Michigan, USA, showing variability in numbers both spatially and daily. Graph by John Hribljan, with permission.



Figure 51. Evidence of eaten apical portions of *Pleurozium schreberi* by *Porcellio scaber*. Photo courtesy of John Hribljan.



Figure 52. Evidence that *Porcellio scaber* prefers leaves to stems in feeding experiments on *Rhytidiadelphus triquetrus*. Photo by John Hribljan, with permission.

Mites (Acari)

Edwards (1978) found protonemal gemmae of *Schistostega pennata* (Figure 53) attached to the legs of mites. The gemmae, like the spores of this species, are very sticky (Ignatov & Ignatova 2001). While mites themselves most likely do not travel far, they can become passengers on other animals – birds and mammals – that might travel considerable distances. Risse (1986, 1987) suggested that this might also be a possible vector for rhizoid tubers, presumably because the mites move about amid the spaces in the soil.

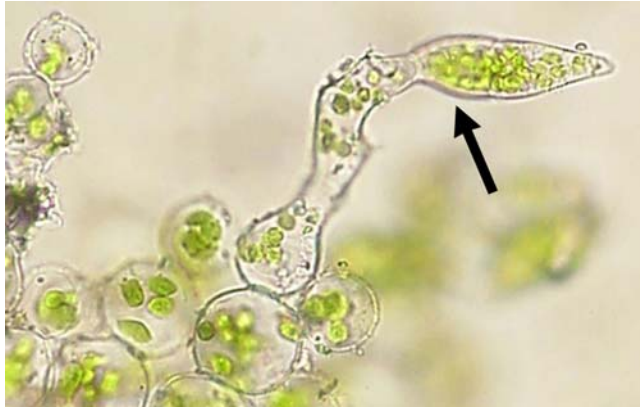


Figure 53. Protonemal gemma (arrow) of *Schistostega pennata*. Photo by Misha Ignatov, with permission.

Zhang *et al.* (2002) observed spider mites (*Halotydeus* sp.; Figure 54) eating the gemmae of *Octoblepharum albidum* (Figure 54) in Hong Kong. It is possible that some of these gemmae will get trapped among the hairs on the legs, thus getting transported by the mite. Others might be knocked off, falling to a new substrate.



Figure 54. *Halotydeus* sp. feeding on gemmae of *Octoblepharum albidum* in Hong Kong. Arrow indicates bases remaining where gemmae have been chewed. Photo by Li Zhang from Zhang *et al.* 2002, with permission.

Harvestmen

Some arthropods have an unusual mode of transporting bryophytes – they grow them on their bodies. These include liverworts on Neotropical harvestmen (Machado & Vital 2001).

Insects

Insects are often responsible for releasing small fragments of bryophytes (Lepp 2008). Larger insects can break dry bryophytes due to the insect weight, and a number of insects actually eat the bryophytes. Some live among the cushions where they often find food and thus move around, potentially transporting the fragments from a cushion to an open space.

Slocum and Lawrey (1976) report that the green lacewing larva (*Nodita pavidata*) carries about a "packet" of camouflage constructed of bits of lichen, lichen soredia, pieces of bark, pollen grains, fungal spores, moss gametophyte fragments, and other debris. They demonstrated that the lichen fragments were viable but did not test the mosses. It is likely that they not only were alive, but that some of these fragments also would land somewhere and grow. Larvae of Diptera (flies, especially craneflies) and Trichoptera (caddisflies) construct houses of various shapes and may incorporate bryophyte fragments in them, as will be discussed later in the chapter on aquatic insects.

Aquatic organisms can be dispersed by aquatic insects that carry adhering cells on their bodies (Stewart & Schlichting 1965, 1966; Stewart *et al.* 1970), but their role in bryophyte dispersal is mostly unknown. For example, some caddisfly larvae may construct their homes from mosses, leafy liverworts, or narrow thallose liverworts like *Riccia fluitans* (Figure 33; Glime 1978). When these homes (cases) are discarded, the bryophytes can potentially grow in this new location.

Cairns and Wells (2008) reported that the microcaddisfly *Scelotrichia willcairnsi* (Figure 55) in Australia fed on the moss *Platyhypnidium muelleri* (Figure 56), an activity that could permit transport of fragments that survive travel through the gut. But in addition, and more likely to survive, are fragments that they weave into their case. The case travels with the caddisfly, which may travel considerable distance if it breaks loose from its substrate and becomes part of the drift.



Figure 55. The caddisfly *Scelotrichia willcairnsi* with *Platyhypnidium muelleri* case. Photo courtesy of Andi Cairns.



Figure 56. The moss *Platyhypnidium muelleri* with the caddisfly *Scelotrichia willcairnsi* showing numerous cases. Photo courtesy of Andi Cairns.

Weevil Gardens – A few insects disperse mosses in an unusual way. Certain weevils (Curculionidae) have pits on them where mosses are able to grow. This is the case for the moss *Daltonia angustifolia* (Figure 57) that attaches in pits on the hardened exoskeletons of weevils, including the weevil *Gymnopholus reticulatus* (Figure 57; Gradstein *et al.* 1984).

Gressitt and coworkers (1965, 1968) reported gardens on the backs of several species of weevils, including *Gymnopholus* spp. (Figure 57) among others. These weevils live in areas with moss cover on forest ridges and summits in eastern New Guinea (Gressitt *et al.* 1965, 1968). *Gymnopholus* species with epizotic bryophytes live more than three years and have hairs or specialized scales not present on species without plants growing on them (Gressitt & Sedlack 1970). In experiments where weevils were kept in cages, older weevils lost their plants, demonstrating the usefulness of these species as dispersal vectors. They are usually sedentary, but they can travel up to 0.25 km in half an hour by walking.



Figure 57. The moss *Daltonia angustifolia* living epizootically on the weevil *Gymnopholus reticulatus*. Photo courtesy of Rob Gradstein.

Ants – Rudolphi (2007) found that ants on stumps served as dispersal vectors, passively carrying the bryophyte dispersal units for a significant time. Rudolphi (2009) used experiments to demonstrate that the ant *Lasius platythorax* (Figure 58) may disperse the gemmae of *Aulacomnium androgynum* (Figure 59). Both the ants and the *A. androgynum* occur on dead wood in Sweden. When the ants were permitted to run over a moss tuft, gemmae adhered to 33% of the ants within only two minutes! Half the gemmae remained attached for about four hours. This is most likely passive dispersal, with no special adaptations by either organism. Since these are active organisms that can travel considerable distances quickly, this could be an important dispersal mechanism.



Figure 58. *Lasius platythorax*, an ant that disperses gemmae of *Aulacomnium androgynum*. Photo by April Nobile, through Creative Commons.



Figure 59. *Aulacomnium androgynum* gemmae, known to sometimes have dispersal by ants. Photo by Des Callaghan, with permission.

One interesting way that ants (*Formica rufa* group; Figure 60) contribute to dispersal is in their nest building. Heinken *et al.* (2007) sampled nesting material from 25 ant nest mounds in Germany. They found fragments of 20 bryophyte and 10 lichen species in these mounds. Among the bryophytes, wefts were particularly well represented, whereas tall turfs were poorly represented relative to their abundance. The researchers suggested that fragments lost along the way provided a means of dispersal. Other successful dispersal may occur among fragments in the

mound when the mound decays. Healthy mounds with live ants do not provide a safe site for the bryophytes. The ants are active in maintaining the mound and keep burying the fragments. Any that do manage to remain at the surface are subject to greater drying than those on the surrounding soil. In addition to these problems, disturbance by the ants, birds, and even boars further dislodges them, interrupting growth and detaching the fragments.



Figure 60. *Formica rufa*, an ant that disperses bryophytes through its nest building. Photo by Richard Bartz, through Creative Commons.

The most common species on these ant mounds were *Hypnum cupressiforme* s.l. (Figure 145) in 16 of the 25 samples (Heinken *et al.* 2007). These accounted for 67.5% of the fragments. In addition, *Brachythecium* spp. (Figure 144) and *Pleurozium schreberi* (Figure 61) were often abundant. Species differed by forest type. Five of the 20 bryophyte species rarely produce any spores or vegetative structures, making fragments important in their dispersal. The territory size for this species ranges 200-1500 m² and the travelling ranges extend 20-30 (65) m from the nest, making a reasonable dispersal distance.



Figure 61. *Pleurozium schreberi*, a moss known from ant mounds. Photo by Janice Glime.

Modern genetic techniques permit us to learn even more about insect roles. Korpelainen *et al.* (2011) studied *Barbilophozia attenuata* (Figure 62) in an area traversed by ant trails, using spatial genetic structure to unravel the history of the liverwort dispersal. They found significant kinship of colonies along the trails up to 8 m. At distances greater than 25 m, kinship correlation was nearly zero. Gemmae were most important up to 8 m, but spores were important for distances of 25 m or greater. Plants on logs

and other raised surfaces can achieve even greater distances by spores. They considered that the large gemmae permitted greater opportunity for establishment than the small sexual spores and gemmae account for the aggregated distribution of the species in the study area. They also concluded that gemmae are favored over spores in areas with frequent disturbance, such as ant trails. Nevertheless, at greater distances, spores become important.



Figure 62. *Barbilophozia attenuata* with apical gemmae. Photo by Michael Lüth, with permission.

