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CHAPTER 18-2
LARGE MAMMALS: RUMINANTS – NON-CERVIDAE

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LARGE MAMMALS – RUMINANTS

Figure 1. ***Ovis aries*** (Soay sheep) resting on mat of mosses and grasses. Their herbivory on grasses can benefit the mosses. Photo from Biopix, through Creative Commons.

Moschidae – Musk Deer – *Moschus*

Green (1987) found that for Himalayan musk deer (***Moschus chrysogaster***; Figure 5), the choice of mosses as food was highly seasonal and usually avoided. They preferred forbs and woody plants in autumn and winter, positively avoiding bamboo leaves and mosses.

Ihl and Barboza (2007) compared the digestible value of a typical ruminant food for Arctic muskoxen (***Ovibos moschatus***; Figure 2) with that of the mosses ***Hylocomium splendens*** (Figure 3) and ***Tomentypnum nitens*** (Figure 4) from two locations in Alaska, USA. First they acclimated the muskoxen to mosses for 15 consecutive days. Using forages from ruminally **fistulated** muskoxen (having passageway cut from rumen to outside) they determined that ruminal degradation was not affected by previous acclimation to mosses.

Ruminal digestion caused a loss of dry matter during 48 hours of ruminal incubation of grasses (-49%), but mosses actually gained dry matter (44-57%) (Ihl & Barboza 2007). These changes were unaffected by suspending the forages in the rumen for 15 consecutive days, a procedure that could induce digestive enzymes in response to previously uneaten food sources. The incubated mosses gained 435-680% N and 18% fiber!

Figure 2. ***Ovibos moschatus***, a species that does not acclimate to digestion of mosses. Photo by Laurent Bélanger, through Creative Commons.

Figure 3. ***Hylocomium splendens***, a species common in the habitat of Arctic musk oxen. Photo from Botany Website, UBC, with permission.

Figure 4. ***Tomentypnum nitens***, a species common in the habitat of Arctic musk oxen. Photo by Jutta Kapfer, with permission.

Ihl and Barboza (2007) suggested that the gain in mass by the mosses was due to microbial colonization and adsorption of fibrous particles onto the absorbent mosses. When digested with acid-pepsin, the ruminally incubated mosses lost little nitrogen, whereas the hay lost 23% nitrogen. Ihl and Barboza suspected that winter consumption of mosses may be the result of selecting other plants that grow mixed within the moss community, thus explaining the presence of mosses in feces. The times when mosses occurred in the feces of these animals indicated low availability of preferred foods. As noted in an earlier chapter, Arctic birds likewise experience periods of low availability of desired foods, but their digestive processes differ, so studies on ruminants may not be indicative of digestibility for birds, or *vice versa*.

Figure 5. Himalayan musk deer (***Moschus moschiferus***), a species that eats mosses seasonally. Photo by Николай Усик, through Creative Commons.

Bovidae – Antelopes, Cattle, Gazelles, Goats, Sheep, and Relatives

Sheep – *Ovis*

Sheep can have a serious impact on the bryophyte communities. Downing (1992) suggested their impact on limestone bryophyte vegetation at Attunga, Australia. Rieley *et al.* (1979) reported that sheep graze in Welsh oakwoods on grasses until ultimately the bryophytes increase in abundance. Austrheim *et al.* (2007) found a similar increase in bryophytes, particularly ***Plagiothecium*** (Figure 6) and ***Rhodobryum roseum*** (Figure 7), under heavy grazing pressure of sheep in an alpine habitat in southern Norway.

Figure 6. ***Plagiothecium succulentum***, member of a moss genus that increases under heavy grazing of sheep in alpine areas of southern Norway. Photo by Hermann Schachner, through Creative Commons.

Figure 7. ***Rhodobryum roseum***, a moss species that increases under heavy grazing of sheep in alpine areas of southern Norway. Photo by Hermann Schachner, through Creative Commons.

