The Impacts of Sheep Grazing on Bryophyte Communities in Iceland

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**Faculty of Life and Environmental Sciences
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90 ECTS thesis submitted in partial fulfillment of a
Magister Scientiarum degree in Biology

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Abstract

Depending on grazing intensity and growing conditions, disturbances caused by large herbivores have strong effects on vascular plant communities. However, it is not well known how sheep grazing activity affects bryophyte communities in tundra ecosystems.

The aim of this study was to assess the impacts of sheep grazing activity on the structure and composition of bryophyte communities in Iceland. Bryophyte communities were compared in three grazed and three ungrazed valleys, in two regions in Northwest and North Iceland. Sampling was stratified to allow for an investigation of different growing conditions with respect to exposure, elevation, and landform. Bryophyte layer depth, species diversity and abundance were measured, and species were grouped by growth form and life-history.

This study found that growing conditions shape bryophyte communities in Iceland, and within certain conditions sheep grazing activity has a detectable impact. There were more pronounced effects on the bryophyte communities in the west than the east-facing slopes, and in low than high elevation. The bryophyte layer was significantly deeper in ungrazed than grazed valleys, which indicates that sheep grazing may have impacts on ecosystem function. Species diversity did not differ greatly but was somewhat higher in grazed valleys within slopes that had a west-facing exposure. Pleurocarpous mosses, the most abundant growth form, were more abundant in grazed than ungrazed valleys, suggesting this growth form tolerates herbivore disturbances relatively well. Competitive and stress tolerate species were more abundant in grazed valleys, suggesting they cope with disturbances caused by sheep grazing activity. While the main drivers in shaping bryophyte communities are the growing conditions, sheep grazing activity also has some impacts to these communities in Iceland.

Útdráttur

Þung beit stórra grasbíta raskar samfélögum háplantna, en þó mismikið eftir vaxtarskilyrðum. Það er hins vegar lítið vitað um hver beitaráhrifin eru á mosasamfélög í túndruvistkerfum. Lítið er hins vegar vitað um áhrif beitar á samfélög mosa í túndruvistkerfum.

Markmið rannsóknarinnar var að meta áhrif sauðfjárbeitar á Íslandi á samfélög mosa og byggingu þeirra. Mosasamfélög í þremur dölum sem notaðir eru sem sumarhagar fyrir sauðfé voru borin saman við mosasamfélög í annars sambærilegum dölum með engri beit á Norðvesturlandi og Norðurlandi. Gagnasöfnun var lagskipt með tilliti til átta, hæðar í landi og landforms til að ná yfir mismunandi vaxtarskilyrði. Þykkt mosamottu, tegundafjölbreytni og samsetning voru mæld og tegundir flokkaðar eftir vaxtarformum og lífsögugerðum.

Niðurstöður sýndu að vaxtarskilyrði mótuðu samfélög mosa og að við vissar aðstæður hafði beitin einnig áhrif. Mosamottan var marktækt þykkara í dölum með engri beit sem bendir til að sauðfjárbeit hafi áhrif á starfsemi vistkerfa. Tegundafjölbreytni í hlíðum á móti vestri var heldur meiri í dölum með beit en án beitar. Algengasta vaxtarformið meðal mosategunda var pleurocarp sem eru mosar með gróhirslur til hliðar á stönglum fremur en á stöngulendum, og var þetta vaxtarform enn algengara í beittum dölum sem bendir til að það þoli rask af völdum sauðfjár fremur vel. Enn fremur voru lífssögugerðir sem sýna mikla samkeppnishæfni og eru stressþolnar algengari í beittum dölum en óbeittum. Þó vaxtarskilyrði virðist sterkasti mótunarþáttur mosasamfélaga sýnir þessi rannsókn að sauðfjárbeit hefur einnig talsverð áhrif.

To my son, Alex Ægir

Table of Contents

List of Figures

List of Tables

Acknowledgements

1 Introduction

1.1 What are bryophytes and why are they important?

The bryophyte group consists of mosses (*Bryopsida*), hornworts (*Anthocerotopsida*), and liverworts (*Hepaticopsida*) (Vitt, 1984; Steere & Schofield, 1985; Steere & Schuster, 1984). "Bryophyte" is a traditional term still used because until this point it is not clear whether these organisms are a monophyletic or a paraphyletic group (Goffinet & Shaw, 2000) (Vanderpoorten & Goffinet, 2009). Some of the earliest lineages of embryophytes (land plants) are found in the bryophyte group and they are generally regarded as transitional between aquatic plants and higher land plants (Goffinet & Shaw, 2000) (Vanderpoorten & Goffinet, 2009) (A. J. Shaw, Szovenyi, & Shaw, 2011). This group of plants does not have vascular tissue and are referred to as non-vascular plants (Steere & Schofield, 1985). Bryophytes do not flower and can be considered as cryptogams in this sense, and they reproduce via spore production and have an alternation of generations like all other land plants. (Goffinet & Shaw, 2000) (Vanderpoorten & Goffinet, 2009). Conservative estimates state there are more than 1,000 genera and over 20,000 species of bryophytes worldwide (Steere & Schofield, 1985) (A. J. Shaw et al., 2011). Because of the uniqueness of this group in regards to other land plants, they offer an opportunity to investigate a "primitive" group of plants and could offer insight on the structure and function of entire plant communities.

Studying bryophytes is crucial to understanding the complexities of an ecosystem because they play important roles in these systems, and can shape their structure and function in different ways. For example, the bryophyte layer may influence temperature and moisture within soil, and microbial biomass and activity, depending on its depth (Gornall, Jónsdóttir, Woodin, & Van der Wal, 2007), (Gornall, Woodin, Jónsdóttir, & Van der Wal, 2011). Furthermore, the bryophyte layer may sequester atmospheric pollutants, enhance soil surface-stability, and host elaborate food webs (Jónsdóttir, 2014; Jónsdóttir, Callaghan, & Lee, 1995; Jónsdóttir, Magnusson, Gudmundsson, Elmarsdottir, & Hjartarson, 2005; Lindo & Gonzalez, 2010; Turetsky et al., 2012). Bryophytes can shape vascular plant communities as well, and certain species may act as seed traps and build the basis for vascular plant establishment, and they even inhibit the spread of non-native species (Gornall et al., 2007; 2011; Jónsdóttir, 1991; Lindo & Gonzalez, 2010; Morgan, 2006; Virtanen, Johnston, Crawley, & Edwards, 2000).

In tundra ecosystems like what is found in Iceland, bryophytes are abundant and account for a significant portion of the species pool and overall vegetative biomass, however, there are large gaps in our understanding of these systems (Longton, 1988) (Jónsdóttir, 2011).

1.2 Herbivore disturbances on bryophyte communities

Large herbivores can cause disturbances to the composition of vascular plant communities, total biomass within a community, and can have impacts on ecosystem functioning due to their selection or avoidance of certain species (Adler, D, & W, 2001; Augustine & McNaughton, 1998; Jónsdóttir, 1991). Herbivores help to control abundance of plants because they often consume, trample, and otherwise impact these organisms (Milchunas, Sala, & Lauenroth, 1988; Olofsson, Kitti, Rautiainen, Stark, & Oksanen, 2001; Sørensen, Mikola, Kytöviita, & Olofsson, 2009). The intensity of the herbivory and the environmental conditions play major roles in determining the degree of the disturbance (Austrheim et al., 2008; Proulx & Mazumder, 1998). While grazing impacts on vascular plant communities are comparably well studied in the tundra, less is known about the effects of grazing animals on the structure and composition of bryophyte communities (Van der Wal & Brooker, 2004).

Disturbances caused by livestock herbivory will shift the state of bryophyte communities to more grass-dominated systems (Van der Wal, 2006). It has been observed that heavy grazing by pink-footed geese (*Anser brachyrhynchus*) could contribute to the compaction of the bryophyte layer (Jónsdóttir, 2014). This would lead to differences in the associated soil parameters and the entire plant community (Jónsdóttir, 2014). Large herbivores such as reindeer (*Rangifer tarandus*), will decrease the depth of the bryophyte layer, in turn this will have impacts on other ecosystem properties, for example, warming the soil (Van der Wal, van Lieshout, & Loonen, 2001). The two main avenues of how reindeer will decrease the depth of the bryophyte layer are by trampling and consumption (Van der Wal et al., 2001). Trampling is particularly damaging to bryophytes, due to their fragile structures (Jägerbrand & Alatalo, 2015). Reindeer trampling has been shown to be the largest impact of herbivores on plant communities when compared to defoliation and fertilization (Sørensen et al., 2009). The herbivore of interest for this study are sheep (*Ovis aries*), and it has been shown that most sheep do not commonly consume bryophytes, however, they certainly trample them and have the potential to have large impacts like what has been observed with reindeer (Prins, 1982; Van der Wal et al., 2001). If sheep have impacts on the depth of the bryophyte layer in the Icelandic tundra, this may be similar to the trampling impact that has been observed from reindeer, and this will ultimately alter the functioning of the ecosystem (Van der Wal et al., 2001). In this thesis, "sheep grazing" is referring to all the activity involved when sheep graze vegetation, e.g., consumption, as well as, trampling.

1.3 Objectives of this study

The main objective of this study is to contribute to a better understanding of how disturbance by sheep grazing influences bryophyte communities in Iceland. This is of interest because a natural ecosystem is able to deal with a certain degree of disturbance, however, introducing an anthropogenic disturbance, for example livestock grazing, will cause a shift in the ecosystem (Van der Wal, 2006). This is important in the fragile tundra like what is found in Iceland, because mammalian herbivory is a relatively new disturbance (arriving when humans first settled) and understanding the impacts from grazing can help to better maintain this system (Brown et al., 2012; Lawson et al., 2007; Thórhallsdóttir,

2002). Bryophytes act as a foundation to many different ecosystem functions, and it is important to investigate how a disturbance might restructure bryophyte communities, and thus disrupt ecosystem stability.

To understand how sheep grazing may affect different aspects of plant communities, it will be helpful to look at the impacts on bryophytes. To evaluate the impacts of sheep grazing on bryophytes, an investigation into three main aspects of bryophyte communities will be addressed. Does sheep grazing impact (1) the depth of the bryophyte layer, (2) bryophyte community diversity, (3) various bryophyte growth forms and life-history groups?