Lepidoptera – Larvae of *Aenetus virescens* (Figure 63) feed on the leaves and rhizoids of both live and dead mosses and liverworts, among other things (Grehan 1984). These bryophytes have the potential of being dispersed in feces, but tests must be made to see if they survive the gut. It is also possible that fragments adhere to these larvae, thus being dispersed.



Figure 63. *Aenetus virescens* adult, looking perfectly suited to living among bryophytes, where it might complete its emergence, but it lives only 48 hours as an adult. Its larvae feed on bryophytes, among other things. Photo by Tony Wills, through Wikimedia Commons.

Molluscs

Mollusks such as slugs eat bryophytes, but their sticky surfaces also cause fragments to adhere, effecting their dispersal. The moss *Orthodicranum flagellare* (Figure 2) lives on logs and stumps where snails can readily gain

access and contribute to dispersal of the flagelliform branches that serve as propagules (Stolzenburg 1995). Kimmerer and Young (1995) found that this species depends on its asexual brood branches to colonize new logs, with slugs as their primary dispersal vector. In fact, the propagules adhere to the slime trails, with evidence that the slugs (*Philomycus* sp.; Figure 64) can transport them at least 23 cm. However, the distance is more commonly only about 3.7 cm. The slime helped the propagules adhere to the substrate without interfering with success of germination.



Figure 64. *Philomycus carolinianus* on a log, crawling over worms. Photo by Rebekah D. Wallace, through Creative Commons.

Aquatic molluscs also facilitate the dispersal of bryophytes. Both *Fissidens fontanus* (Figure 26) and *Leptodictyum riparium* (Figure 65) are known from the shells of mussels, a moving substrate that is likely to drop off fragments as it moves (Neumann & Vidrine 1978). Species of *Fissidens* are especially vulnerable to grazing by snails and slugs (Figure 66), so it is likely that fragments also get dispersed in the feces of the bodies of these molluscs.



Figure 65. *Leptodictyum riparium*, a moss that is known to grow on mussel shells. Photo by Michael Lüth, with permission.

Amphibians

Like slugs, most amphibians have moist, sticky skin (Evans & Brodie 1994). Therefore, it is likely that bryophyte fragments and propagules get broken off as they traverse the bryophytes and that many of these same fragments and propagules get transported to new locations. My own pet frog was usually covered by empty seed coats dropped by the finches that shared the room. Evans and

Brodie found moss fragments were among the debris they washed from amphibians at the beginning of their sampling. In their experiments, Evans and Brodie found that *Dyscophus antongilii* and *D. guineti* had the strongest glue among the eleven amphibians tested. D. Bruce Means has captured this adherence to *Ceuthomantis smaragdinus* in the image below (Figure 67).



Figure 66. *Fissidens* sp. being traversed by a slug. Photo by Janice Glime.

Figure 68 through Figure 73 demonstrate some of the variety of anurans that are able to carry bryophyte fragments. These six images were selected from my collection of 494 anuran images based on discernible adhering debris, giving a very crude estimate of the frequency of such passage. Figure 74-Figure 75 demonstrate that salamanders are also able to carry bryophytes that adhere to the sticky surface.



Figure 67. *Ceuthomantis smaragdinus* with several fragments of bryophytes adhering. Photo by D. Bruce Means, through public domain, USFWS.



Figure 68. *Trachycephalus resinifictrix* with debris attached to its breast. Photo by John White, with permission.



Figure 69. *Craugastor bransfordii* with an adhering bryophyte at the arrow. Photo by Jason Folt.



Figure 70. *Oophaga pumilio* on moss, with debris adhering to its skin. Photo by Brian Gratwicke, through Creative Commons.



Figure 71. *Rana arvalis* with a bryophyte fragment adhering to its leg. Photo by Petr Balej, with permission.



Figure 72. *Ascaphus truei* with an adhering moss fragment on its back. Photo by James Bettaso, USFWS, through public domain.



Figure 73. *Bufo bufo* with adhering plant material, demonstrating that even the dry skin of a toad can carry plant fragments. Photo by Karamel, through Wikimedia Commons.



Figure 74. *Hynobius tokyoensis* carrying a bryophyte fragment on its head. Photo ©Henk Wallays, through Creative Commons.



Figure 75. *Nototriton abscondens* with large bryophyte fragments on its back. Photo by Eduardo Boza Oviedo, with permission.

Turtles

I have experienced this dispersal first-hand by inference. When I (Glime, unpubl) grew *Conocephalum conicum* (Figure 76) and *Fissidens* (Figure 77) in my garden room in the company of a box turtle (*Terrapene*; Figure 78), both bryophytes spread quickly around the room, something they never did in the absence of the turtle. But eventually the zebra finches discovered the liverwort and each day it grew smaller, with triangles cut from its edges. Alas, the birds seemed to be agents of destruction and not dispersal because *C. conicum* soon disappeared completely. The *Fissidens* likewise stopped spreading and within some months it too disappeared.



Figure 76. *Conocephalum conicum*, a liverwort that is eaten by birds and carried by turtles. Photo by Robert Klips, with permission.



Figure 77. *Fissidens taxifolius*, a moss that seems to be carried by turtles. Photo by David Holyoak, with permission.



Figure 78. *Terrapene carolina*, a potential bryophyte dispersal vector. Photo through Wikimedia Commons.

McGregor (1961) has a more documented story. He found living thalli of *Riccia rhenana* (Figure 79) on the carapace of a snapping turtle (*Chelydra serpentina*; Figure 80) that had ventured nearly 1 km from the nearest pond. This liverwort species grows among cattails, sedges, rushes and grasses of shallow water where it multiplies by growth and division of thalli, mostly in April. The thallus dries up to its growing apex in summer, and McGregor observed it in that dry state for up to 33 days, when it was rehydrated by rains and resumed growth. Its ponds often freeze solid, freezing the thalli in ice. Once again, the thalli die except the growing apex. McGregor reports that these thalli can survive more than five weeks in the ice.



Figure 79. *Riccia rhenana*, a liverwort known to be carried by a snapping turtle. Photo by Jan-Peter Frahm, with permission.



Figure 80. *Chelydra serpentina* (snapping turtle) female searching for a nesting site. Photo by D. Gordon E. Robertson, through Wikimedia Commons.

Birds

Aquatic organisms living in isolated wetlands could have real difficulty being dispersed. But Figuerola and Green (2002) found that widespread distributions of aquatic organisms typically coincide with pathways of migratory waterbirds. They considered that small propagule size would favor dispersal, but we have seen that birds are important dispersers of bryophyte fragments (Lewis *et al.* 2014). Behling *et al.* (2002) have further demonstrated dispersal through **endozoochory** – ingestion of fragments by birds. Birds travel long distances, and rather quickly. Their frequent stops for food makes them ideal dispersal agents because in most cases any adhering bryophyte parts won't be in the atmosphere for very long. (See further details of long migration flights in Chapter 4-8.)

The introduction of the aquatic liverwort *Ricciocarpus natans* (Figure 81) into Norway may be the result of transport by waterfowl or some other form of epizooic transport (Skulberg 1978). This has been shown for a number of algae that travel on the feathers and feet of ducks, arriving in viable condition (Schlichting 1958). Both mechanisms seem reasonable for bryophyte spores and leaf fragments, or even small branches.

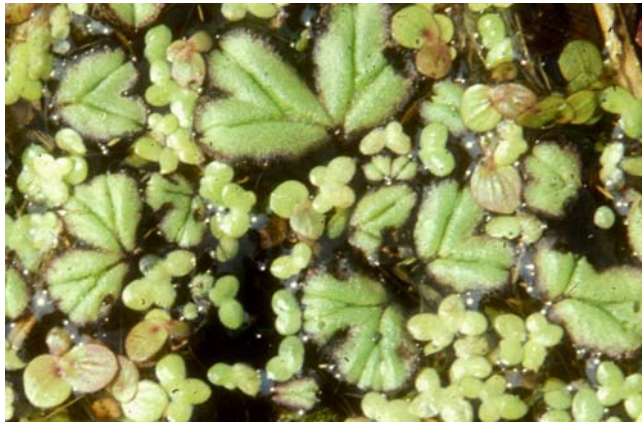


Figure 81. Thalli of *Ricciocarpus natans* floating with the duckweeds *Lemna minor*, *Wolffia* sp., and *Spirodela polyrrhiza*. Since duckweeds are common foods for waterfowl, it is likely that *Ricciocarpus* gets mixed in with the food and stuck to feathers or feet as the birds wade and eat. It may also be eaten, if only inadvertently, and could possibly be dispersed in feces. Photo by Janice Glime.

The **Kelp Gull** (*Larus dominicanus*; Figure 82) in the Argentine Island region of the Antarctic uses bryophytes and other plant material for building its nest (Parnikoza *et al.* 2012). Some of these bryophytes are able to establish in their new locations. If the gull can survive a long flight, most likely the bryophyte can as well.

McGregor (1961) actually found evidence that ducks indeed disperse living bryophytes. A fragment of *Riccia fluitans* (Figure 33) was attached to a feather at the back of the neck of a pintail duck (*Anas acuta*; Figure 83) that was soon to become a hunter's dinner. The duck was intercepted just before it descended to land on the Kansas River.