In a study of ruminants from the Canary Islands, Rodríguez Suárez *et al.* (1990) found that mouflons [wild sheep; ***Ovis aries musimon*** (Figure 8) – an endangered species that has been successfully cloned (Loi *et al.* 2001; Trivedi 2001)] and Barbary sheep (***Ammotragus lervia***; Figure 9), native of northern Africa and introduced to Europe in the late 1800's) consumed bryophytes. Rodríguez Suárez and coworkers examined the stomach contents of 46 Corsica mouflons and 19 Barbary sheep from the highest area of La Palma and Tenerife islands. They found that 11 stomachs contained ***Grimmia laevigata*** (Figure 10), ***Grimmia*** sp., ***Racomitrium heterostichum*** (Figure 11), and 2 ***Didymodon*** sp. (Figure 12). These species grow on rocks in very dry habitats where other plants usually considered more suitable for consumption are generally absent. This suggests that the consumption of mosses is deliberate.

Figure 8. Mouflon (***Ovis aries musimon***), a moss consumer. Photo through Creative Commons.

Figure 9. Barbary sheep (***Ammotragus lervia***), a moss consumer, eating. Photo by Peripitus, through Creative Commons.

Figure 10. ***Grimmia laevigata***, a moss species consumed by mouflons and Barbary sheep in the Canary Islands. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Racomitrium heterostichum***, a moss species consumed by mouflons and Barbary sheep in the Canary Islands. Photo by J. C. Schou, with permission.

Figure 12. ***Didymodon rigidulus*** var ***icmadophilus***, in a moss genus sometimes consumed by mouflons and Barbary sheep in the Canary Islands. Photo by Michael Lüth, with permission.

Like the roe deer (***Capreolus capreolus***; Figure 13), grazing sheep are often transporters of bryophyte fragments and other propagules (Müller & Heinken 2011). Pauliuk *et al*. (2011) compared transport by two breeds of sheep. The twelve sheep in the study carried 16 species of mosses, but these represented only 40% of the moss species in the pasture (Figure 14). The belly and tail (Figure 13) were especially good at transport. The two breeds favored different species and frequencies. Those sheep that had a dense, curly fleece were able to carry larger species and more fragments than the breed with a fine, smooth fleece. The horizontally growing pleurocarpous mosses, as with roe deer, were more common than upright acrocarpous species; small species and mats were likewise more common than other forms. Large species, acrocarpous species, wefts, and turfs were underrepresented. Hooves, on the other hand, carried primarily acrocarpous colonist species.

Figure 13. Roe deer (***Capreolus capreolus***) lying down, a position that can put bryophyte fragments on the underbody and tail. Photo through Creative Commons.

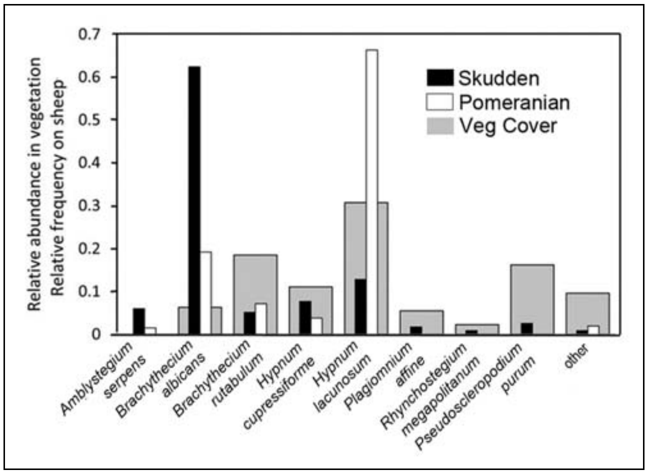

Figure 14. Comparison of bryophyte transport by two breeds of sheep: Skudden (n = 5, 117 fragments) and Pomeranians (n = 7, 2096 fragments). Grey bars indicate relative cover in the vegetation of the study site. Modified from Pauliuk *et al*. 2011.

It appears that at least some bryophytes receive other benefits from the sheep. They appear to maintain a habitat where these bryophytes can thrive. When the pasture is abandoned, bryophytes disappear due to their limited ability to compete with the invading tracheophytes (Takala *et al*. 2012). In southwestern Finland, cover, species richness, species density, and species diversity of bryophytes were all significantly higher in pastures that had been continuously grazed than those in abandoned grasslands. Takala defined three grassland habitats: (1) continuously grazed pastures, (2) previously abandoned pastures where grazing was re-established during 1990s, and (3) abandoned pastures. Among these, 17 species of bryophytes were suitable indicators of the three grassland types. Four of these indicated valuable grassland habitat.