To address the research questions, a hierarchically designed investigation of currently grazed and ungrazed valleys in Iceland was conducted. Bryophyte layer depth, species richness, species diversity, and community function and structure were measured. An investigation into different habitats within the valleys was devised to determine in which habitats the grazing impacts were most detectable.

1.3.1 Assessment of bryophyte layer depth

As mentioned above, it has been shown that large herbivores have impacts on the depth of the bryophyte layer due to trampling (e.g., Van der Wal et al., 2001). It has also been shown that the depth of the bryophyte layer is directly linked to many other ecosystem processes (e.g., Gornall et al., 2007). The assumption is, during the act of grazing, sheep trample bryophyte mats and will impact their depth, thus having impacts to the ecosystem as a whole. It is predicted that trampling from sheep will decrease the depth of the bryophyte layer. The bryophyte layer depth will be less in grazed than in ungrazed valleys.

1.3.2 Assessment of bryophyte species diversity

There are different ways to assess community diversity, by addressing the within community diversity (*alpha*, *α*), among community diversity (*beta*, *β*), and the diversity within a landscape (*gamma*, *γ*) (Crist, Veech, Gering, & Summerville, 2003; Huston, 1979; Jost, 2007; Pélissier & Couteron, 2007; R. H. Whittaker, 1960; 1972; R. J. Whittaker, Willis, & Field, 2001). Some accepted indexes of *alpha* diversity and richness are: species richness (R. H. Whittaker, 1972), Simpson index (here also referred to as the Gini–Simpson index) (Simpson, 1949), and the Shannon index (Shannon, 1948). While both the Simpson and Shannon index give good measures to the abundance of species, they must be interpreted differently and thus can be used to answer different questions; these concepts will be discussed later in the methods section.

There are many factors that influence diversity in a biological community, and defining their importance can be challenging (Jost, 2006). The challenge comes from the idea that these factors are operating at different scales and are carried out under different timeframes (Jost, 2006). In scale sensitive analysis, it is important to link the scale at which the measurement of diversity is being taken with the scale that is affected by the recorded process (Huston, 1999).

As mentioned above, understanding the grazing intensity is a crucial component in research on disturbances caused by herbivory. When assessing questions pertaining to the impacts of grazing on diversity, some prior knowledge of the intensity is beneficial and can

help in making more accurate predictions. Grazing can cause a decrease in the competitive ability of plants in fertile habitats, which will result in a higher degree of species diversity, whereas, grazing in nutrient poor habitats can cause a reduction in species diversity (Proulx & Mazumder, 1998). Goose foraging supports the coexistence of bryophyte species at the centimeter scale and will thus increase richness at that scale (Jasmin, Rochefort, & Gauthier, 2008). In some larger scale investigations it was found that heavy grazing pressures by reindeer decrease bryophyte species richness and diversity (Eskelinen & Oksanen, 2006; Olofsson et al., 2001). In another large scale investigation it was found that heavy grazing by sheep actually increased the abundance of certain bryophyte species (Austrheim et al., 2008). The disturbance from low intensity grazing is hard to detect and bryophyte species richness does not always show signs of being affected by minimal grazing pressures (Austrheim et al., 2008). In another large scale investigation it was shown that lemmings can cause significant reductions in bryophyte cover depending on their population size (Moen, Lundberg, & Oksanen, 1993). Sometimes the disturbance from grazing is hard to detect and bryophyte species richness does not show any signs of being affected (Austrheim, Mysterud, Hassel, Evju, & Økland, 2007).

The grazing impact on bryophyte communities is a complex set of interactions, and there is certainly a range to the severity of this disturbance. This has to do directly with grazing intensity and the environmental conditions. The Intermediate Disturbance Model (IDM) offers a framework to help explain this range of impacts. The IDM expects communities to have maximum diversity while experiencing intermediate levels of disturbance (Connell, 1978; Fox, 1981; Fox & Connell, 1979; Shea, Roxburgh, & Rauschert, 2004; Wilkinson, 1999). Under intermediate levels of disturbance, species coexistence is maintained at a nonequilibrium state and no strong competitor can dominate completely (Connell, 1978; Grime, 1973). The IDM describes a unimodal or hump-shaped relationship where towards the ends of the disturbance spectrum there is a minimum level of diversity, and at the center or intermediate levels of disturbance, there will be a maximum level of diversity (Fox, 1981; Fox & Connell, 1979).

1.3.3 Assessment of structural and functional aspects of bryophyte communities

Similar to other land plants, bryophytes can be grouped into different classes based on structure and function. Research into growth form classification and life-history groups of bryophytes is limited and even more so when looking at grazing and trampling impacts on these groups (e.g., Austrheim et al., 2007; Gornall, Woodin, Jónsdóttir, & Van der Wal, 2009; Jägerbrand & Alatalo, 2015; Van der Wal et al., 2001). To understand how sheep grazing may affect functional aspects of bryophyte communities, it is helpful to study the abundance of bryophyte growth forms and life-history groups.

Growth form types can be defined as groups of plants that are similar in architecture or general physiognomy (During, 1992). Even though bryophytes are relatively small when compared to vascular plants, their growth can be very diverse, which makes finding a universally accepted definition of growth form types challenging. This is due to ongoing debate on the exact characteristics that define each group and inconsistent use of these terms in previous literature (La Farge-England, 1996). Grouping bryophytes into growth forms has been a strategy in studying these plants for sometime, perhaps the first classification of bryophyte growth-forms occurred over one hundred years ago

4

(Giesenhagen, 1910). Throughout the years these definitions have be tailored and improved to include the complete diversity of bryophyte growth forms throughout the world. One of the most recent classifications of bryophytes into growth forms comes from (La Farge-England, 1996). La Farge-England, (1996), was able to put forth four essential points to help define this terminology, and these were used in this study to define growth forms of bryophytes: 1) growth form is not synonymous with life form; 2) direction of growth does not necessarily imply perichaetial position; 3) cladocarpy is distinct from acrocarpy and pleurocarpy; 4) pleurocarpy is defined as having perichaetia terminal on lateral innovations that appear sessile and swollen along supporting axes. Juvenile leaves are morphologically different from those of vegetative branches. Perichaetial innovations lack lateral branch primordia and thus do not produce subperichaetial branches (Glime, 2007; La Farge-England, 1996). The specific groups used in this study will be discussed in more detail in the methods section.

The most likely impact of sheep on bryophytes is trampling, and while there has not been research investigating this specific interaction, there are some recent studies examining the impacts from human caused trampling on the various growth forms of bryophytes and this might help to predict the impacts of sheep (Gremmen, Smith, & van Tongeren, 2003; Jägerbrand & Alatalo, 2015; Van der Wal et al., 2001). Acrocarpous mosses seem to be more fragile when it comes to trampling, and pleurocarpous mosses increase closer to a trampling site (Jägerbrand & Alatalo, 2015). However, the responses of bryophyte growth forms to trampling are not always clear, opposite results have been found in another study addressing similar questions (Gremmen et al., 2003). These studies do show that trampling has some impact on bryophyte communities, but there is room for further research to try and determine how bryophyte species will respond.

The growth form types of bryophytes are based on the architecture of the plant alone, while life-history groupings also attempt to incorporate the organism's adaptations to its environment (During, 1992). In order to understand the theory behind the life-history groupings of bryophytes, one must first discuss plant strategies (Grime, 1977), the relative growth rate (RGR), and the notion of life strategies (During, 1979). Plant strategies are mechanisms that plants use to reproduce, defend, survive, and compete in an environment, and are based on two environmental factors, stress and disturbance (Grime, 1977). In this context stress is defined as something that restricts aspects such as available light, water, and nutrients, whereas, disturbance refers to impacts from things like herbivores, pathogens, anthropogenic influences, or natural catastrophes (Grime, 1979). In environments that have low levels of both environmental factors, competition becomes a key factor in determining community structure (Grime, 1977). The model from Grime, (1977), is best pictured as a triangle where each side represents a gradient from high to low competition, stress, and disturbance (also referred to as: the C-S-R model). Competitors are characterized by moderate to long life span, low reproductive effort, and high RGR or the growth rate relative to the size of the population (Grime, 1977; During, 1992). Species that are considered stress tolerators are characterized as having a long to very long life span, low reproductive effort, and low RGR, whereas the ruderals or those species that are first to colonize disturbed lands are characterized as having very short life spans, high reproductive effort, and high RGR (Grime, 1977; During, 1992).

The theory of life strategies for bryophytes is complex and the most notable attempt at defining these was proposed by During, (1979), and later revised (During, 1992). They were proposed based on three major trade-offs: 1) few large spores versus many small, 2)

5

survival of the difficult season as spores only (avoidance), versus survival of the gametophore (tolerance), and 3) for the tolerance group, potential life span of the gametophore versus reproductive investment (During, 1992) (Austrheim, Hassel, & Mysterud, 2005). The specific groups used in this study will be discussed in more detail in the methods section.

The life-history groups of bryophytes might respond differently to grazing pressures, certain life-history groups may be better adapted to withstand disturbance by herbivores than others, and conversely, certain groups may be more susceptible to herbivore disturbances. There has been limited research addressing issues dealing with grazing and the various life-history groups of bryophytes, one study found that early successional bryophyte species respond the quickest to a location where the grazing pressure is removed (Austrheim et al., 2007).

1.4 Predictions of this study

For this study, an investigation on bryophyte communities was carried out in the strongest possible grazing contrasts in Iceland. This study was conducted in conjunction with the doctorial study of Martin A. Mörsdorf where he assessed vascular plant communities in the same habitats (Mörsdorf, 2015b). Because this thesis research and that of Mörsdorf, (2015b), had the same design, it will allow for robust comparisons. An overall manuscript dealing with both studies is planned for the future and this thesis will only be addressing those questions pertaining to the impacts of sheep grazing on bryophyte communities.

For this study, three valleys were selected in Iceland that had not be grazed by sheep for anywhere between 30-60 years and compared to similar valleys in close proximity that were currently grazed (Figure 2.1, Table 2.1). Each valley was divided into different growing conditions based on topography. The growing conditions of each valley were characterized by changes in topography due to contrasting slope exposures, elevations within each slope, and convex and concave landforms within each elevation (Figure 2.3). These conditions were examined based on soil fertility defined by soil pH and nutrient content, which allowed for a test of the assumptions that these were contrasting growing conditions.