In Hungary, geese (Figure 84) are known to carry such fugitives as *Riccia frostii* (Figure 85) on their feathers, feet, or muddy bills, making these liverworts common – you

guessed it – along goose trails (Crum 1973). But might they also be transported in the feces? Bryophytes such as *Riccia fluitans* (Figure 33-Figure 32) exist among duckweeds (Lemnaceae) and thus will almost certainly be eaten along with them. With 0.7 kg of defecation (French & Parkhurst 2009) occurring every 20 minutes (Bowen & Valiela 2004), there is considerable opportunity for transport, albeit not very far if it has only 20 minutes of residence time. Jasmin *et al.* (2009) found that bryophytes increased in areas of goose foraging in the Arctic, but this may have been due to an increase in available habitat.



Figure 82. *Larus dominicanus* (Kelp Gull), a bird that spreads bryophytes by putting them in its nest in the Antarctic. Photo by Steve and Jem Copley, through Creative Commons.



Figure 83. Male and female Northern Pintails (*Anas acuta*). Photo by J. M. Garg, through Wikimedia Commons.



Figure 84. Domestic goose (*Anser*). These are among the known vectors of bryophytes through fragments stuck to feathers or feet. Note bits of mud on lower feathers and feet. Photo through Wikimedia Commons.



Figure 85. *Riccia frostii*, a liverwort that is a known goose hitchhiker. Photo by Rosemary Taylor, with permission.

Crows seem to be favorites as the villains in moss destruction. Misha Ignatov (Bryonet 23 February 2013) reports seeing the rare (in Moscow) moss *Dicranum viride* (Figure 86) scattered over the ground rather than in place on the tree trunks. As he wondered who the destructive villain was, he heard crows overhead, then noticed a number of crow nests. He concluded that the crows were the likely vandals. He hoped that they might be forgiven if in the process the crows succeeded in dispersing the mosses to new locations where they could establish.



Figure 86. *Dicranum viride* on tree trunk in Michigan, USA. Photo by Janice Glime.

Erkamo (1976) reported observations of mosses being upturned, especially on flat, open rocks. These were mostly only a few cm in size, but some were 10-15 cm across. He considered the agents of this upheaval to be possible by voles, pheasants, seagulls, or crows, but considers crows (Figure 87) to be the most likely. He has actually seen crows in such activity, and considered that they were probably looking for food such as insects or worms under the moss cover. Erkamo lamented the destruction of beautiful rock scenery that will most likely take years to recover.



Figure 87. *Corvus brachyrhynchos*, a crow that scatters mosses to find food. Photo by Walter Siegmund, through GNU Free Documentation.

Blackbirds (*Turdus merula*; Figure 88) have found another use for bryophytes that is likely to disperse them. Robin Stevenson (Bryonet 15 April 2010) reported observing **displacement activity** in this species. He observed a male throwing clumps of moss off a rooftop, alternating the activity with altercations with another blackbird. This displacement behavior was most likely part of a fight over territory and the mosses permitted them to take a break that prevented them from killing each other. The battered mosses included *Grimmia pulvinata* (Figure 89), *Hypnum cupressiforme* (Figure 90), and *Syntrichia montana* (Figure 91).



Figure 88. The Blackbird, *Turdus merula*, resting among lichens. Photo by Mario Modesto Mata, through GNU Free Documentation.



Figure 89. *Grimmia pulvinata* (Grey-cushioned Grimmia), a rooftop species that was thrown off by quarrelling blackbirds. Photo by Barry Stewart, with permission.



Figure 90. *Hypnum cupressiforme* var. *cupressiforme*, a species tossed from a rooftop by quarrelling blackbirds. Photo by David Holyoak, with permission.



Figure 91. *Syntrichia montana*, a species tossed about by quarrelling blackbirds. Photo by Barry Stewart, with permission.

Terrestrial bryophytes may get transported, at least for short distances, by bird behavior. For example, blackbirds (*Turdus merula*; Figure 88) forage among mosses to find insects or worms, tossing them aside to gain access (Davison 1976). It is likely that such food items and earthworms are closer to the surface under mosses where the moisture is greater. Davison reports that *Mnium hornum* (Figure 92) and *Polytrichastrum formosum* (Figure 93) may be tossed 1-2 m in these activities. In an area of 5 sq m, Davison found that 34 clumps with an average diameter of 2 sq cm were displaced in this way over a two-month period in Great Britain. Furthermore, an additional 18 clumps were moved into that same 5 sq m during the same time period (October-November).



Figure 92. *Mnium hornum*, a moss that can be a victim of crow scavenging. Photo by Janice Glime.



Figure 93. *Polytrichastrum formosum*, a moss often disturbed by crows seeking food. Photo by Michael Lüth, with permission.

Gathering bryophytes for nests is a likely means of dispersal for nearly every kind of nest in which bryophytes are used, *e.g.*, the Picaflor Rubi (*Sephanoides sephaniodes*; Figure 94-Figure 95) and White-sided Hillstar (*Oreotrochilus leucopleurus*) construct their nests primarily of mosses, especially those with falcate leaves (Calvelo *et al.* 2006). Fragments are likely to be dropped on the way, and many more are broken off or dropped or discarded during the construction of the nest and subsequent usage. For some, the lofty position of a nest in a tree provides the advantage of more opportunity to gain access to air movements that can carry the fragments even further.



Figure 94. Picaflor Rubi (*Sephanoides sephaniodes*), a bird related to the hummingbird that uses bryophytes to build its nest. Photo by Suemili, through Wikimedia Commons.



Figure 95. Picaflor Rubi (*Sephanoides sephaniodes*) on nest that is constructed of mosses, showing how its coloration blends with the moss. Photo by Diucón, through GNU Free Documentation.

When Surtsey was colonized after its ascension from the sea, the moss *Racomitrium* (Figure 96) was among the first invaders (Magnússon *et al.* 2009). The Lesser Black-backed Gull (*Larus fuscus*; Figure 97) invaded the island, forming a dense colony. Its primary nesting material was *Racomitrium*, but it is unclear if it was brought to the island by the birds or it arrived by fragments or spores and spread.



Figure 96. *Racomitrium lanuginosum*, one of the first mosses to arrive on Surtsey when it arose as a volcanic island. Photo by Juan Larraín, with permission.



Figure 97. *Larus fuscus* (Lesser Black-backed Gull) adult and juvenile, probably dispersal agents for *Racomitrium* sp. to Surtsey. Photo by Pline, through Wikimedia Commons.

Even when bryophytes are not transported to make nests, the nearness of a nest to bryophytes increases the chances that the bryophytes will become dislodged, and some may adhere to the birds. For example, the Peg-billed Finch (*Acanthidops bairdi*) is a rare bird in Costa Rica and Panama (Elizondo C. 2000). It has rarely been observed, but Mathias Jaschhof was able to photograph four fledglings in the nest (Figure 98). The nest was built in myrtle (*Vaccinium consanguineum*) and consisted of a bulky cup developed from *Frullania* sp. (Figure 99) with amendments of *Leptodontium* sp. (Figure 100), *Pilotrichella*, and *Plagiochila* sp. (Figure 102) as well as fruticose lichens and a mix of unidentified leafy liverworts and mosses (Elizondo C. 2000). The egg chamber had a layer of fern rhizomes, a thin layer of grass inflorescences, and finally an external layer of *Thuidium* sp. (Figure 107).

This latter layer may extend to the outside of the nest and may be surrounded by *Frullania*.



Figure 98. *Acanthidops bairdi* (Peg-billed Finch), a rare bird that builds a cup-shaped nest, sometimes in moss banks, as seen here. Photo by Mathias Jaschhof, with permission.



Figure 99. *Frullania*, leafy liverwort that is predominant in the nest of the Peg-billed Finch (*Acanthidops bairdi*). Photo by Li Zhang, with permission.



Figure 100. *Leptodontium*, a secondary moss in the nest of the Peg-billed Finch (*Acanthidops bairdi*). Photo by Felipe Osorio Zúñiga, with permission.



Figure 101. *Pilotrichella* sp., a minor component of nests of the Peg-billed Finch (*Acanthidops bairdi*). Photo by Lena Struwe, through Creative Commons.



Figure 102. *Plagiochila adianthoides*, member of a genus used as a secondary bryophyte in nests of the Peg-billed Finch (*Acanthidops bairdi*). Photo by Michael Lüth, with permission.

Mammals

The role of mammals in dispersal of propagules seems to have gotten less attention than it deserves. Only recently are we seeing documentation that mammals can serve as dispersal vectors through feces, fur, and hooves, and in some habitats these may play a major role. Among these dispersal units are fragments that cling easily to the fur and feathers of some animals. Dispersal of fragments is most likely more important than we have considered (Heinken *et al.* 2001).

Rodents

I have blamed the chipmunks in my moss garden for tearing up my recent moss plantings. They seem to like frolicking across the bryophytes, and more than occasionally the bryophytes end up upside down as the chipmunks (Figure 103-Figure 104) kick them up or drag them with their feet. They seem to especially like *Leucobryum glaucum* (Figure 105-Figure 106) and *Thuidium delicatulum* (Figure 107). At least those are the most likely to get torn up in my garden, and one chipmunk insisted on making an entrance to a burrow in the middle of the *T. delicatulum*, destroying the integrity of the mat, hence causing its death. *Leucobryum* species have the ability to develop rhizoids on the upturned surface that contacts the soil (Figure 106) and may recover as a moss ball. Mine did not. Gray squirrels (Figure 108), and certainly others, have the same potential to serve as dispersal agents.