In some areas, sheep graze in bogs (Rawes 1983). In two high altitude blanket bogs in the North Pennine uplands of England, cessation of sheep grazing led to major changes in the species composition, vegetation pattern, and structure of the bogs. Colonization of bare peat was slow in the exclosures. In particular, the leafy liverwort ***Diplophyllum albicans*** (Figure 15) declined, whereas it had previously been a constant companion for the cottongrass *Eriophorum* (Figure 16).

Figure 15. ***Diplophyllum albicans***, a leafy liverwort species that declines in the absence of sheep. Photo by Hermann Schachner, through Creative Commons.

Figure 16. Cottongrass (*Eriophorum vaginatum*), member of a common genus in peatlands of English uplands. Photo through Creative Commons.

Lee *et al*. (2013) examined blanket bog plant communities following various types of disturbance, including low-intensity sheep grazing. In the low-intensity grazing areas, ***Hypnum jutlandicum*** (Figure 17) cover and bryophyte species richness both increased in the least-disturbed plots. Overall bryophyte cover, however, did not. In fact, low-level grazing had little impact on the bryophyte communities. The most-disturbed plots, with a 10-year burn cycle, had an increase in ***Sphagnum*** spp. (Figure 18) over a 10-year period. I have to wonder if drafts created by the burning contributed to dispersal from neighboring communities.

Figure 17. The moss ***Hypnum jutlandicum*** with capsules. Photo by J. C. Schou, through Creative Commons.

Figure 18. ***Sphagnum girgensohnii***, representing a genus that increases in number of represented species following fire disturbance. Photo by Jutta Kapfer, with permission.

A common bryophyte in northern open areas is the moss ***Racomitrium lanuginosum*** (Figure 19). On a Scottish montane plateau, an area was fenced to provide a ski corridor (Scott *et al*. 2007). This area was used to establish permanent quadrats for a 12-year study. The fencing created a gradient in snow-lie and sheep use. ***Racomitrium lanuginosum*** cover was initially lower immediately adjacent to the fence. After 12 years, cover was reduced significantly in the 10 m adjoining the fence, whereas it was relatively stable further away. Scott and coworkers attributed the decline near the fence to greater snow-lie and heavier sheep usage. Grass cover near the fence increased. At the same time, ***Dicranum fuscescens*** (Figure 20) increased significantly near the fence. At more interior locations, there was a significant increase in ***Polytrichastrum alpinum*** (Figure 21) (Welch *et al*. 2005).

Figure 19. ***Racomitrium lanuginosum*** (white), a common moss species in Arctic and alpine areas, in Iceland. Photo by Manfred Morgner, through Creative Commons.

Figure 20. ***Dicranum fuscescens***, a moss species that increased near the exclosure fence. Photo by Michael Lüth, with permission.

During and Willems (2003) reported that many species of mosses have disappeared "almost completely" from the Dutch chalk grasslands (see Figure 22) after grazing ceased. These included characteristic acrocarpous mosses such as ***Tortella*** spp. (Figure 23), ***Trichostomum*** spp. (Figure 24), ***Aloina*** spp. (Figure 25), and ***Pleurochaete squarrosa*** (Figure 26), but also the pleurocarpous species ***Abietinella abietina*** (Figure 27) and ***Homalothecium lutescens*** (Figure 28) have experienced drastic reductions. Litter indicator species such as ***Brachythecium rutabulum***

(Figure 29) are concurrently increasing. As in other studies, these changes seem to be the result of cessation of grazing.

Figure 21. Alpine hairy cap moss, ***Polytrichastrum alpinum***, with capsules, a species that increased in interior regions of exclosure fence. Photo by David T. Holyoak, with permission.

Figure 22. Chalk grassland similar to those in the Netherlands. Photo by Rose and Trev Clough, through Creative Commons.