The overall prediction of this study is that disturbance caused by sheep grazing may alter bryophyte layer depth, species diversity, and community structure, and these differences will occur under different growing conditions. The IDM and previous studies on grazing impacts to bryophytes can be used to help guide predictions on how disturbance caused by sheep will affect bryophyte communities in Iceland. It is predicted that bryophyte species diversity will be higher in grazed locations when compared to ungrazed locations. This grazing effect will be dependent on the growing conditions. Based on previous research looking at the impacts of trampling on the different bryophyte growth forms, and knowledge on the architecture of the growth forms, it is predicted that sheep grazing and trampling will alter the growth form composition of bryophyte communities. The abundance of acrocarpous mosses will decrease and pleurocarpous mosses will increase under the pressures caused from herbivory. Based on the characteristics of certain life-history groups and the limited previous research on this subject, it is predicted that early successional groups, like the colonist group, will be more abundant in ungrazed than grazed locations.

6

2 Methods

2.1 Site descriptions

Six different valleys, in the Vestfirðir and Norðurland regions of Iceland were selected as study locations and represented the largest available contrasts of grazing pressure (Figure 2.1 & Figure 2.2). In order to limit the influence of unmeasured environmental variables, as well as, allow for comparison between the valleys, criteria of valley selection included similar physical characteristics like exposure to solar radiation, climate, and topography, as well as, current sheep grazing pressure and similar sheep densities (Table 2.1). All of the valleys fell into the low arctic subzone E of the arctic bioclimatic zonation classification (CAVM Team, 2003) and were located above 66° N. The 50 year average (1950-2000) growing season (June to August) temperature ranged from 7.6-8.1 °C and during the same timeframe the annual precipitation ranged from 667-1202mm with continuous snow cover from October until mid-June (WorldClim, 2015) (Table 2.1). The range of precipitation values was likely due to the amount of snow cover, where Ingjaldssandur likely received the most snow and Nesdalur received the least out of all the valleys in this study. All valleys were outside the Icelandic volcanic zone and were considered stable. All valleys were glacially eroded and were positioned on basic and intermediate extrusive rocks with intercalated sediments from the Neogene Period (Jóhannesson, Jakobsson, & Sæmundsson, 1990). The Vestfirðir region's topography was considered eroded basalt plateau, while Norðurland had higher mountains, however, all localities showed similar valley shape and exposure (Figure 2.2). The soil in these areas were not heavily influenced by frequent deposits of volcanic ash or tephra like in other places in Iceland, and can be classified as brown andosols with a pH that typically ranges from 4.5 to 6.5 (Arnalds, 2015).
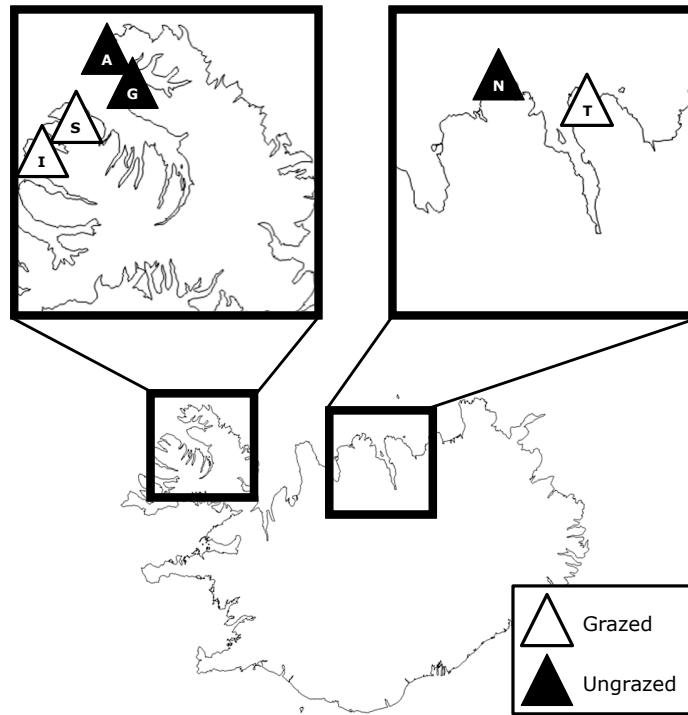
Figure 2.1. A map, north-up oriented, showing the locations of grazed and ungrazed valleys in Iceland that were used in this study. The Vestfirðir region contained four valleys and the Norðurland region contained two valleys. The filled triangles are the ungrazed valleys, and the open triangles are the grazed valleys. Ingjaldssandur (I), Skálavík (S), Thorgeirsfjördur (T), Aðalvík (A), Grunnavík (G), and Nesdalur (N).

Table 2.1. The valleys, located in Iceland, that were used in this study, with latitudinal (lat) and longitudinal (lon) locations. Temperature (temp) data represent averages during the growing season (June to August) and precipitation (prec) data are annual averages, both are based on a 50-year period (1950-2000) and obtained from http://www.worldclim.org. The current grazing pressure within each valley as reported by local farmers, and historical grazing pressure when that information was available.

Valley Name	Lat. Lon.	Temp. (°C)	Prec. (mm)	Current Grazing	Historical Land Use
Ingjaldssandur (I)	66.04N 23.69W	8.1	1202	~200 sheep	Heavily grazed
Skálavík (S)	66.17N 23.46W	7.8	1132	~500 sheep	Heavily grazed
Thorgeirsfjördur (T)	66.14N 18.16W	7.6	744	~1000 sheep	Unknown
Aðalvík (A)	66.34N 23.08W	7.7	989	0 sheep	Abandoned 1952
Grunnavík (G)	66.24N 22.86W	7.6	937	0 sheep	Abandoned 1962
Nesdalur (N)	66.17N 18.80W	7.6	667	0 sheep	Abandoned ~1990
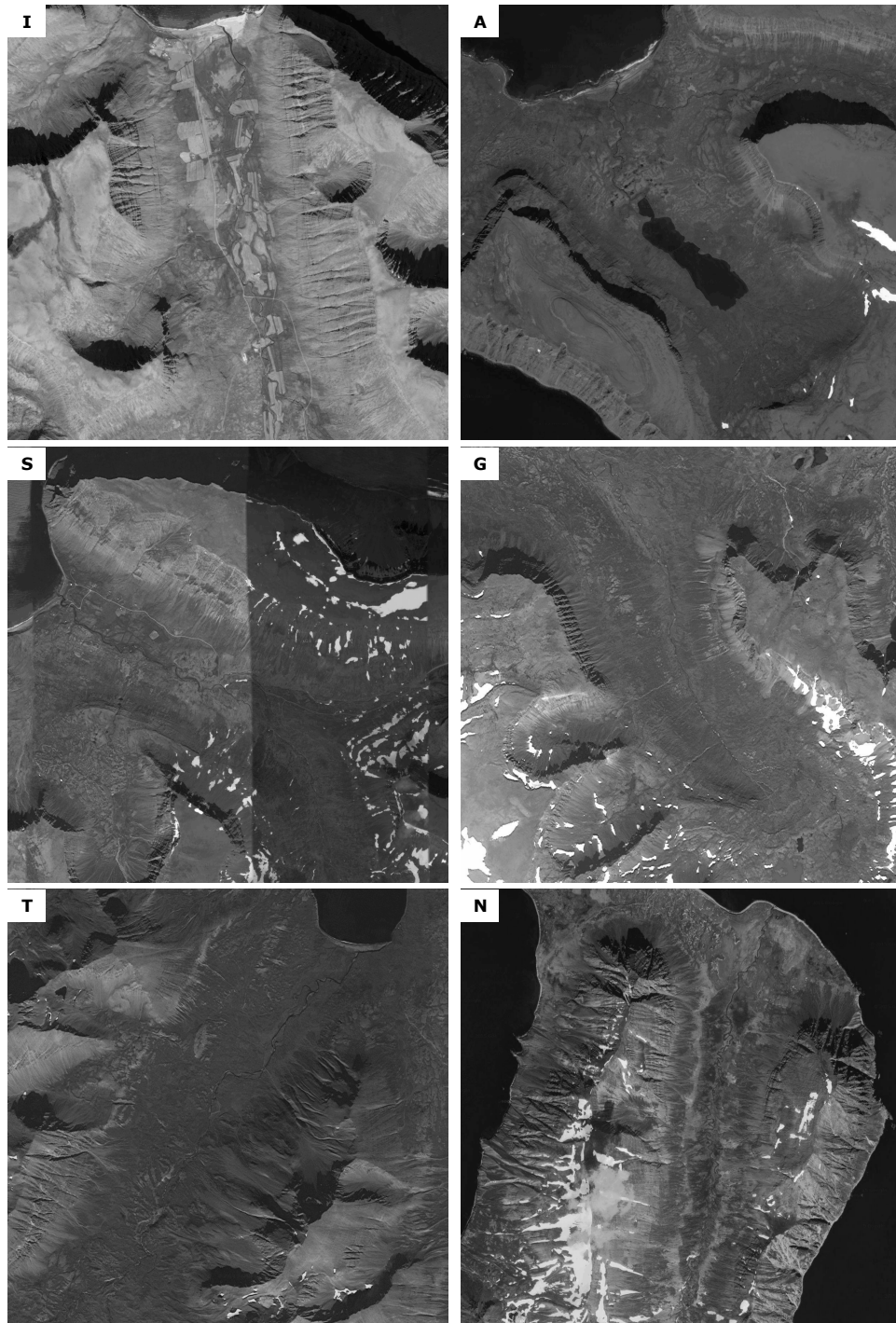
Figure 2.2. Maps, north-up oriented, showing the valleys in Iceland that were used in this study. The three maps on the left side (I, S, T) represent the grazed valleys, whereas the three maps on the right side (A, G, N) represent the ungrazed valleys. Ingjaldssandur (I), Skálavík (S), Thorgeirsfjördur (T), Aðalvík (A), Grunnavík (G), and Nesdalur (N). (Kahle, 2013).