Figure 103. *Tamias sciurus* (eastern chipmunk) is responsible for kicking up loose mosses and most likely transports fragments. Photo by Oleksii Voronin, through Wikimedia Commons.



Figure 104. *Tamias sciurus* (eastern chipmunk) with bark stuck to its fur, showing how easily it could transport bryophyte propagules and fragments. Photo by Janice Glime.



Figure 105. Moss garden showing upturned *Leucobryum glaucum* at lower left and mist netting covering clumps to prevent further upheaval. Photo by Janice Glime.



Figure 106. *Leucobryum glaucum* with leaf rhizoids (arrow) that develop after the clump has been overturned. Photo by Kristian Peters, through Wikimedia Commons.



Figure 107. *Thuidium delicatulum*, a moss that a chipmunk used to make an entrance to reach its underground tunnels. Photo by Bob Klips, with permission.



Figure 108. Eastern gray squirrel (*Sciurus carolinensis*) amid mosses. This frisky animal is a likely dispersal agent for gemmae and fragments, especially when scratching to grab seeds, as seen here. Photo by Janice Glime.

In the Arctic, rodents, including moles and lemmings, eat the bryophytes (Ericson 1977), so dispersal of spores and fragments in their whiskers and fur is likely. Hribljan (unpubl) has cultured feces of rodents, collected from Alaska, that had protonemata germinate from them (Figure 109). It is likely that these came from fragments that were present in the feces, but could also have been from spores. Kimmerer and Young (1996) suggested that rodent activity may help *Orthodicranum flagellare* (Figure 2) disperse in two ways, by helping to produce gaps among the bryophytes on the logs and possibly by carrying the flagelliform propagules among the locations visited. In this regard, squirrels and chipmunks are likely agents. Could it be that they also inadvertently eat bryophytes as they forage and thus carry them in their guts? At the very least, they probably dislodge epiphytes, aiding their dispersal.



Figure 109. Protonemata and young gametophores germinated from microtine rodent scat collected in Alaska. Photo by John Hribljan, with permission.

Ericson (1977) showed that many of the most abundant forest mosses in northern Sweden are a preferred food for *Myopus schisticolor* (wood lemming; Figure 110). *Ptilidium ciliare* (Figure 111) and *Plagiothecium denticulatum* (Figure 112) are rejected, as are most herbaceous species. When the snow is gone, they feed on green tips of mosses, whereas when they are living under snow the lemmings bite the shoots off at the base. In 1974 and especially in 1975, following heavy grazing in 1973, *Dicranum scoparium* (Figure 113) spread to areas where no *D. scoparium* occurred in 1973. These rodents appear to have been the agents of both fragmentation and dispersal.



Figure 110. *Myopus schisticolor* (wood lemming) by its path amid *Hylocomium splendens*. Photo by Risto S. Pynnönen, through Wikimedia Commons

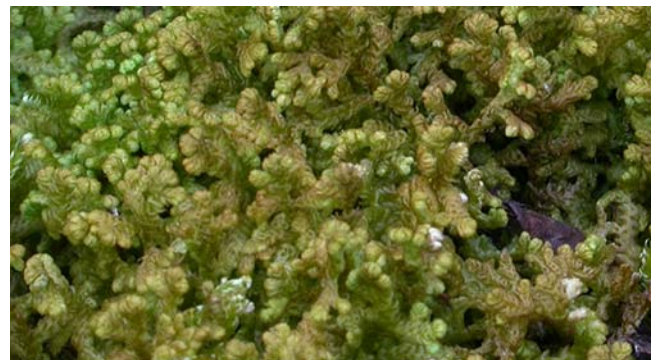


Figure 111. *Ptilidium ciliare*, a leafy liverwort rejected by the wood lemming (*Myopus schisticolor*). Photo by Li Zhang, with permission.



Figure 112. *Plagiothecium denticulatum*, a moss rejected by the wood lemming (*Myopus schisticolor*). Photo by Michael Lüth, with permission.



Figure 113. *Dicranum scoparium*, a moss most likely distributed by rodents in northern Sweden. Photo by Janice Glime.

Eskelinen (2002, 2004) likewise demonstrated that mosses are preferred food of the wood lemming in northern Finland, and that they also are selective. They consume *Dicranum* spp. (Figure 113) and *Polytrichum* (Figure 114-115) in greater quantities than would be expected, but avoid *Hylocomium splendens* (Figure 110) and *Pleurozium schreberi* (Figure 61). Nevertheless, Ericson (1977) found that *H. splendens* diminished, presumably due to rodent consumption. Eskelinen (2002, 2004) suggested the preference for *Polytrichum* and *Dicranum* may relate to their higher N content. If so, preferences may change with habitat and available food choices.



Figure 114. *Polytrichum commune* var. *commune*, demonstrating the clone that can result from its branching rhizomes. Photo by David Holyoak, with permission.



Figure 115. *Polytrichum juniperinum*, a moss that spreads by rhizomes. Photo by Janice Glime.

Ericson (1977) followed the changes in moss cover in Scandinavia for four years and discovered that rodents played a major role in the changes. Only the mosses on windthrows and tree stumps maintained constant cover. The fascinating realization was that different species of bryophytes seemed to suffer declines and increases in different years. In 1974, *Ptilium crista-castrensis* (Figure 116) suffered 73% reduction and *Dicranum scoparium* (Figure 113) suffered 57%. However, in 1975, the strongest decrease was in *Hylocomium splendens* (Figure 110), which suffered 49% reduction, while *P. crista-castrensis* increased 43% and *D. scoparium* increased 70%! Ericson felt that this might indicate increased growth as a response to fragmentation caused by grazing. However, to increase cover values so significantly, it would seem that at least some dispersal must have been effected.



Figure 116. *Ptilium crista-castrensis*, a preferred moss for rodent consumption. Photo by Janice Glime.

Ericson (1977) felt that several types of regeneration were common for these species. *Polytrichum commune* (Figure 114) and *P. juniperinum* (Figure 115), as well as others, can recolonize from protonemata, juvenile plants, and rhizoid fragments (Meusel 1935, Wigglesworth 1947). *Hylocomium splendens* (Figure 110; Correns 1899) and species of *Dicranum* (Figure 113; Meusel 1935) grow easily from broken parts of stems, and *Polytrichum commune* and species of *Dicranum* regenerate from isolated leaves (Correns 1899). Callaghan *et al.* (1978) pointed to the need for *Polytrichum commune* to reproduce by underground branching into clones because of its finite life expectancy. *Hylocomium splendens* solves the problem of life expectancy by producing new shoots in a stair-step fashion, with the oldest part of the plant senescing and decomposing (Callaghan *et al.* 1978), a feature seen also in *Pseudocalliergon trifarium* (Figure 117; Bisang *et al.* 2008). However, if the young branch shoot of *Hylocomium splendens* is damaged, the entire plant will die (Callaghan *et al.* 1978). On the other hand, it seems to have a low branching rate for the main stem, limiting its clonal growth.

Bank voles (*Clethrionomys glareolus*) include small quantities of mosses in their diets (Watts 1968). Bank voles were caught in the act of eating mosses in The Netherlands. Andrew Spink was able to capture these on film (Figure 118).

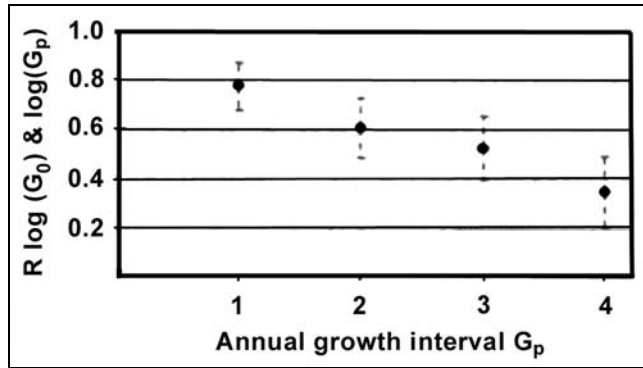


Figure 117. Diminishing growth rates of *Pseudocalliergon trifarium* through four years of growth. Redrawn from Bisang *et al.* 2008.



Figure 118. Bank vole eating mosses and most likely carrying fragments from one place to another. Photo by Andrew Spink, with permission.

Flying Fox

The spectacled flying fox (*Pteropus conspicillatus*; Figure 119), a fruit bat, passes bryophyte fragments in its feces (Figure 120-Figure 121), including chloronemata, rhizoids, and shoots (Parsons *et al.* 2007). These are capable of germinating (Figure 122) and may even benefit from nutrients in the adhering feces. Fifteen families of bryophytes were represented in these feces. Among the 48 fragments cultured, 52% germinated, producing rhizoids or shoot extensions. Even rotifers among the bryophytes were still alive. Included among the species were *Metzgeria* sp. (Figure 123), *Acroporium* sp. (Figure 124), *Leucobryum juniperoideum* (Figure 125, and *Racopilum* sp. (Figure 126). The germination rate was higher from samples taken during the early part of the season (17 out of 28 fragments) compared to those taken in the later part of the season (7 out of 20). This could represent a shift in diet, change in brittleness of bryophytes (resulting from desiccation) that changes ease of fragmentation, or a change in viability of the bryophytes. It is likely that the bryophytes were eaten unintentionally along with fruit.