Figure 23. ***Tortella tortuosa***, a species that has disappeared from pastureland after grazing ceased. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Trichostomum crispulum***, in a moss genus that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.

Figure 25. ***Aloina aloides***, in a moss genus that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.

Figure 26. ***Pleurochaete squarrosa***, a moss species that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.

Figure 27. ***Abietinella abietina***, a species that has experienced severe decreases from pastureland after grazing ceased. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Homalothecium lutescens***, a species that has experienced severe decreases from pastureland after grazing ceased. Photo by J. C. Schou, Biopix, with permission.

Figure 29. ***Brachythecium rutabulum*** with capsules, a species that has increased in Dutch chalk grasslands after grazing was withdrawn. Photo by J. C. Schou, with permission.

Maelfait *et al.* (2007) similarly found that when dune vegetation was short-grazed by sheep (***Ovis aries***; Figure 30), the previously lichen-moss domination decreased. But one site changed during the same time to a cover of ~95% clipped grasses, mosses, and herbs, a physiognomy created by the grazing of sheep.

Figure 30. ***Ovis aries***, domestic sheep that causes lichen-moss domination to decrease. Photo through Creative Commons.

One of the operators in the moss vs tracheophyte story in pastureland is nitrogen (van der Wal *et al.* 2003). Air pollution has increased nitrogen deposition, causing massive invasion of grasses, sedges, and rushes in habitats ranging from forests to upland heaths. At the same time, grazing by livestock has increased in many locations, further degrading natural ecosystems. In the Scottish montane ecosystem, grazing and nitrogen deposition interact, causing a loss of the moss-dominated habitat and takeover by grasses and sedges.

One of our techniques to maintain diversity is to create green spaces where normal (non-pasture) vegetation is allowed to grow. However, even in these situations adjacent land use can significantly alter the bryophyte (and tracheophyte) communities of the natural vegetation (Piessens *et al.* 2008). Fortunately, these effects occur only within 5 m or less of the borders into heathland patches. In these transition zones adjacent to the borders, the invasive moss ***Campylopus introflexus*** (Figure 31) is common at grazed sites.

Figure 31. ***Campylopus introflexus***, an invasive moss species common in transition zones of grazed areas. Photo by Fitis-Sytske Dijksen, with online permission through <freenatureimages.com>.

Hill *et al.* (1992) found that ***Polytrichum commune*** (Figure 32) declined steadily in sheep exclosures (Figure 34) in Snowdonia, Wales. When sheep were fenced out of some areas, ***Polytrichum commune*** declined consistently, presumably due to competition for light by larger tracheophytes. Subsequent to sheep exclosure (Figure 33-Figure 35), voles became dominant among the herbivores and considerable growths of pleurocarpous mosses like ***Hylocomium splendens*** (Figure 3) and ***Pleurozium schreberi*** (Figure 36) invaded the mats of dead grass.

Figure 32. ***Polytrichum commune*** with capsules, a species that declines when sheep are removed. Photo by Bas Kers, through Creative Commons.

Figure 33. Nature Reserve, Helfdi, Iceland, in area where sheep are allowed to browse. Photo by Janice Glime.

Figure 34. Nature Reserve, Helfdi, Iceland, in exclosure where sheep are unable to browse. Photo by Janice Glime.

Figure 35. Wool on fence and plants on near side of fence in Iceland where grasses have been eaten by sheep. The exclosure prevents browsing on the opposite side where the grass is abundant. Photo by Janice Glime.

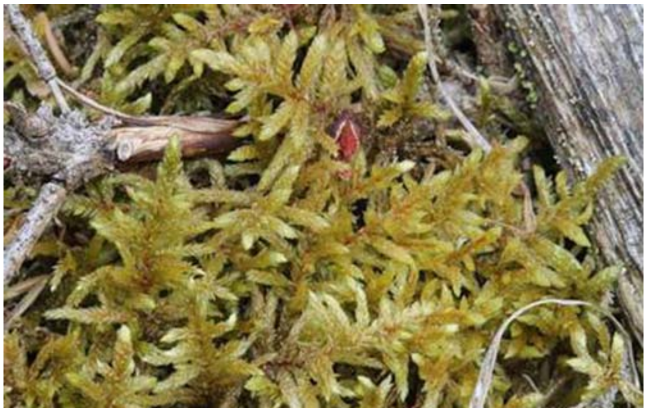

Figure 36. ***Pleurozium schreberi***, a species that becomes dominant among dead grass in sheep exclosures when voles invade. Photo by Rob Routledge, through Creative Commons.