The vegetation in all valleys was described as "low shrub tundra" which is defined as tundra that is dominated by low shrubs > 40 centimeters tall (CAVM Team, 2003). The prevailing wind direction for all selected valleys was from the east and northeast (Einarsson, 1976). Due to the wind direction, snow will accumulate more on the west-

facing than the east-facing slopes (Evans, Walker, Benson, Nordstrand, & Petersen, 1989). High elevations within each valley were characterized as having a shorter duration of snow cover and being xeric, being more exposed to weather differences, and having lower nutrient availability; the opposite conditions could be found in low elevations. Within the slopes of each valley, small streams shaped the topography and tended to create two main landform divisions, the first was classified as a concave unit, and the other was classified as a convex unit. This pattern leads to differences in growing conditions.

2.2 Experimental design and sampling

A stratified random design was devised to investigate the relationships between bryophyte communities and grazing pressure under different growing conditions. In order to properly investigate these relationships, emphasis was put on transparency and clearly defined criteria (Mörsdorf et al., 2015a). Using GIS software (ESRI, 2011) each of the valleys in this study were divided into three zones to ensure a complete investigation of the entire valley (Figure 2.3A). Zone A was closest to the sea (1-2km from the coastline), while zone C was the furthest from the sea (3-4km inland) (Table 2.2). Each zone was divided in half by the long axis of the valley where the main river was located, each of these divisions represented a valley slope (Figure 2.3B). Each slope had one randomly selected major transect out of twenty, going perpendicular from the long axis of the valley and from the river at the valley floor up the slope, for a total of six major transects per valley. The major transects each had two elevations (Figure 2.3C), for a total of twelve minor transects. The elevations were the same for all the valleys, and were selected to avoid anthropogenic hay fields, extreme slopes, and based on valley floor elevation (Table 2.2). Each minor transect was divided into two landforms. One landform was in a concave, snow-bed-like habitat; the other was in a convex, exposed habitat (Figure 2.3C). Each of these topographical units were regarded as different growing conditions, i.e., east/west-facing slopes, high/low elevation, and concave/convex landforms.
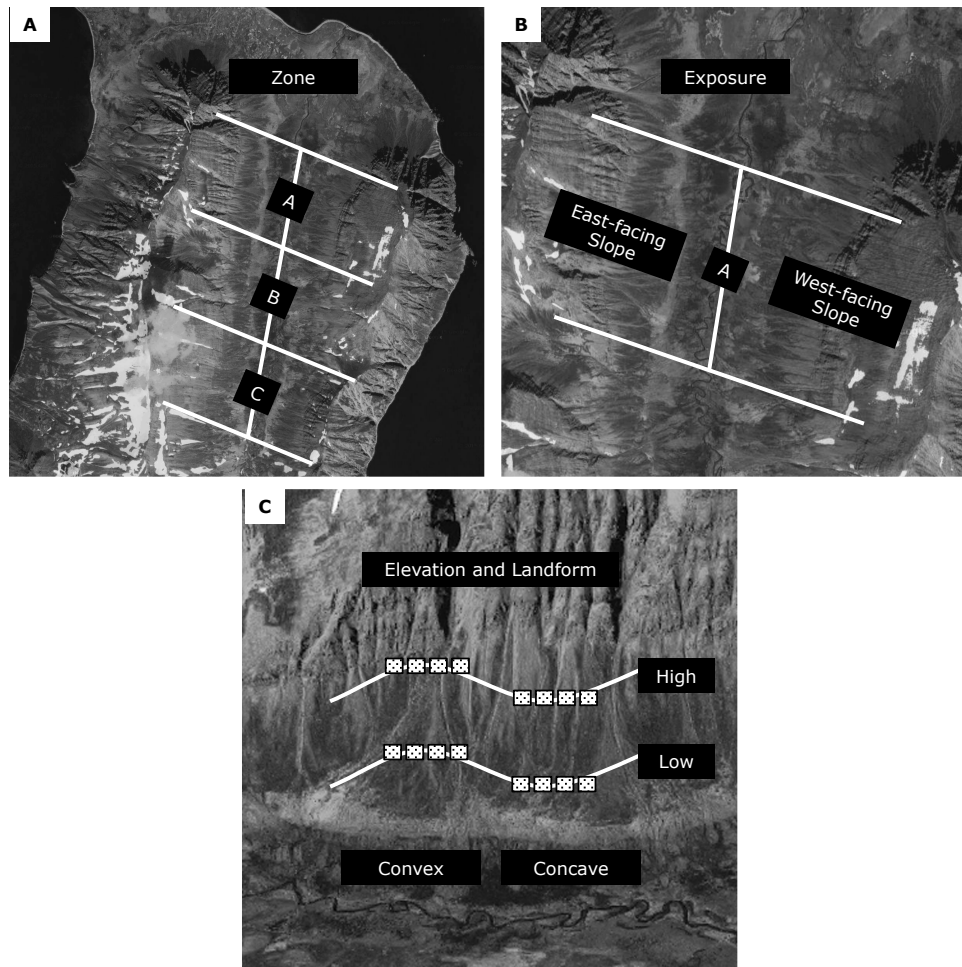
Figure 2.3. (A) A map, north-up oriented, showing how each valley used in this study and located in Iceland, was divided into three zones to insure investigation of the entire valley (in this case it is depicting Nesdalur valley, but the same procedure was used for all valleys). (B) A map, north-up oriented, showing how each zone was divided into two exposure divisions (east and west-facing slopes) (in this case it is depicting zone 'A', but the same procedure was used for all zones). (C) A projection showing how each slope was divided into two elevations (high and low) and two landforms (convex and concave), small dotted boxes represent the approximate location of the sampling plots (in this case it is depicting the east-facing slope, but the same procedure was used for both slopes). White lines are not drawn to scale. (Kahle, 2013).

Table 2.2. The three zones within each of the valleys that were used within this study and located in Iceland. Each zone was defined based on distance from the sea. They were divided into two elevations on each slope. Elevation was determined based on sea level and the elevation of the valley floor due to a general increase in valley floor elevation as one moves to the inner zones.

Zone	Distance from Sea (km)	Low Elevation (masl)	High Elevation (masl)
A	1-2	40	100
B	2-3	60	120
C	3-4	80	140

Data were collected in the year 2012 from the dates of July 12th until August 15th. In the field, two GPS coordinates were randomly selected that corresponded with the major transects constructed beforehand. Upon arrival at the location, a previously established set of guidelines determined if the location was a suitable sampling site. This included avoiding boulder and hay fields. If the site was not suitable, another transect was randomly selected. Upon arrival at a suitable location, a transition zone between concave and convex landforms was located and a 30-meter measuring tape was placed at this transition with each end extending into each landform.

Sampling included four plots (40x40 centimeters) within each landform (concave and convex) at an interval of three meters apart, for a total of 96 plots per valley (576 plots for all valleys) (Figure 2.3C). The point intercept method (PIM) was used to obtain frequencies and relative abundances of bryophyte species within each plot using a custom-built frame that had five pins with a diameter of two millimeters each. The pins were located in each corner of the square frame with one pin in the middle. This was a modified version of the traditional PIM and followed the notion of "many plots and few points per plot" which allows for vegetation sampling over extensive spatial scales (Bråthen & Hagberg, 2004).

Abundance measurements were made based on the recording of the first bryophyte species that was intercepted by each pin, receiving a value of 1.0. Bryophyte species present within the plot, but were not intercepted by a pin, were also identified and given a value of 0.1. Samples of bryophytes not identified in the field were taken to the lab for later identification (see bryophyte identification section). The depth of the bryophyte layer at each of the five pins was recorded by carefully placing a wooden pin through the bryophyte layer until it was stopped by the soil surface underneath the mat and measuring the distance on the pin that was enveloped by the bryophyte layer (Jónsdóttir, Crittenden, & Jägerbrand, 1999). This allowed for a calculation of the average depth of the bryophyte layer within each plot.

Soil samples were taken next to each plot, stored under cool conditions (maximum of four days), and later transported to the lab for analysis. Each sample was approximately 50 grams, and was taken to a depth of five centimeters. The soil samples were pooled by each concave and convex landform, meaning there were four samples per landform for a total of 24 samples per valley (144 samples for all valleys). The samples were air dried and then sieved in the lab using a two-millimeter mesh sieve. After sieving, the soil was crushed into a homogenized sample via mortar and pestle. Soil pH was recorded via a 1:5 soil to distilled water ratio (Oakton pH 510 series) (Blakemore, Searle, & Daly, 1987). Soil carbon and soil nitrogen for each landform was calculated by weighing approximately three milligrams of homogenized soil into a metal cylinder, this was put in a gas chromatography analyzer (Elementar Vario MAX Cube). A rough approximation of soil fertility was calculated using the soil pH, soil carbon, and nitrogen.

2.3 Bryophyte identification and classification

2.3.1 Identification

When it was possible, Edwin Liebig identified all bryophyte species in the field. For species that were not identified in the field, samples were carefully dried and packed for transportation back to the lab where Edwin Liebig made identifications. Bryophyte identification training came from Kristian Hassel et al. from the Museum of Natural History and Archaeology, Norwegian University of Science and Technology, located in Trondheim, Norway. All samples collected during this study are kept in a private collection. Literature used for identification included: (Hallingbäck, Lönnell, & Weibull, 2008; Hallingbäck, Lönnell, Weibull, & Hedenäs, 2006; Jóhannsson, 1985; 1989a; 1989b; 1990a; 1990c; 1990b; 1991; 1992a; 1992b; 1992c; 1993; 1995b; 1995a; 1996a; 1996b; 1997; 1998b; 1998a; 1999; 2000; 2001; 2002; 2003).

2.3.2 Species diversity

Within this study, the term diversity is referring to *alpha* diversity, or the within community diversity. *Alpha* diversity is useful because it allows analysis of the mean species measurements in a particular habitat at a more local scale, in this case, the plot scale. Species richness was defined as the number of species present in a sample, community, or taxonomic group. In this study, species richness was a measure used to address the differences in within community diversity (*alpha*) in terms of species occurrences (Table 2.3).

The Gini–Simpson index was used as a measure of probability that two individuals randomly selected from a sample belonged to different species, the probability of interspecific encounter (PIE). It is a dominance index that squares the abundance of all species, giving more weight to common species, thus rare species might be reduced relatively more than that of more abundant species (Jost, 2006). In this study, the Gini–Simpson index was a measure used to address the differences in *alpha* diversity in terms of relative abundance of species without giving extra weight to rare species (Table 2.3).