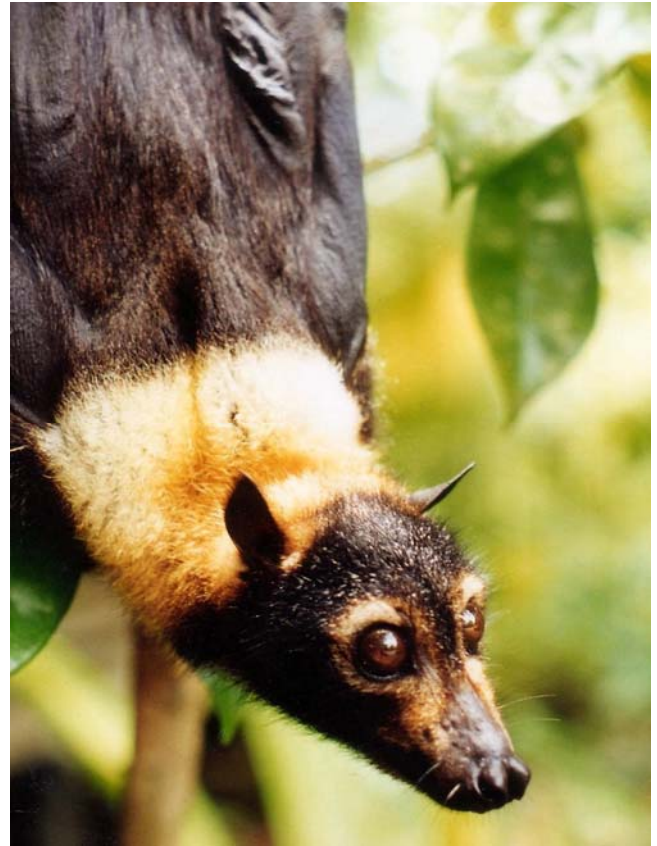


Figure 119. Spectacled flying fox (*Pteropus conspicillatus*). Photo courtesy of Andi Cairns.



Figure 120. Splat (feces) of flying fox on leaf. Photo courtesy of Andi Cairns.



Figure 121. Jennifer Parsons with flying fox splat trap. Photo courtesy of Andi Cairns.



Figure 122. Culture tube with flying fox feces. Photo courtesy of Andi Cairns.



Figure 125. *Leucobryum juniperoideum* leaf fragment germinating from flying fox feces. Photo courtesy of Andi Cairns.

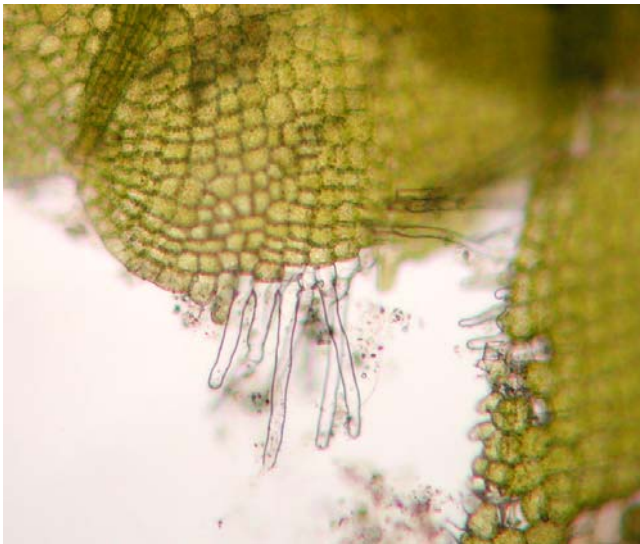


Figure 123. *Metzgeria* germinating from flying fox feces. Photo courtesy of Andi Cairns.



Figure 126. *Racopilum* sp. germinated from flying fox feces (splat). Photo courtesy of Andi Cairns.

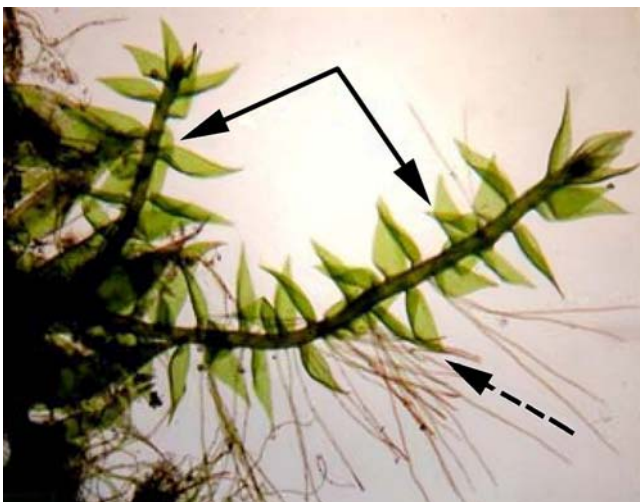


Figure 124. *Acroporium* sp. feces from flying fox. Solid arrows indicate new shoots; dashed arrows indicate rhizoids. Photo by Andi Cairns.

Lessons from a Dog

Heinken (2000) conducted an interesting and most instructive study on dispersal of fragments by using a dog. Dogs act as good surrogates to demonstrate the ability of diaspores to adhere to fur, but their habit of wallowing on the ground is unusual among many wild mammals, making some predictions limited. In one year, Heinken walked his dog 49 times in the forest near his home in Germany. He found no seasonal differences in fragment attachments of bryophytes compared to the seasonal pattern observed for seed plant diaspores.

The forest used in the dog study had 20 species of bryophytes occupying 1% of the cover (Heinken 2000). The dog presented 29 bryophyte stem fragments from at least 10 bryophyte species. All the stem fragments had leaves and most had terminal buds. Only 13 of the fragments had branches and these were often numerous. The most frequent species were *Eurhynchium hians* (Figure 127) and *Ceratodon purpureus* (Figure 128). Other taxa included *Barbula* sp., *Amblystegium varium* (Figure 129), *Hypnum cupressiforme* (Figure 145),

Eurhynchium praelongum (Figure 130), *Plagiomnium* sp., *Rhynchostegium* cf. *megapolitanum* (Figure 131), *R. murale* (Figure 132), and *Rhytidiadelphus squarrosus* (Figure 133). On the other hand, two species [*Atrichum undulatum* (Figure 134), *Mnium hornum* (Figure 92)] that were frequent in the study area were not represented at any time on the dog's fur.



Figure 127. *Eurhynchium hians*, one of the two most common species on dog fur in a German experiment. Photo by Michael Lüth, with permission.



Figure 128. *Ceratodon purpureus*, one of the two most common species on dog fur in a German experiment. Photo by Michael Lüth, with permission.



Figure 129. *Amblystegium varium*, a species found on dog fur in a German experiment. Photo by Jan-Peter Frahm, with permission.



Figure 130. *Eurhynchium praelongum*, a species found on dog fur in a German experiment. Photo by Michael Lüth, with permission.



Figure 131. *Rhynchostegium megapolitanum*, a species found on dog fur. Photo by Michael Lüth, with permission



Figure 132. *Rhynchostegium murale*, a species found on dog fur in a German experiment. Photo by David Holyoak, with permission.



Figure 133. *Rhytidiadelphus squarrosus*, a species found on dog fur in a German experiment. Photo by Brian Eversham, with permission.



Figure 134. *Atrichum undulatum*, a moss that did not adhere to dog fur in a German experiment. Photo by Janice Glime.

Sources of the adhering bryophytes were primarily tree trunks, walls, paved places in the city, a grassland plot, and the lawn of the owner (Heinken 2000). The dog would frequently wallow on the ground, then shake and groom himself to remove annoying diaspores, especially seeds. The bryophytes that adhered were primarily wefts or short turfs with acute and often erect or squarrose leaves. Tall turf species with rounded leaves were very under-represented. Mats were likewise rare. Loose wefts, on the other hand, seemed to hitch a ride rather easily. Heinken concluded by saying that for a moss to be transportable it must fragment and that this most probably occurs when the moss is dry, perhaps explaining the seasonal difference found for flying fox feces.

Hoofed Mammals

Larger animals contribute to dispersal in somewhat different ways. Their fur, hair, spaces between toes, feathers, and other parts can trap bryophyte parts and easily transport them for the distance travelled by the animal. Among these are large, hoofed mammals. Cattle and other farm animals are able to transport terrestrial taxa wedged in their hooves, causing certain bryophyte species to frequent cattle trails and ruts made by machinery (Crum 1973). The fur and hairs of hoofed mammals can provide a protective location for diaspores to hitch a ride and may take these diaspores for long distances (de Pablos & Peco 2007). Erika Péntzes-Kónya demonstrated the ability of overturned *Leucobryum juniperoideum* to form rhizoids on the overturned clump (Figure 125, Figure 135) after cattle traffic.



Figure 135. *Leucobryum juniperoideum* cushion with leaf rhizoids after overturn by cattle. Photo by Erika Péntzes-Kónya, with permission.

When Poschlod (pers. comm. 6 March 2013) applied diaspore traps in grasslands, he found many fewer vegetative parts than in peatlands. Rather, he found grazing animals, especially sheep, serving as long-distance dispersers of vegetative parts, especially from those moss species which do not form capsules (at least not in central Europe where he is familiar with the flora) such as *Abietinella abietina* (Figure 136). And this species is astonishingly widespread in all the dry calcareous (and man-made) grasslands there.