But do sheep eat bryophytes? Rodriguez Suárez *et al.* (1990) reported 15 cryptogams in the stomachs of goats and sheep. The winter diet of feral Soay sheep (***Ovis aries***; Figure 30) at St. Kilda, Scotland, is comprised of 20-30% mosses (Milner & Gwynne 1974). When Virtanen and Crawley (2010) assessed the relationships of bryophytes with these St. Kilda sheep, they found that bryophytes and tracheophytes had opposite trends relative to elevation and sheep preference. The bryophytes reached their highest species richness at mid to high elevations and were negatively correlated with levels of sheep preference.

In a 1500 m^2 plot in a sheep pasture of the Netherlands, the moss layer disappeared almost totally, concomitant with the introduction of artificial fertilizer application and liquid manure (Arnolds 1989). This coincided with changes in the fungal populations, and those fungi associated with litter or bryophytes decreased in numbers.

In the alpine communities of the Scottish Highlands (Figure 37), one can find rare species (Miller *et al.* 2010). Nevertheless, this community is often heavily grazed by sheep. Many have suggested that the sheep hold the community in a **plagioclimax** (habitat or area in which influences of humans have prevented further ecosystem development). By excluding sheep from spring until fall for 10 years, Miller and coworkers found that graminoids initially increased in cover and the vegetation became taller. However, this stage did not last, and a decline in graminoid cover followed, with bryophytes becoming much more abundant. Permanent removal of sheep could cause a shift to a bryophyte-rich habitat tall-herb or scrub vegetation.

Figure 37. Alpine area in Scotland, where sheep often graze. Photo through Flickr Creative Commons.

Large herbivores can have an especially severe effect on bryophytes and other plants in Arctic and alpine regions (Austrheim *et al*. 2007). Using exclosures in an oceanic alpine ecosystem to stop sheep grazing, Austrheim and coworkers found that tracheophyte height increased, but the grass ***Deschampsia flexuosa*** (Figure 38) was the only tracheophyte that increased in cover in these exclosures. At the same time, six bryophyte species changed in abundance, favoring successional bryophytes. The mosses ***Straminergon stramineum*** (Figure 39) and ***Pohlia nutans*** (Figure 40) and the leafy liverwort ***Cephalozia bicuspidata*** (Figure 41) increased when sheep grazing ceased.

Figure 38. *Deschampsia flexuosa*, the only seed plant in an oceanic alpine ecosystem that increased in cover inside sheep exclosures. Photo by M. Porto, through Creative Commons.

Figure 39. ***Straminergon stramineum***, a species in an oceanic alpine ecosystem that increases when sheep grazing stops. Photo by Jutta Kapfer, with permission.

Figure 40. ***Pohlia nutans*** in Svalbard, a moss that benefits when sheep grazing stops. Photo by Michael Lüth, with permission.

Figure 41. ***Cephalozia bicuspidata***, a leafy liverwort species that increases when sheep grazing stops. Photo by Botany Website, UBC, with permission.

For ***Pohlia nutans*** (Figure 40), this is a surprise as it tends to occur in open, disturbed sites, and it also typically disappears when reindeer are fenced out (see above). Species of the mosses ***Brachythecium*** (Figure 29) and ***Plagiothecium*** (Figure 6) likewise decreased in the exclosures, while ***Polytrichum*** (Figure 32) species actually increased with grazing, as already noted in Wales by Hill *et al*. (1992) and elsewhere (Helle & Aspi 1983; Väre *et al*. 1996; Virtanen 2000; Olofsson *et al*. 2004), causing Austrheim *et al*. (2007) to consider the genus to be grazing resistant. The leafy liverworts ***Barbilophozia lycopodioides*** (Figure 42) and ***B. floerkei*** (Figure 43) decreased with grazing, whereas the latter disappeared in the exclosures in the Arctic reindeer study by Väre *et al.* (1995), where it was replaced by the lichen ***Cladina*** (Figure 44), a preferred food of reindeer. Nevertheless, exclosures did not result in changes in tracheophyte or bryophyte species richness or total cover of bryophytes and lichens in the Austrheim *et al*. study. A side effect of the exclosures and cessation of sheep grazing was that rodent grazing was also reduced.