The Shannon index was used as a transformation of the relative abundance of species. The weight of all species was reduced relative to more rare species because of this transformation. The Shannon index increases as both the richness and the evenness of the community increase. In this study, the Shannon index was a measure used to address the differences in *alpha* diversity in terms of proportion of species while giving extra weight to rare species (Table 2.3).

Table 2.3. Equations used to calculate the bryophyte diversity measures addressed in this study.

Diversity Measure	Equation
Species Richness	$= \sum (n_i)$
	n_i: the occurrence of species i in a community
Gini-Simpson index	$= 1 - \sum (p_i^2)$
	p_i: the relative abundance of species i in a community
Shannon index	$= - (\sum (p_i * \ln (p_i)))$
	p_i: the relative abundance of species i in a community

2.3.3 Growth forms

To evaluate whether different growth forms respond to grazing, each species was classified into different groups. The growth form groups that were used for mosses were: acrocarpous, pleurocarpous, and *Sphagnum*. Acrocarpous mosses bear a capsule at the tip of their main stem, rhizoids, which draw nourishment from the soil, at the lower end of the stem, and have a radial arrangement of leaves (Figure 2.4A). Pleurocarpous mosses bear their capsules on short side branches, have a branching and creeping nature, and have the distinction of possessing leaves of different shape on its main stem and branches (Figure 2.4B). Additionally, liverworts were grouped together for analyses. The estimated effects of grazing on the abundance of these growth forms were analyzed. These groups were chosen based on guidance from Kristian Hassel and based on the species encountered in this study. A complete list of all bryophyte species encountered in this study and their growth form classification can be found in the appendix (Appendix Table 5.1).
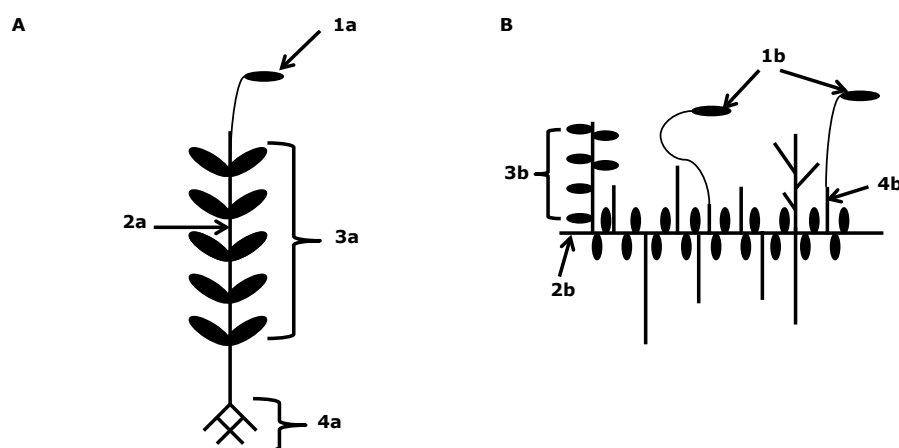
Figure 2.4. (A) Acrocarpous moss diagram, showing the capsule (1a), the main stem (2a), the radial leaves (3a), and the rhizoids (4a). (B) Pleurocarpous moss diagram, showing the capsules (1b), the main stem (horizontal)(2b), the leaves (3b), and the branching stems (vertical)(4b).

2.3.4 Life-history groups

The life-history groups used in this study were: 1) colonists, 2) colonist pioneer, 3) long-lived shuttle, 4) perennial competitive, 5) perennial stress tolerant (During, 1979; During, 1992). The colonist group can be characterized as those species that colonize open habitats, occurring in early stages of secondary succession and could be successful in productive habitats, whereas pioneers can be described as species that are able to colonize in harsh environments and tend to occur in the early stages of primary succession (During, 1992). In general, both of these groups have a potential life span of a few years and have relatively high reproductive effort, either asexually or sexually with small spores (During, 1992). These groups can often be found in habitats that are suitable for some years but can disappear later (During, 1992). The shuttle group can be characterized as having large spores and often found in microhabitats that periodically but predictably disappear and then reappear frequently within the same area as the original community (During, 1992). The perennial groups can be characterized by being present in more permanent habitats, with small spores (During, 1992). Pleurocarpous mosses are common in this group and certain tall acrocarpous mosses also belong to this group (During, 1992). The difference between the competitive and stress tolerant perennial species is primarily shown in varying growth rate (Furness & Grime, 1982), morphological plasticity (Rincon & Grime, 1989), and their degree of stress tolerance (During, 1992) (Table 2.4).

Table 2.4. Revised system of bryophyte life strategies (During, 1992). Italicized text marks bryophyte life-history groups used in this study (Colonists, Colonist pioneers, Long-lived shuttle, Perennial competitive, and Perennial stress-tolerant).

Potential life span (yr)	Spores		Reproductive effort
	Numerous, light (<20 µm)	Few, large (>20 µm)	
<1	Fugitives	Annual shuttle	High
Few	*Colonists*	Medium	
	Ephemeral colonists	Short-lived shuttle	
	Colonist pioneers	*Long-lived shuttle*	
Many	*Perennial competitive*	Dominants	Low
	Perennial stress-tolerant		

The estimated effects of grazing on the abundance of these life-history groups were analyzed. These groups were chosen based on guidance from Kristian Hassel and based on the species encountered in this study. A complete list of all bryophyte species encountered in this study and their life-history classification can be found in the appendix (Appendix Table 5.1).

2.4 Statistical analyses

The R statistical language and environment was used for all data evaluations (R Core Team 2016). The data were first assessed to determine if the defined growing conditions were characterized by differences in soil variables. Linear mixed effect models were fitted to detect differences in soil characteristics based on the different habitats representing different growing conditions in each valley, using the nlme package (Pinheiro, 2016) in R

(R Core Team 2016). The soil variable (soil nitrogen concentration, soil carbon concentration, or soil pH) was set as the response and each growing condition was individually set as a fixed factor. This procedure was followed for all soil variables and all growing conditions for exposure (east and west-facing slopes), elevation (high and low), and landform (concave and convex), for a total of nine models. The structure of these models were:

Soil Variable ~ Exposure | Random = Valley/Zone/Elevation/Landform

Soil Variable ~ Elevation | Random = Valley/Zone/Exposure/Landform

Soil Variable ~ Landform | Random = Valley/Zone/Exposure/Elevation

In order to get a picture of each valley, the most dominant species, growth forms, and life-history groups will be identified. Bryophyte layer depth, the diversity measures (species richness, Gini-Simpson, and Shannon index), growth forms and life-history groups will be investigated per valley. Species that were only found in each grazing regime will be documented in tables.

For bryophyte layer depth and for the various diversity measures, linear mixed effect models were fitted individually for each respective model. Grazing regime, by itself and including each growing condition, was included as a fixed factor to test for significant interactions. Models were fitted by including grazing, exposure and grazing, elevation and grazing, or landform and grazing as fixed effect interactions for a total of twelve models. Random variables based on the study design were assigned to the applicable models. The structure of these models were:

Response Variable ~ Grazing Regime | Random = Valley/Zone/Exposure/Elevation/Landform

*Response Variable ~ Grazing Regime * Exposure | Random = Valley/Zone/Elevation/Landform*

*Response Variable ~ Grazing Regime * Elevation | Random = Valley/Zone/Exposure/Landform*

*Response Variable ~ Grazing Regime * Landform | Random = Valley/Zone/Exposure/Elevation*

Using the same model structure as was used for the diversity measures, the abundances of all growth form groups (acrocarpous, pleurocarpous, *Sphagnum*, and liverworts) and life-history groups (colonists, colonist pioneer, long-lived shuttle, perennial competitive, and perennial stress tolerant) were analyzed. In these models all response variables had to be log transformed to fulfill the model assumptions for a total of 40 models dealing with these groups. These data were later back-transformed for graphical purposes.

When assessing all 61 linear mixed effect models used for this study, statistically significant model estimates were based on a five percent significance level, and marginally significant model estimates were based on a ten percent significance level.

3 Results

In general, *Hylocomium splendens, Pleurozium schreberi, Racomitrium lanuginosum (Raclan), Rhytidiadelphus squarrosus,* and *Sanionia uncinata* were the most common species observed in this study. The three most dominant bryophyte species found in grazed and ungrazed valleys, and within each growing condition is given in table 3.1.

Table 3.1 List of total number of hits to the three most dominant bryophyte species in the valleys used in this study, located in Iceland. The differences in total number of hits to the dominant bryophyte species are shown in ungrazed (U) and grazed (G) valleys, as well as, in these valleys and under different growing conditions based on east and west-facing slopes, high and low elevations, and concave and convex landforms. The species given in this table are: Hylocomium splendens (Hylspl), Pleurozium schreberi (Plesch), Racomitrium lanuginosum (Raclan), Rhytidiadelphus squarrosus (Rhysqu), and Sanionia uncinata (Sanunc).