Figure 136. *Abietinella abietina* in Europe, a moss that is easily broken when dry, as it is here. Photo by Michael Lüth, with permission.

Several researchers have examined sheep and cattle coats (Figure 137) for propagules, primarily seeds, and found that greater seed weight was likely to prevent attachment on vertical surfaces but not on horizontal ones (de Pablos & Peco 2007). The same relationship is not likely to be a problem for the light-weight bryophyte diaspores. Sheep wool held more diaspores than the smoother coats of cattle. Both animals rest by lying down (Figure 138-Figure 139), providing ample opportunity for bryophyte adherence in rocky, mountainous pastures. In addition to clinging to the coats of hoofed mammals, the bryophytes can lodge on the hooves, particularly in the company of mud.



Figure 137. Sheep with full coat of wool before shearing in North Wales. At this stage, bryophyte fragments can easily adhere to the wool. Photo by Janice Glime.



Figure 138. Sheep resting under a tree near Swallow Falls, Wales. In areas where bryophytes are prevalent, this behavior contributes to attaching bryophyte fragments to the wool, facilitating dispersal. Photo courtesy of Kim Barton.

Sheep seem to be particularly good dispersal vectors, particularly those with a dense, curly fleece (Figure 137) (Pauliuk *et al.* 2011). The curly fleece is able to carry more fragments and larger species of bryophytes than those with smooth, fine hair (Figure 139-Figure 140). Twelve sheep representing two breeds were examined and revealed fragments from 16 species of mosses, representing 40% of the species present in the pasture. It is interesting that these were particularly common on the belly and tail! Some species disperse better than others, with pleurocarpous species, small species, and mats being over-represented compared to the pasture vegetation. On the other hand, large species, acrocarpous taxa, wefts, and turfs were under-represented among those cultured. The hooves transported mostly acrocarpous colonists. Short fragments were more likely to occur on the hooves; longer fragments were more common on the wool (Figure 141).



Figure 139. Sheep with closely sheared wool, creating a smooth surface to which bryophyte fragments don't adhere as well as they do to long, curly wool. Photo by Janice Glime.

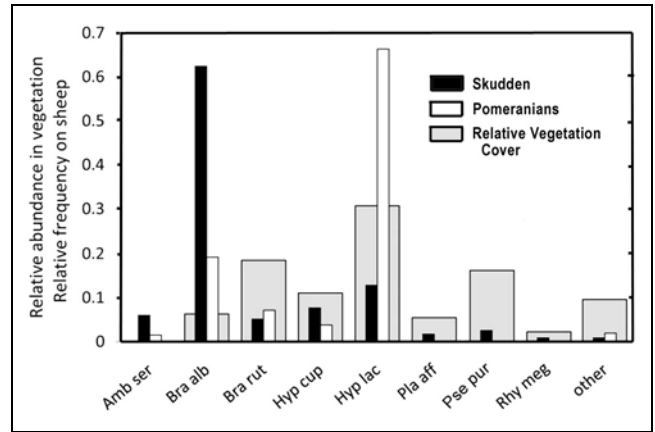


Figure 140. Comparison of proportions of bryophyte species carried by two different breeds of sheep, superimposed on the relative cover of the vegetation where the sheep were grazing. Skudden $n = 5,117$ fragments, Pomeranians $n = 7,2096$ fragments. Amb ser *Amblystegium serpens*, Bra alb *Brachythecium albicans*, Bra rut *B. rutabulum*, Hyp cup *Hypnum cupressiforme* var. *cupressiforme*, Hyp lac *H. cupressiforme* var. *lacunosum*, Pla aff *Plagiomnium affine*, Pse pur *Pseudoscleropodium purum*, Rhy meg *Rhynchostegium megapolitanum*. Modified from Pauliuk *et al.* 2011.

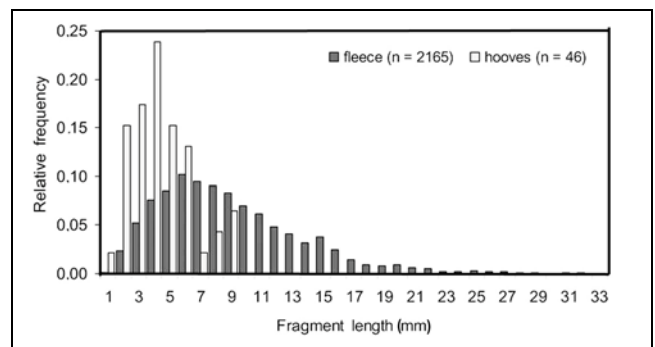


Figure 141. Size distribution of visible bryophyte fragments in fleeces and hooves from 12 sheep grazing on a dry grassland pasture. $n = 2206$. Modified from Pauliuk *et al.* 2011.

Heinken *et al.* (2001) further elucidated hoofed mammal dispersal by examining 25 shot roe deer (*Capreolus capreolus*; Figure 142) and 9 wild boar (*Sus scrofa*; Figure 143) in deciduous forests in Germany. They located a total of 106 bryophyte fragments (102 stem fragments, 4 leaves), representing 12 species, on the animals in their coats and hooves. This was proportionally somewhat less than the representation of tracheophytes based on percent cover (bryophyte:tracheophyte diaspores 1:30; bryophyte:tracheophyte cover 1:22.5).

Mean fragment length on the animals was 3.6 mm, but ranged 0.5-35 mm (Heinken *et al.* 2001). The fragments came mostly from the **terricolous** (on the soil) species, especially *Brachythecium velutinum* (Figure 144), *Hypnum cupressiforme* (Figure 145), *Eurhynchium hians* (Figure 127), and *Ceratodon purpureus* (Figure 128). Robust acrocarpous species in tall turfs were predominantly excluded, whereas the slender pleurocarpous species with erect, acute leaves, growing in wefts, were common. As in the dog study, some species that were frequent in the study area failed to adhere: *Atrichum undulatum* (Figure 134), *Plagiomnium affine* (Figure 146), *Pohlia nutans* (Figure

147), *Polytrichastrum formosum* (Figure 93). Others [*Brachythecium rutabulum* (Figure 148), *Mnium hornum* (Figure 92), and *Plagiomnium* sp.] only had a few fragments attached. The liverworts in the study area were completely absent on the animals, despite the scattered occurrence of *Chiloscyphus profundus* (= *Lophocolea heterophylla*; Figure 149) throughout the study area.



Figure 142. *Capreolus capreolus* (roe deer) male and female. Photo through Wikimedia Commons.



Figure 143. *Sus scrofa* (wild boar) in forest, lying among mosses. Photo by Rizzo, through Wikimedia Commons.



Figure 144. *Brachythecium velutinum* with capsules in southern Europe. Photo by Michael Lüth, with permission.



Figure 145. *Hypnum cupressiforme*, a species whose fragments commonly appeared on a dog in a German dispersal experiment. Photo by Dick Haaksma, with permission.



Figure 146. *Plagiomnium affine*, a species that failed to adhere to a dog in a German dispersal experiment. Photo by Michael Lüth, with permission.



Figure 147. *Pohlia nutans*, a species that failed to adhere to a dog in a German dispersal experiment. Photo by Michael Lüth, with permission.

The bristly coat of the wild boar was more adept at taxi service than the sleek hairs of the deer (Heinken *et al.* 2001). Furthermore, the boars wallow and root in the mud, giving them greater contact for picking up their hitchhikers. In addition to these fur and hair dwellers, they also travelled in the hooves.



Figure 148. *Brachythecium rutabulum* (Rough-stalked Feather-moss), a moss that is uncommon among the fragments on a dog in a German dispersal experiment. Photo by Barry Stewart, with permission.



Figure 149. *Chiloscypus profundus* (= *Lophocolea heterophylla*), a liverwort that does not seem able to hitch-hike a ride on roe deer or wild boar. Photo by Michael Lüth, with permission.

Heinken and coworkers (2001) tested the ability to pick up bryophyte fragments by experimenting with a dummy deer. This dummy was placed on its stomach on the forest floor and used to mimic wallowing by giving it a gentle rolling motion. They repeated the experiment 300 times between July and October, cleaning all adhering fragments each time. This "behavior" produced 51 bryophyte fragment hitchhikers. Four of the six terricolous bryophyte species in the sample plots adhered to the ventral hair, with strong differences among bryophyte species. *Eurhynchium hians* (slender with erect, acute leaves, forming wefts; Figure 127) had 47 adhering stem fragments, whereas the similarly dominant *Plagiomnium undulatum* (robust with rounded leaves, forming tall turfs; Figure 150) had only one adhering fragment.



Figure 150. *Plagiomnium undulatum*, showing its large, rounded leaves that do not adhere easily to fur. Photo by Des Callaghan, with permission.

Heinken *et al.* (2001) concluded that most of the attachment to fur occurs when the animals lie down or wallow on the ground, or when they rub against rocks, walls, or tree trunks. The hooves can also transport fragments, particularly in adhering mud (Figure 151). The type of fur matters. The boar provides further advantages by its frequent rooting and wallowing, extensive resting periods, and difficulties with grooming. Even their feces (Figure 152) could carry diaspores, but we don't know if they will survive. Since wild boars can travel as much as 5 km per day through the European forests, they could facilitate transport for quite some distance.