Figure 42. ***Barbilophozia lycopodioides***, a leafy liverwort species that diminishes with sheep grazing. Photo by Hermann Schachner, through Creative Commons.

Figure 43. ***Barbilophozia floerkei***, a species that decreases with grazing but can disappear in exclosures. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Cladina*** spp., a genus that replaces ***Barbilophozia floerkei*** in reindeer exclosures in the Arctic. Photo by Peder Curman, through Creative Commons.

Goats – *Capra*

Goats are known to eat everything, right? So we shouldn't be surprised that in Washington State's Olympia National Park (Figure 45), invasive goats, introduced from Canada and Alaska for hunting, were destroying the sensitive ecosystem (Wright 1996). In particular, the very rare Olympic Mountain milk vetch (*Astragalus cottonii*; Figure 46) was a favorite food. But like we might expect of goats, these goats ate everything, including mosses. They further affected the habitat by trampling and wallowing. Rodriguez Suárez *et al*. (1990) also found that goats on the Canary Islands consumed mosses.

Figure 45. Olympic rainforest, Washington, USA, with bigleaf maples and epiphytic mosses. Photo from NPS, through public domain.

Figure 46. *Astragalus cottonii*, a rare but favorite food of goats in the Olympic Mountains, USA. Photo by Paul Slichter, with permission.

Nevertheless, feral goats (*Capra hircus*; Figure 47-Figure 48) in New Zealand avoided mosses, even though mosses were very abundant compared to preferred foods like *Schefflera digitata* (Figure 49) and ferns (Mitchell *et al*. 1987).

Figure 47. *Capra hircus aegagrus*, a feral goat and moss avoider in New Zealand. Photo by Murat Göktas through Creative Commons.

Figure 48. Wild goat, *Capra hircus aegagrus*, a goat that avoids eating mosses. Photo by Quartl, through Creative Commons.

Figure 49. *Schefflera digitata* in New Zealand, a preferred food of feral goats. Photo by Kahuroa, through Creative Commons.

Cattle – *Bos*

It is hard to imagine a big cow choosing to eat mosses, but Esteban *et al*. (2012) reported that in the Southern Patagonian *Nothofagus* forests (Figure 50), mosses, along with grasses, were the most grazed vegetation by cattle (***Bos taurus***; Figure 51). But contrasting with many rodent herbivores, the cattle consumed erect herbs and mosses in the summer, switching to shrubs in spring and winter. In fact, while sheep primarily grazed prostrate herbs, cattle grazed mosses, except in autumn.

With this kind of preference for mosses, it might be surprising that removing cattle herbivory can cause a decline in bryophytes. But further examination in southwestern Finland reveals that these weak moss competitors are actually disappearing as tracheophyte biomass increases (Takala *et al*. 2012). By contrast, in continuously grazed grasslands, bryophyte cover, species richness, species density, and species diversity were significantly higher than in abandoned grasslands. The importance of cattle grazing for maintaining the bryophyte species richness is further supported by Humphrey and Patterson (2000) in a riparian pasture and an upland conifer forest of the UK. Furthermore, they found almost no evidence that trampling had any effect on the bryophytes.

Figure 50. ***Nothofagus pumilio*** forest in Patagonia, a forest type where mosses are grazed by cattle (***Bos taurus***). Photo by through public domain.

Figure 51. ***Bos taurus***, Italian cattle, a species that consumes mosses and herbs in summer, but shrubs in spring and winter. Photo by Justine Peacock, through Creative Commons

Yet Ludvíková *et al*. (2014a, b) found that in their experimental comparisons in temperate *Agrostis capillaris* (Figure 52) grassland, it was the non-trampled plots that had the highest composition of bryophytes, with ***Rhytidiadelphus squarrosus*** (Figure 53) being the dominant species (95%). However, the non-trampled plots also had the lowest evenness index, indicating few dominant species and lots of uncommon species. Soil compaction played an important role in determining species composition (Ludvíková *et al*. 2014b).