Bryo. spp.	Growing Condition													
	All		West-Facing		East-Facing		High Elev.		Low Elev.		Concave		Convex	
	G	U	G	U	G	U	G	U	G	U	G	U	G	U
Hylspl	201.6	235.8	108.9	95.6	92.7	140.2	118.3	88.4	83.3	147.4	73.8	110.1	127.8	125.7
Plesch				45.5	71.3				78.4	64.0				64.1
Raclan		112.6				81.4		78.4					67.9	89.5
Rhysqu	207.4	162.3	138.5	82.5	68.9	79.8	61.5	68.9	145.9	93.4	109.2	105.8	98.2	
Sanunc	136.5		81.7				63.7				82.3	44.4		

3.1 Soil variables

Within all valleys, soil nitrogen concentration ranged from 0.04% to 2.35%, soil carbon concentration ranged from 1.01% to 38.47%, and the soil pH ranged from 4.3 to 6.7. Statistically significant differences in these soil variables were detected in growing conditions based on elevation and landform. There were no significant differences in any of the soil variables based on exposure. Both nitrogen and carbon concentrations were significantly higher in low [1.00% N; 18.47% C] than in high elevation [0.69% N; 13.42% C] (Figure 3.1A&B, Table 3.2), and significantly higher in concave [0.92% N; 17.47% C] than in convex landforms [0.76% N; 14.41% C] (Figure 3.1D&E, Table 3.2). Soil pH was significantly higher in high [5.58] than in low elevations [5.39] (Figure 3.1C), and in convex [5.58] than in concave landforms [5.40] (Figure 3.1F, Table 3.2). Based on the soil carbon and nitrogen concentrations observed in this study, the assumption that soil fertility was higher in low elevations and higher in concave landforms, when compared to their contrasting habitats, was supported. These results also support the assumption that these topographical units offer different growing conditions.
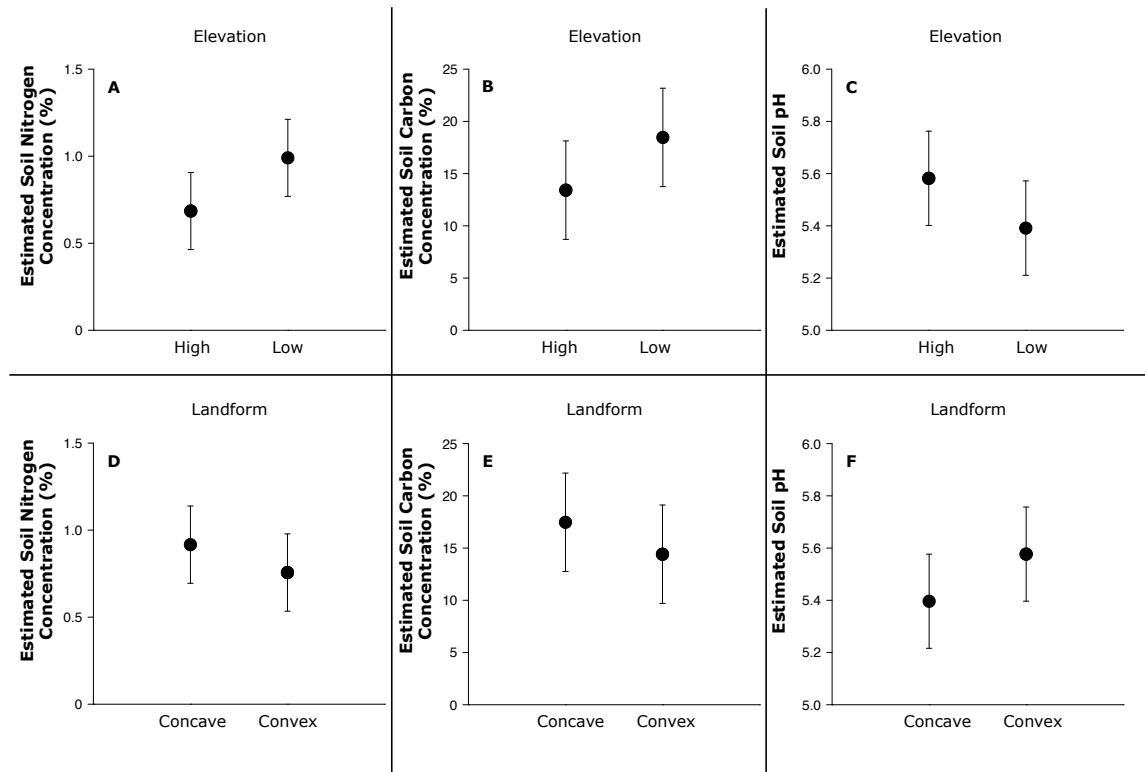
Figure 3.1. Model estimates (mean ± 95% confidence intervals) representing the soil chemistry found in the valleys used in this study, located in Iceland. The differences in soil nitrogen, carbon, and pH, are shown under different growing conditions based on high and low elevations (A, B, C), and concave and convex landforms (D, E, F). Values are given as estimates from linear mixed effects models and all differences are statistically significant based on a 5% level.

Table 3.2. Soil variables within each growing condition. All valleys used in this study, located in Iceland, are represented.

Soil Variable	Growing Condition	Model Estimate	Std. Error	df	t-value	p-value
Soil Nitrogen Concentration	High Elev.	0.69	0.12			
	Low Elev.	1.00	0.06	114	5.16	<0.001
	Concave	0.92	0.12			
	Convex	0.76	0.07	114	-2.36	0.020
Soil Carbon Concentration	High Elev.	13.42	2.46			
	Low Elev.	18.47	1.30	114	4.45	<0.001
	Concave	17.47	2.43			
	Convex	14.41	1.35	114	-2.56	0.012
Soil pH	High Elev.	5.58	0.10			
	Low Elev.	5.39	0.08	114	-2.72	0.007
	Concave	5.40	0.10			
	Convex	5.58	0.09	114	2.22	0.029

3.2 Bryophyte layer depth

Nesdalur valley had the highest bryophyte layer depth per plot [7.3 centimeters (cm)], whereas Ingjaldssandur and Skálavík valleys had the lowest depth per plot [3.6cm; 3.9cm] (Figure 3.2). The lowest recorded bryophyte layer depth, other than zero, was 0.2cm. The highest recorded bryophyte layer depth was 23.8cm found on an east-facing slope under low elevation, and convex growing conditions in Grunnavík valley. Recordings for bryophyte layer depth were not made on a species-specific scale, but field observations suggest that the deepest layers were found in mats of *Racomitrium lanuginosum*, *Pleurozium schreberi*, and *Hylocomium splendens*. The thinnest layers could be found under numerous species, for example species found in *Dicranum spp*.
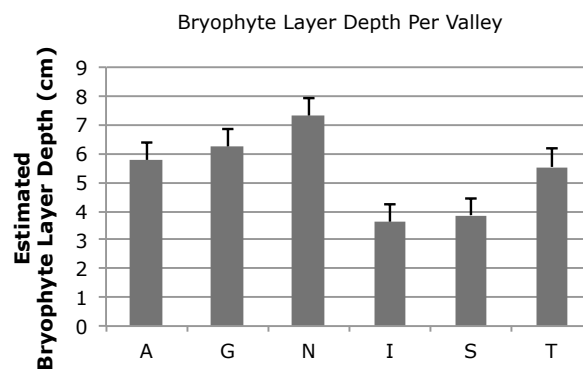
Figure 3.2. Model estimates (mean ± one standard error) representing the average depth of the bryophyte layer per plot in all valleys used in this study, located in Iceland. The valleys shown in this figure are: Aðalvík (A), Grunnavík (G), Nesdalur (N), Ingjaldssandur (I), Skálavík (S), and Thorgeirsfjördur (T). The three valleys on the left represent ungrazed, while the three on the right represent the grazed valleys.

Within grazed valleys, the depth of the bryophyte layer was less when compared to ungrazed valleys, and this difference was marginally significant based on a 10% level (Table 3.3). The model estimates on mean depth of the bryophyte layer per plot was 1.95cm less in grazed [4.30cm] than ungrazed [6.25cm] valleys (Figure 3.3, Table 3.3). This difference becomes stronger when stratified by growing conditions.

All Growing Conditions

Figure 3.3. Model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on bryophyte layer depth in the valleys used in this study, located in Iceland. The filled triangle is the estimated bryophyte layer depth per plot for ungrazed, and the open triangle is the estimated depth per plot for grazed valleys. Values are given as estimates from linear mixed effects models and are marginally significant based on a 10% level.

Within habitats found on east-facing slopes there was a statistically significant difference in the depth of the bryophyte layer based on a 5% level (Table 3.3). Under growing conditions found on east-facing slopes, the model estimates on mean depth of the bryophyte layer per plot were 3.0cm less in grazed [4.88cm] than in ungrazed [7.88cm] valleys (Figure 3.4A, Table 3.3). The lowest recorded value of bryophyte layer depth in ungrazed east-facing conditions, other than zero [0.4cm], was twice that of the grazed counterpart [0.2cm]. Within ungrazed valleys, the mean depth of the bryophyte layer per plot was 3.14cm greater in east-facing [7.88cm] than in west-facing [4.74cm] slopes (Figure 3.3A&B, Table 3.3).

East-Facing Slope   West-Facing Slope

Figure 3.4. Model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on bryophyte layer depth in the valleys used in this study, located in Iceland. Illustrating differences found in different growing conditions based on exposure ('A' east; 'B' west-facing slope). The filled triangles are the estimated bryophyte layer depths per plot for ungrazed, and the open triangles are the estimated depths per plot for grazed valleys. Values are given as estimates from linear mixed effects models and "" indicates statistically significant effects based on a 5% level.*

Within habitats found in low elevation there was a statistically significant difference in depth of the bryophyte layer based on a 5% level (Table 3.3). Under growing conditions found in low elevation, the model estimates on mean depth of the bryophyte layer per plot were 2.59cm less in grazed [4.87cm] than in ungrazed [7.46cm] valleys (Figure 3.5B, Table 3.3). Within ungrazed valleys, the mean depth of the bryophyte layer per plot was 2.31cm greater in low [7.46cm] than in high [5.15cm] elevations (Figure 3.5A&B, Table 3.3).
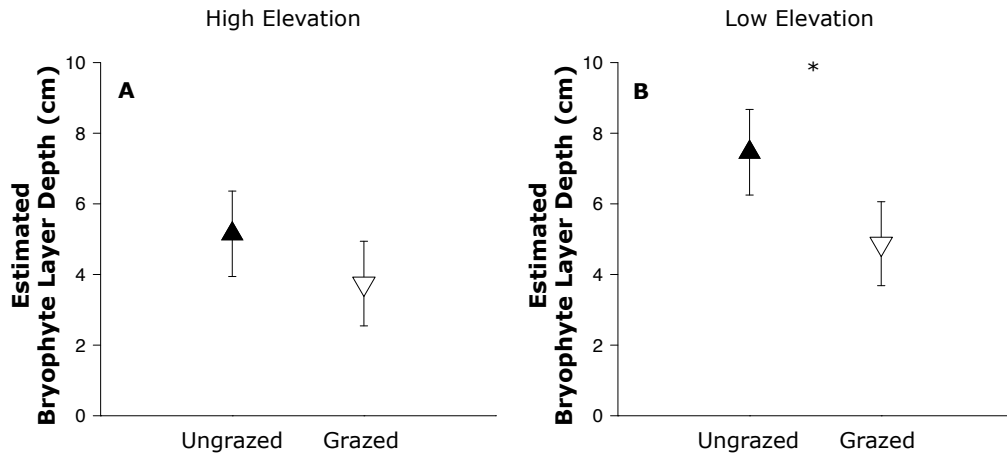
Figure 3.5. Model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on bryophyte layer depth in the valleys used in this study, located in Iceland. Illustrating differences found in different growing conditions based on elevation ('A' high; 'B' low). The filled triangles are the estimated bryophyte layer depths per plot for ungrazed, and the open triangles are the estimated depths per plot for grazed valleys. Values are given as estimates from linear mixed effects models and "" indicates statistically significant effects based on a 5% level.*