Figure 151. *Sus scrofa* (wild boar) tracks showing the mud that is a common part of the boar's environment. Mud on the hooves can help to carry bryophyte diaspores. Photo by James K. Lindsey, with permission.



Figure 152. *Sus scrofa* (wild boar) scat, a potential but untested means of dispersal. Photo by James K. Lindsey, with permission.

Pérez (2010) considered goats as contributors to dislodging mosses, particularly *Grimmia trichophylla* (Figure 153) and *G. torquata* (Figure 154) on Haleakala's Crater, Maui, Hawai'i, USA. These were transported downslope to new locations where they could grow, perhaps a combination of fragmentation by goats and gravity.



Figure 153. *Grimmia trichophylla* on rock. This moss may be dislodged by goats on Maui, Hawaii, and subsequently roll down the slope, making moss balls. Photo by Michael Lüth, with permission.



Figure 154. *Grimmia torquata* on rock. This moss may be dislodged by goats on Maui, Hawaii, and subsequently roll down the slope, making moss balls. Photo by Michael Lüth, with permission.

Bears

When I was searching for images of bears in streams, I found one with a group of bears in a moss-laden tree in the temperate rainforest of Canada (Figure 155). It occurred to me that these bears, and most likely monkeys, big cats, and other climbers, would dislodge some of the bryophytes, hence facilitating their dispersal. Another image of a black bear climbing over a rock with a vascular plant draped around its head suggested that especially for pendent mosses, they could carry them away, perhaps for some distance, and if the bryophyte is lucky, it might even be deposited in another tree.

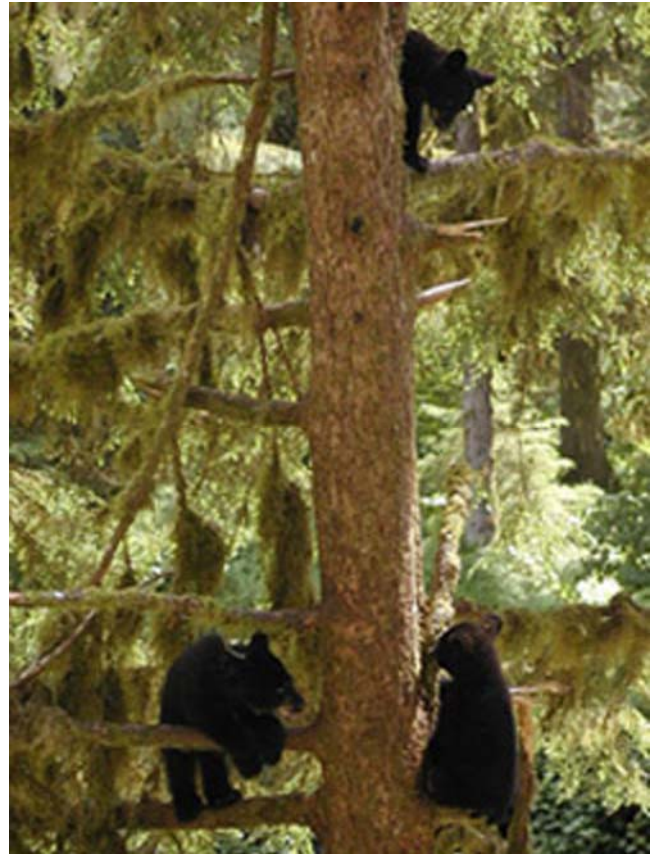


Figure 155. *Ursus americanus* among pendent mosses in Tongass National Forest. Photo by Interpretive staff, Tongass National Forest, Alaska, USA, through public domain.

In addition to dispersal of plants on the fur, bears may also disperse them through feces. Wilson and Ruff (1999) report that mosses are included among the food, but we have no information on the viability of mosses that pass through the digestive tract of the bear.

Bryophyte vegetative structures generally are not adapted for animal dispersal. Nevertheless, just by their location they are likely to be carried on amphibian skin, turtle carapaces, slug slime, insect guts and surfaces, hairs of mites and spiders, stuck to feathers and beaks of ducks, and on animal hooves and fur. Nest-building birds that line their nests with mosses often drop pieces, or the moss can even grow while within the nest. It appears that most vegetative parts do not survive the guts of most animals well, but some do and can thus be carried to new locations.

Human Dispersal

Humans are often inadvertent dispersal agents. For example, van Zanten and Pócs (1981) report on fragmentation of mosses by lawn mowers. These are then carried further by the lawn mower or by the human raking up the scraps. Others are torn apart during logging operations, adhering to the equipment, and potentially

being carried many kilometers to another site. And certainly back packs and collecting bags carry small scraps of bryophytes that escape the fate of a herbarium packet. Van Zanten and Pócs (1981) noted that when they walked in a dry meadow in New Zealand, their socks became transport agents of fragments of *Thuidiopsis furfurosa* (Figure 156). This suggests that other animals could likewise transport this species on fur or feathers.



Figure 156. *Thuidiopsis furfurosa*, a species that is known to cling to socks of bryologists. Photo by David Tng, with permission.

Bryum argenteum (Figure 29) is commonly dispersed by humans. It has deciduous shoot apices that apparently attach to shoes and other clothing as well as to small animals. It is common along paths in cemeteries, around tennis courts, and in golf courses. Clare and Terry (1960) used matchbooks in an elegantly simple experiment to demonstrate dispersal in this species. They "walked" the matchbook across patches of *B. argenteum*, then across soil. As a control, they walked matchbooks that had not contacted *B. argenteum* across other patches of soil. The *B. argenteum* became established on the plots where the matchbook had previously visited the mosses, but not on the others, demonstrating how easily it could be dispersed on shoes and feet.

There are several documented cases of bryophytes dispersed by humans. One of the most recent reports is that of Ireland and Shchepanek (1993) for the spread of *Hyophila involuta* (Figure 157) in Canada. This species was known only from a few localities in Ontario. However, it is growing abundantly on the sides of most of the locks in the Rideau Canal and the authors suspect that it arrived in both Michigan and Canada from more southern localities by travelling there on boats. The locks are constructed of limestone and sandstone or concrete, and the plants seem to get started along the mortar seams.



Figure 157. Gametophytes of *Hyophila involuta* growing on concrete. Photo by Michael Lüth, with permission.

I still recall Iwatsuki commenting in Japan that he didn't need to check what was growing on the concrete retaining walls along the roads – it was all *Hyophila* (Figure 157). However, on the locks in Ontario it is nearly devoid on the concrete blocks, occurring predominately on the limestone and sandstone blocks which are more similar to the construct in Japan (Ireland & Shchepanek 1993). In the Ontario locks, it grows only below the water level, sometimes even on the bottom of the locks. Frequent wetting and drying and low light intensity seem to favor its growth, but the plants must also survive seven months out of the water in winter when the locks are drained. These plants never have sporophytes, and with only one report of sporophytes in the United States, it appears that they rely on their numerous multicellular gemmae (Figure 158).



Figure 158. *Hyophila involuta* showing numerous gemmae that form at leaf bases. Photo by Michael Lüth, with permission.

Logging vehicles, all-terrain vehicles, and other forest transport have giant tires with the potential to pick up fragments of bryophytes along with soil. Some of these could travel considerable distances to another location before falling off. It appears that hitch hiking is a common mode of travel for *Riccia* – in Michigan, USA, *R. huebeneriana* (Figure 159) and *R. cavernosa* (Figure 160) are often dwellers along disturbed soil of 2-track roads, suggesting a vehicular means of dispersal (Crum 1973).

Horticulture provides several means of introducing species to new locations. *Marchantia polymorpha* (Figure 34) is frequently spread throughout a greenhouse by the force of the watering system. This and other bryophytes then travel in the pots with the purchaser. *Polytrichum longisetum* (Figure 161) is an introduced horticultural weed in West Cornwall, Great Britain (Holyoak 1995).



Figure 159. *Riccia huebeneriana*, a common liverwort along two-track roads. Photo by Des Callaghan, with permission.

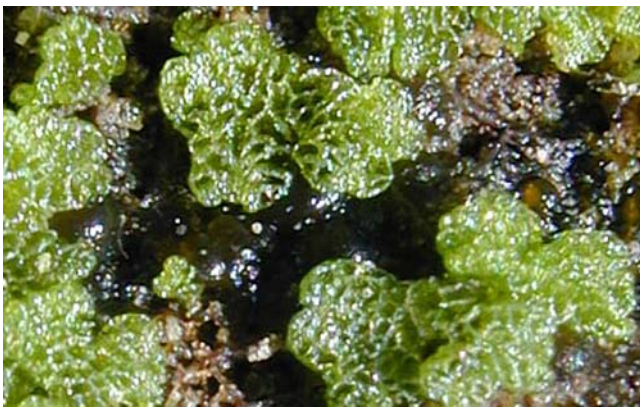


Figure 160. Thalli of *Riccia cavernosa* on disturbed soil. Photo by Michael Lüth, with permission.



Figure 161. *Polytrichastrum longisetum*, an introduced horticultural weed in West Cornwall, Great Britain. Photo by Michael Lüth, with permission.

Bryophytes used as packing material are potential propagules. Degener *et al.* (1969) reported such dispersal to explain the "unnatural distribution" of *Sphagnum palustre* (Figure 162). Its appearance in Hawaii seems to be from use of this moss as packing material for tree seedlings. Bryophytes used for packing can escape and become established, as in the case of *Pseudoscleropodium purum* (Figure 163), in widely ranging parts of the world (Allen & Crosby 1987).