Figure 52. *Agrostis capillaris*, a dominant grass where the moss ***Rhytidiadelphus squarrosus*** co-exists where trampling is limited. Photo by Kristian Peters, through Creative Commons.

Figure 53. ***Rhytidiadelphus squarrosus***, the dominant bryophyte in non-trampled plots in temperate grassland. Photo by Michael Lüth, with permission.

Ingerpuu and Sarv (2015) studied 15 Estonian coastal meadows (Figure 54) to compare effects of two different grazing pressures. During a 10-year period, the intensive grazing area experienced an increase in bryophyte diversity, but tracheophyte diversity did not increase, nor did that of the diaspore bank. Litter cover suppressed tracheophyte diversity. Nevertheless, tracheophyte and bryophyte diversity were positively correlated. And species composition remained unaffected by grazing intensity.

Figure 54. Estonian coastal meadow. Photo by KalervoK, through Creative Commons.

The Austrian agricultural landscapes (Figure 55) are rich in bryophytes, with a total of 506 species, 135 of which are considered to be endangered (Zechmeister *et al.* 2002). The upland landscapes dominated by moderately intensive cattle farming have significantly more endangered species than do the lowland landscapes with primarily intensive farming styles. Similarly, in comparing 24 grazed and 24 abandoned sites, Oldén *et al.* (2016) demonstrated that grazing had more impact on tracheophytes than on bryophytes in boreal wooded pastures. These are low-intensity livestock grazing areas in forested sites.

Figure 55. Austrian agricultural landscape. Photo through Creative Commons.

In Finnish seminatural grasslands, Takala *et al.* (2014) used 420 plots in 21 grasslands to examine species richness and cover of bryophytes. They found that grazing promotes bryophyte species richness, with colonists and perennial bryophytes in particular increasing. As expected, colonists were strongly associated with sites having a high proportion of bare ground.

Among the most sensitive ecosystems that must endure grazing are the cryptogamic crusts (Figure 56) in prairie areas. In a study in southeastern British Columbia, Rosentreter (2006) found that rock cover decreased significantly(?), p>0.10, in the Cattle Only Area from 1994 to 2004, whereas in the Wildlife Only Area there were no significant changes in litter, soil, bryophyte, or rock cover. Bryophytes and litter provided the predominant soil cover. But bryophyte cover overall increased nearly 70% from

1991 to 2003 ($p<0.10$), somewhat complicating the comparisons. Decreases in bryophyte cover in the exclosure area was driven by the increases in vascular plants and litter cover. Hence, bryophyte cover decreased with time in the exclosure, only the bryophytes increased in the wildlife and cattle area, and bryophytes did not change in the cattle only or wildlife only areas. Bryophytes are important contributors to these ecosystems by providing soil stability, nitrogen fixation, maintaining greater soil moisture, preventing runoff, facilitating infiltration, and enhancing seed germination and subsequent plant growth (Anderson *et al*. 1982a, b; Johnston 1997; McCune 2000).

Figure 56. Cryptogamic crust in Natural Bridges National Monument, Utah. Photo by Hihonjoe, through Creative Commons.

Some endangered species are benefitted by cattle and pony grazing. The disturbance by the cattle and wheel ruts in salt marshes (Figure 57) where they graze creates open soil patches that can be colonized by ***Bryum marratii*** (Figure 58) (Holyoak 2015). But the occurrence of the species in wheel tracks was short-lived because grazing was light and competitive grasses (*Agrostis stolonifera*; Figure 59) excluded it within two years (Callaghan 2017). In Ireland, when salt marsh grazing stopped, a dense saltmarsh grass cover developed, leading to extinction of the moss in Northern Ireland and threatening the species in other Irish locations (Lockhart *et al*. 2012).

Figure 57. ***Bryum marratii*** habitat at bay of Meallabhan, Scotland, a salt marsh. Photo by Michael Lüth, with permission.