Within habitats found in convex landforms there was a statistically significant difference in depth of the bryophyte layer based on a 5% level (Table 3.3). Under growing conditions found in convex landforms, the model estimates on mean depth of the bryophyte layer per plot were 2.52cm less in grazed [4.92cm] than in ungrazed [7.44cm] valleys (Figure 3.6B, Table 3.3). Within ungrazed valleys, the mean depth of the bryophyte layer per plot was 2.23cm greater in convex [7.44cm] than in concave [5.21cm] landforms (Figure 3.6A&B, Table 3.3).
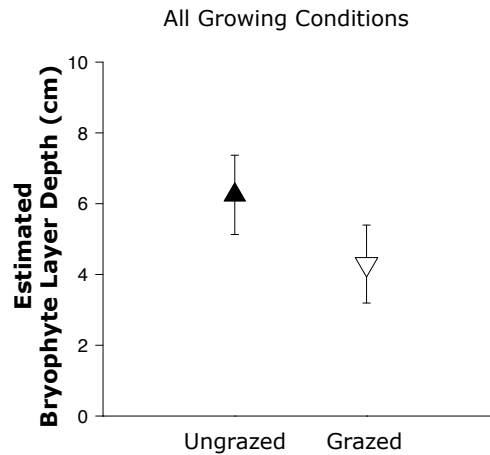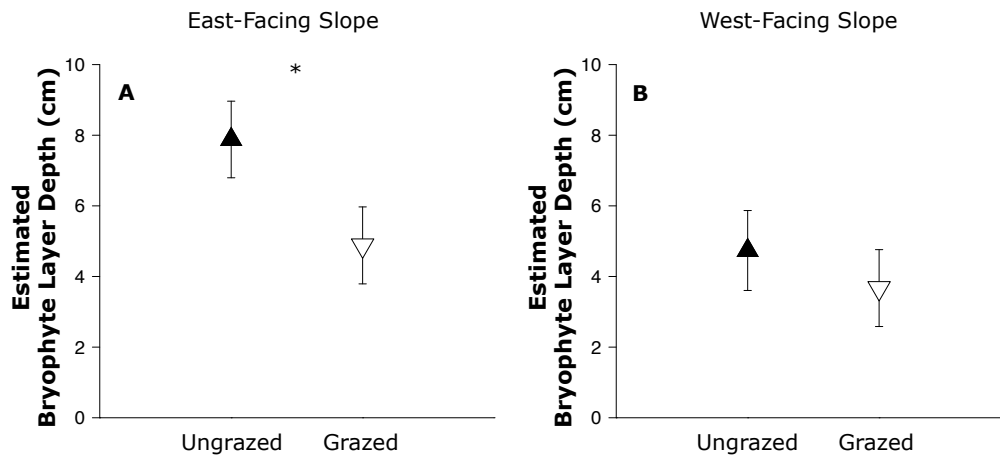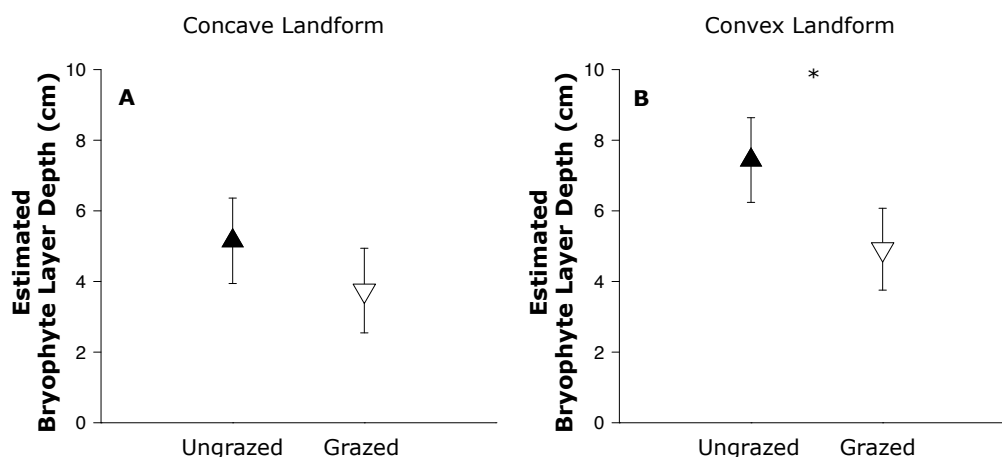
Figure 3.6. Model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on bryophyte layer depth in the valleys used in this study, located in Iceland. Illustrating differences found in different growing conditions based on landform ('A' concave; 'B' convex). The filled triangles are the estimated bryophyte layer depths per plot for ungrazed, and the open triangles are the estimated depths per plot for grazed valleys. Values are given as estimates from linear mixed effects models and "*" indicates statistically significant effects based on a 5% level.

Table 3.3 Differences in bryophyte layer depth between ungrazed and grazed valleys, and within each growing condition. All valleys used in this study, located in Iceland, are represented.

Response Variable	Growing Condition	Estimate Ungrazed	Estimate Grazed	Std. Error	df	t-value	p-value
	All	6.25	4.30	0.80	4	-2.44	0.07
	East-Facing	7.88	4.88	0.78	4	-3.83	0.01
	West-Facing	4.74	3.68	0.80	4	-1.33	0.25
Bryophyte Layer Depth	High Elev.	5.15	3.74	0.87	4	-1.63	0.18
	Low Elev.	7.46	4.87	0.86	4	-3.00	0.04
	Concave	5.21	3.65	0.84	4	-1.86	0.14
	Convex	7.44	4.92	0.85	4	-2.97	0.04

3.3 Community diversity

Nesdalur valley had the highest species richness per plot [6.4], whereas Ingjaldssandur valley had the lowest richness per plot [4.3] (Figure 3.7). Skálavík and Nesdalur had the highest index of both Gini-Simpson [0.56, 0.54] and Shannon diversity [1.08, 1.09], whereas Aðalvík and Grunnavík had the lowest Gini-Simpson index [0.45, 0.45] and Aðalvík, Grunnavík, and Ingjaldssandur had the lowest Shannon index of diversity [0.87, 0.81, 0.86] (Figure 3.7). Within individual plots, the highest recorded value of Gini-Simpson index was 0.83 found on an east-facing slope under high elevation, and convex growing conditions in Aðalvík valley. The highest recorded value of Shannon index was

1.89 found on an east-facing slope under low elevation, and concave growing conditions in Nesdalur valley, and the highest recorded number of species was 13 found in this same plot.

Bryophyte Species Richness Per Valley

Gini-Simpson Diversity Per Valley

Shannon Diversity Per Valley
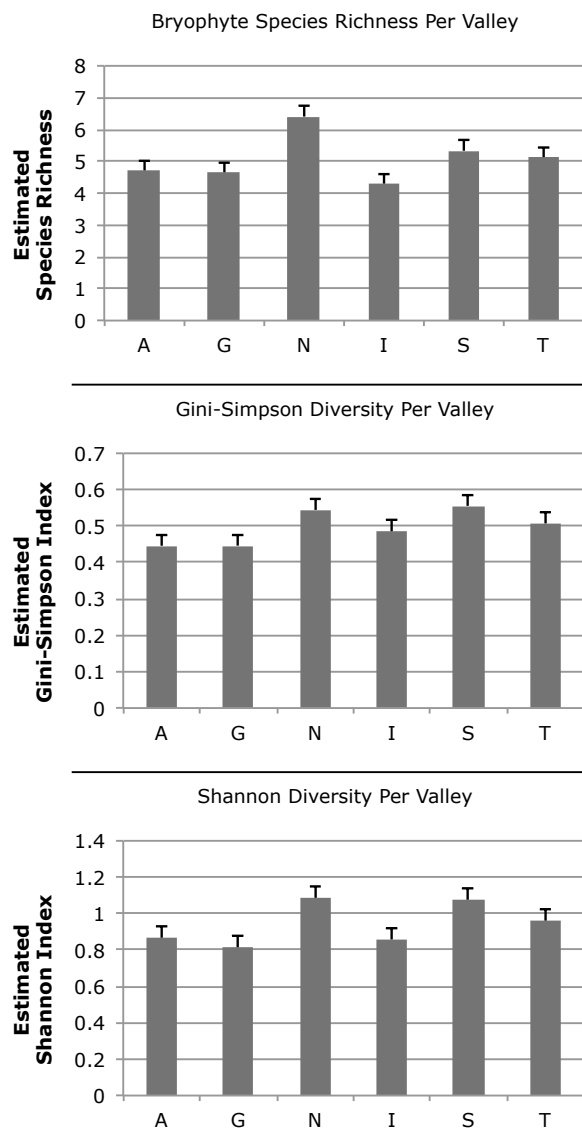
Figure 3.7. Model estimates (mean ± one standard error) representing bryophyte species richness, Gini-Simpson, or Shannon Index of diversity per plot in all valleys used in this study, located in Iceland. The valleys shown in this figure are: Aðalvík (A), Grunnavík (G), Nesdalur (N), Ingjaldssandur (I), Skálavík (S), and Thorgeirsfjördur (T). The three valleys on the left of each figure represent ungrazed, while the three on the right represent the grazed valleys.

There were no significant differences detected in grazed versus ungrazed valleys in general for species richness, Gini-Simpson, or Shannon Index (Table 3.6). However, more species where found in ungrazed [60] than in grazed [56] valleys, and this pattern is the same for all growing conditions (Table 3.4). Within this study, there were 12 species that were only

found in ungrazed valleys and eight species that were only found in grazed valleys (Table 3.5).