Figure 162. *Sphagnum palustre*, a moss that is spread by its use in packing tree seedlings. Photo by Michael Lüth, with permission.



Figure 163. Gametophyte of *Pseudoscleropodium purum*, a widely transported packing material. Photo by Michael Lüth, with permission.

Golf courses and picnic areas seem to be common sites for invasive species because they get considerable foot traffic from a wide range of locations. The first citing of *Fissidens taxifolius* (Figure 77) in Auckland, New Zealand, was reported occurring under a picnic table (Espie 1997). Also *Rhytidiadelphus squarrosus* (Figure 133) first appeared in New Zealand on a Dunedin golf course in 1975, presumably arriving with foot traffic, or perhaps a golf bag.

Paths are often bordered by bryophytes (Figure 164–Figure 165). Such is the case in the Tatra Mountains of the Western Carpathians where one can find 15% of the liverwort species of that area (Górski 2009). Górski refers to "walking down" of high mountain species [*Marsupella brevissima* (Figure 166), *Pseudolophozia sudetica* (Figure 169)] to lower sites, "passing" of alpine scree-bed species to habitats associated with humans [*Anthelia juratzkana* (Figure 170), *Marsupella brevissima*, *Pleurocladula albescens* (Figure 171)], and formation of new combinations of plant communities [with *Cephalozia bicuspadata* (Figure 167)] or expansion of communities already associated with human activity [e.g. *Calypogeietum trichomanis*, *Nardietum scalaris* (Figure 168)]. Although there is no proof or experimentation to support this, it is likely that at least some of these have arrived in these locations due to human dispersal on foot gear. Others are simply opportunists that are able to

occupy a suitable habitat created by humans, possibly facilitated in their dispersal by the openings created by the paths.



Figure 164. Mosses along forest trail at Clear Creek Park in Ohio, USA. The trail opens new habitats on the slopes and foot traffic can bring propagules to the scene. Photo by Janice Glime.



Figure 165. Mosses at edge of a blacktop path at Three Creeks Park, Ohio, USA. These are easily fragmented by human foot traffic, creating dispersal potential. Photo by Janice Glime.



Figure 166. *Marsupella brevissima*, a leafy liverwort that gets "walked down" the mountain along paths. Photo by Jan-Peter Frahm, with permission.



Figure 167. *Cephaloziella bicuspidata*, a species subject to new community combinations due to "walking down" of alpine species. Photo from Botany Website, UBC, with permission.



Figure 168. *Nardia scalaris*, primary species in the *Nardietum scalaris*. Photo by J. C. Schou, with permission.



Figure 169. *Pseudolophozia sudetica*, a leafy liverwort that gets "walked down" the mountain along paths. Photo by Jan-Peter Frahm, with permission.



Figure 170. *Anthelia juratzkana*, a scree-bed species that gets transferred to human habitats. Photo by Michael Lüth, with permission.



Figure 171. *Pleuroclada albescens*, a scree-bed species that gets transferred to human habitats. Photo by Michael Lüth, with permission.

Bryophytes may even be transported deliberately. My favorite story is one in which *Fontinalis antipyretica* (Figure 22) was introduced into South Africa in an attempt to encourage more aquatic insects as food for fish (Richards 1947). The moss spread rapidly and covered the rocks. But at least initially, the attempt to improve the aquatic insect population failed because the native species were adapted to smooth rocks and they in fact lost their habitat.

Despite the role of humans in dispersal, urban areas often exhibit depauperate bryophyte floras. One of the reasons for this is the fragmented nature of the urban landscape, making dispersal difficult (Korpelainen *et al.* 2006), especially for epiphytes. Of course, the inhospitable nature of the urban habitat, especially exposure, makes establishment difficult once a diaspore arrives.

Mystery Dispersal

Most bryophyte dispersal is in fact mystery dispersal. Few species have actually been subjected to experimentation, tagging, or other means to provide scientific data on their dispersal. Dickson *et al.* (pers comm. 23 April 2013) have provided me with one such

story for *Fissidens fontanus* (Figure 172) in France. This species occurs in many of the abandoned lavoirs that still have flowing clean water; abandoned in the 1960s, the lavoirs were communal wash houses where women did family laundry. They were mainly contracted in the nineteenth century and some villages had more than one. These usually have a roof, but they are open on one or more sides and accessible to birds and insects (and probably an occasional frog). They have become inhabited by algae and bryophytes, the moss *Fissidens fontanus* (Figure 173). No capsules are known for this species in Europe. Recent searches of lavoirs have revealed more locations (Piguet *et al.* 2007; Piguet 2009), and it seems to be increasing along rivers in Germany and perhaps in France. Dickson and colleagues raise the question of its dispersal. There are no known connections among the springs that feed them and no ducks have been seen at any of the lavoirs. How does it spread between lavoirs – I'm guessing it was animals.

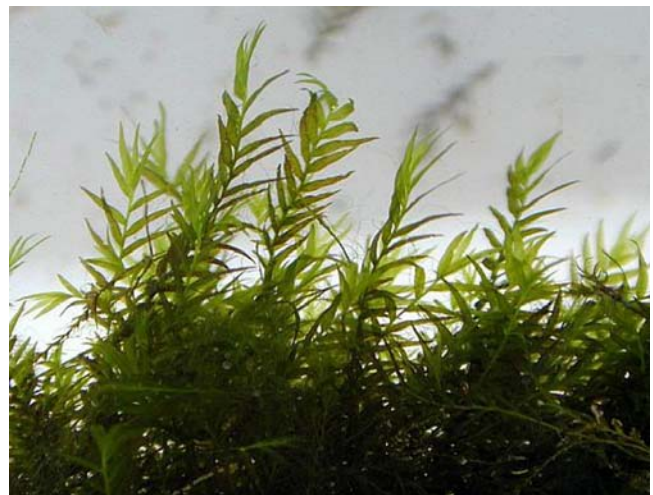


Figure 172. *Fissidens fontanus*, a moss that has appeared in lavoirs in France. Photo by Michael Lüth, with permission.



Figure 173. *Fissidens fontanus* in lavoir at Vouchoux, France. Photo courtesy of James Dickson.

Invasive Species

Invasive species represent the epitome of dispersal. Often it is the human species that serves as the dispersal vector. But whatever the vector, these species are good at getting there and successful at establishment.

One of the best known of the invasive bryophyte species is *Campylopus introflexus* (Figure 174) (Fudali 1992; Schirmel & Buchholz 2013). This species is responsible for altering the invertebrate communities in the acidic coastal dunes of Europe where it is able to form dense carpets. It caused changes in both body size and feeding preference among the arthropods, resulting in changes in hunting mode of spiders. Spiders increased in functional diversity, whereas carabid beetles had a reduction in functional diversity.

Another well-known invasive species is *Orthodontium lineare* (Figure 175) (Herben 1994). The key to success for this species is that it seems to be able to grow on whatever substrate is available, being limited only by available space.



Figure 174. *Campylopus introflexus*, an invasive species in Europe and parts of North America. Photo by Janice Glime.



Figure 175. *Orthodontium lineare*, an invasive species in Europe. Photo by David T. Holyoak, with permission.

Essl *et al.* (2013) assessed bryophyte invasions and what makes them work, using 82 regions spanning five continents as their data sources. They identified 139 species (106 mosses, 28 liverworts, 5 hornworts) that they

considered to be alien in at least one study region. They found that alien numbers were significantly higher on islands than on the studied continental regions. They identified 34 species as accidental hitch-hikers and 27 species as accompanying ornamental plants. These invasive species prefer strongly disturbed habitats [ruderal vegetation (growing on waste ground), roadsides, lawns], whereas forests and rocks are typically avoided. They concluded that the pattern of bryophyte invasions is different from that of tracheophytes.

Summary

Dispersal methods of vegetative diaspores of bryophytes include gravity, wind, water, and animals. Although most bryophytes are suitable for wind dispersal, even for fragments and specialized propagules, gravity accounts for the short distances to which most of these vegetative diaspores travel.

Splash cups are useful in dispersing gemmae in several liverworts and one family of mosses. Bryophytes getting frozen in ice or caught by flood waters can be carried considerable distances and vegetative dispersal in flowing water environs is essentially guaranteed.

Animal dispersal is probably more important than has been presumed, and includes earthworms, arthropods (insects, mites, pillbugs, spiders, harvestmen), slugs, amphibians, turtles, water birds, nest-building birds, and animal feet and fur. Birds and rodents often dislodge bryophytes while searching for food items among them and may carry fragments among their feathers/fur or attached to feet. Humans disperse bryophytes through their own footwear, vehicle tires, horticulture, and packing materials. However, none of the bryophyte vegetative propagules seems to be especially adapted for animal dispersal.

Although most bryophytes are best adapted to wind dispersal, even of fragments and specialized propagules, gravity accounts for the short distances to which most of these vegetative structures travel.

Acknowledgments

Andi Cairns kindly provided me with the flying fox and caddisfly stories and pictures. Geert Raeymaekers provided me with the *Fissidens* paper by Arts and Jan Janssens translated it for me. Thank you to Bryonetters for interesting discussions on diaspores. Steve Trynoski offered several suggestions after a critical reading of this subchapter.

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