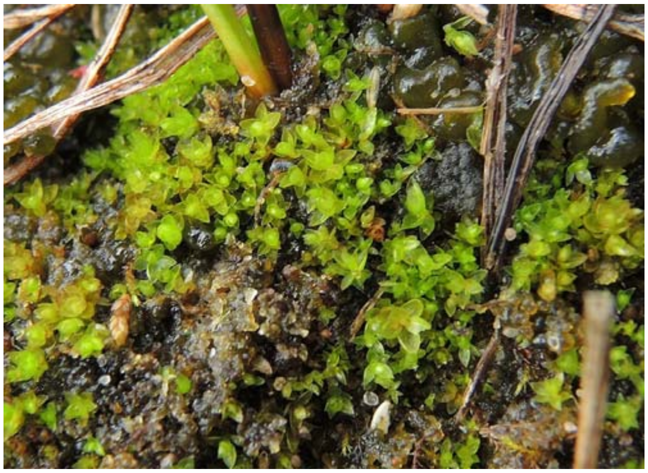

Figure 58. ***Bryum marratii***, in a salt marsh in Scotland. Photo by Michael Lüth, with permission.

Figure 59. *Agrostis stolonifera*, a salt marsh species that crowds out ***Bryum marratii***. Photo by Matt Lavin, through Creative Commons.

Bison – *Bison*

Even large, herbivorous, late Pleistocene mammals such as the Mylakhchinsk bison (see Figure 60-Figure 61) have died with bryophytes in their alimentary tract (Ukraintseva *et al.* 1978; Ukraintseva 1979).

Ukraintseva (1981) examined the gastrointestinal tracts of a variety of herbivorous mammals, including ***Bison*** (Figure 60-Figure 61), preserved from various periods during the Kargin interglacial period in the Indigirka River basin (Wisconsin period, 45,000-30,000 BP). During that time bogs spread, concurrent with the reduction of herbaceous communities suitable for pasturing. At the same time, rumen analysis indicated that the food composition changed for these large mammals, shifting to plants (Ukraintseva *et al.* 1978), including ***Sphagnum*** (Figure 62), from moist and water-logged communities (Ukraintseva 1981). These plants had considerably different nutrient quality, and the diet change led to the extinction of some of the herbivores.

Figure 60. American buffalo, ***Bison bison***, grazing. The Mylakhchinsk bison died with mosses in its gut. Photo through Creative Commons.

Figure 61. The European bison, ***Bison bonasus***, grazing amid grasses and mosses. Photo by Michael Gäbler, through Creative Commons.

Figure 62. ***Sphagnum austinii***; species of ***Sphagnum*** entered the food chain when climate change caused more bogs to develop. Photo by Michael Lüth, with permission.

Summary

Activities of sheep and other ruminants can contribute to dispersal of bryophytes as the fragments adhere to hooves and fur/hair/wool.

Many goats eat mosses, but feral goats in New Zealand seem to avoid them. Musk oxen may actually lose nutrients due to adsorption onto mosses they accidentally ingest. On the other hand, some sheep (***Ovis***) will eat bryophytes as a significant portion of their diet. Some goats (***Capra***) will eat them and others avoid them. In southern Patagonia, cattle (***Bos taurus***) will eat mosses in summer, but not in winter.

When grazing is light, it can favor such mosses as ***Rhytidiadelphus squarrosus***, **Polytrichaceae**, ***Brachythecium***, and ***Plagiothecium***. Colonizers like ***Pohlia nutans*** can benefit from disturbance and increased light. Leafy liverworts like ***Barbilophozia lycopodioides*** and ***B. floerkei*** decrease with grazing. Similarly, the moss ***Straminergon stramineum*** and the leafy liverwort ***Cephalozia bicuspidata*** benefit from exclosures. But the bryophyte communities depend on the site, with Arctic and alpine communities responding differently from more temperate ones. Rodents likewise can have a profound effect on the bryophytes, with communities responding differently depending on the foraging ruminants present.

Bryophytes suffer from manuring and urine, perhaps due to increased microbial decomposition, or to greater competition from the enriched tracheophytes.

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