Table 3.4. The bryophyte species richness for all valleys (all conditions), and divided into growing conditions based on exposure (east and west-facing slopes), elevation (high and low), and topography (concave and convex landforms). In all cases the ungrazed had higher richness when compare to the grazed counterpart. All valleys used in this study, located in Iceland, are represented.

Growing Condition	Bryophyte Species Richness	
	Ungrazed	Grazed
All	60	56
East-Facing	49	45
West-Facing	50	41
High Elevation	46	44
Low Elevation	50	43
Concave	56	50
Convex	47	41

Table 3.5. List of bryophyte species unique to ungrazed and grazed valleys used in this study, located in Iceland. Including growth form (pleurocarpous (P), acrocarpous (A), Sphagnum (S), and liverwort (L)), and life-history group (colonist (COL), colonist pioneer (COP), long-lived shuttle (LLS), perennial competitive (PEC), and perennial stress tolerant (PST)).

Unique to Ungrazed Valleys	Growth form	Life-history	Unique to Grazed Valleys	Growth form	Life-history
Barbilophozia floerkei	L	PST	*Andreaea rupestris*	A	COL
Conostomum tetragonum	A	COL	*Aulacomnium palustre*	A	PEC
Cratoneuron filicinum	P	PEC	*Kiaeria starkei*	A	COP
Ditrichum flexicaule	A	COL	*Lescuraea incurvata*	P	PST
Fissidens osmundoides	A	PEC	*Pohlia nutans*	A	COL
Grimmia longirostris	A	COL	*Racomitrium sudeticum*	P	COP
Jungermannia exsertifolia	L	COL	*Scapania undulata*	L	COL
Mnium spinosum	A	LLS	*Schistidium papillosum*	A	COL
Philonotis seriata	A	PEC			
Racomitrium aciculare	P	COP			
Sphagnum squarrosum	S	LLS			
Timmia austriaca	A	PEC			

Within habitats found on west-facing slopes there was a marginally significant difference in the Gini-Simpson index of diversity based on a 10% level (Table 3.6). Under growing conditions found on west-facing slopes, the model estimates of Gini-Simpson index were 0.11 greater in grazed [0.53] than in ungrazed [0.42] valleys (Figure 3.8B, Table 3.6). This means there was an 11% greater probability of interspecific encounter (PIE) within grazed west-facing slopes than in the comparable ungrazed sites. There were no significant differences detected within these habitats for species richness or Shannon Index (Table 3.6). However, more species where found in ungrazed east-facing slopes [49] than in the

comparable grazed sites [45], and in ungrazed west-facing slopes [50] than in the comparable grazed sites [41] (Table 3.4).
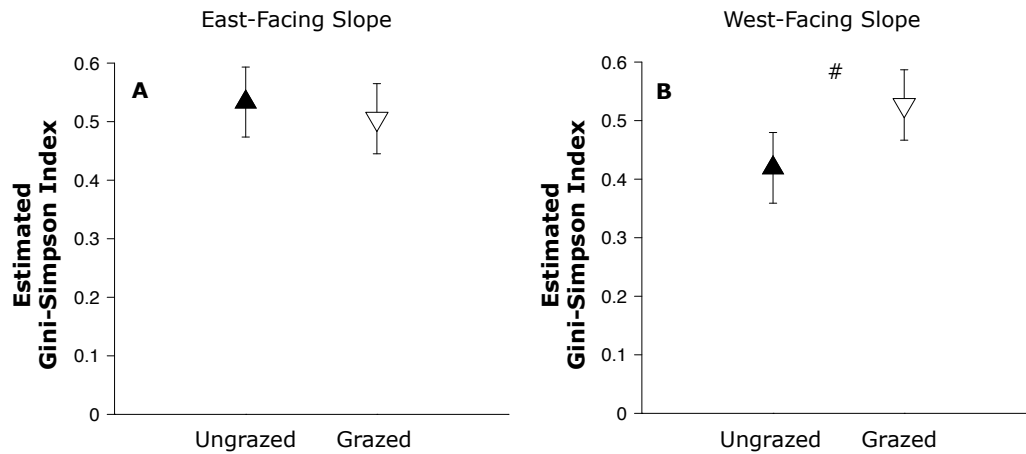
Figure 3.8. Model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on the Gini-Simpson index of diversity in the valleys used in this study, located in Iceland. Illustrating differences found in different growing conditions based on exposure ('A' east; 'B' west-facing slope). The filled triangles are estimated Gini-Simpson index of diversity per plot for ungrazed, and the open triangles are the estimated index per plot for grazed valleys. Values are given as estimates from linear mixed effects models and "#" indicates statistically significant effects based on a 10% level.

There were no significant grazing effects detected on species richness, Gini-Simpson, or Shannon Index between high and low elevation (Table 3.6). However, more species where found in ungrazed high elevations [46] than in the comparable grazed sites [44], and in ungrazed low elevations [50] than in the comparable grazed sites [43] (Table 3.4).

There were no significant grazing effects detected on species richness, Gini-Simpson, or Shannon Index between concave and convex landforms (Table 3.6). However, more species where found in ungrazed concave [56] than in the comparable grazed sites [50], and in ungrazed convex [47] than in the comparable grazed sites [41] (Table 3.4).

26

Table 3.6 Differences in bryophyte species richness, Shannon, and Gini-Simpson index of diversity between ungrazed and grazed valleys, and within each growing condition. All valleys used in this study, located in Iceland, are represented.

Response Variable	Growing Condition	Estimate Ungrazed	Estimate Grazed	Std. Error	df	t-value	p-value
Species Richness	All	5.25	4.92	0.66	4	-0.50	0.64
	East-Facing	6.00	4.82			-1.73	0.16
	West-Facing	4.49	5.00			0.75	0.49
	High Elev.	5.39	5.18			-0.31	0.77
	Low Elev.	5.10	4.64			-0.67	0.54
	Concave	5.40	5.09			-0.46	0.67
	Convex	5.09	4.74			-0.52	0.63
Shannon Index	All	0.92	0.96	0.10	4	0.41	0.70
	East-Facing	1.06	0.89			-1.00	0.37
	West-Facing	0.78	0.98			1.79	0.15
	High Elev.	0.94	0.98			0.32	0.76
	Low Elev.	0.90	0.95			0.46	0.67
	Concave	0.94	0.99			0.46	0.67
	Convex	0.90	0.94			0.33	0.76
Gini-Simpson Index	All	0.48	0.52	0.04	4	1.04	0.36
	East-Facing	0.53	0.50			-0.66	0.54
	West-Facing	0.42	0.53			2.48	0.07
	High Elev.	0.47	0.51			1.02	0.36
	Low Elev.	0.48	0.52			0.84	0.45
	Concave	0.49	0.53			0.83	0.45
	Convex	0.47	0.52			1.07	0.35

3.4 Bryophyte growth forms

Ingjaldssandur and Nesdalur valleys had the highest abundance of pleurocarpous mosses [3.4, 3.3 hits$_p$, mean number of hits per plot], and Grunnavík and Skálavík valleys had the highest abundance of acrocarpous mosses [0.8, 0.8 hits$_p$] (Figure 3.9). Pleurocarpous mosses were more abundant than any other growth form, and acrocarpous mosses were the second most abundant group, this was the case under all growing conditions (Table 3.7). Within all valleys, pleurocarpous mosses were hit over five times more per plot [2.8 hits$_p$] when compared to acrocarpous species [0.6 hits$_p$]. There were no significant differences detected in grazed versus ungrazed valleys in general for pleurocarpous or acrocarpous mosses (Table 3.8). There were not enough data to make any conclusions based on *Sphagnum* or liverwort species.

Table 3.7 List of total number of hits to bryophyte growth forms in the valleys used in this study, located in Iceland. The differences in total number of hits to bryophyte growth forms are shown in ungrazed (U) and grazed (G) valleys, as well as, in these valleys and under different growing conditions based on east and west-facing slopes, high and low elevations, and concave and convex landforms.

| Growing Condition | Acrocarpous | | Pleurocarpous | | Liverwort | | *Sphagnum* | |
	G	U	G	U	G	U	G	U
All	154.5	169.1	857.4	769.9	80.4	66.7	25.8	42.6
East-Facing	88.0	110.8	399.1	432.2	49.7	31.9	17.5	29.6
West-Facing	66.5	58.3	458.3	337.7	30.7	34.8	8.3	13.0
High Elev.	68.4	69.4	403.9	371.1	44.4	28.0	4.1	15.5
Low Elev.	86.1	99.7	453.5	398.8	36.0	38.7	21.7	27.1
Concave	86.7	113.3	390.4	369.4	63.6	42.1	22.6	29.2
Convex	67.8	55.8	467.0	400.5	16.8	24.6	3.2	13.4
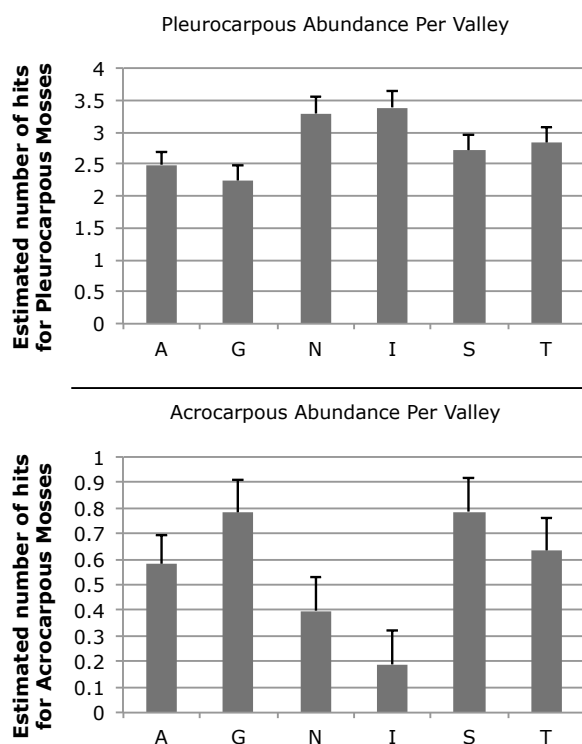
Figure 3.9. Model estimates (mean ± one standard error) representing number of hits to pleurocarpous and acrocarpous mosses per plot in all valleys used in this study, located in Iceland. The valleys shown in this figure are: Aðalvík (A), Grunnavík (G), Nesdalur (N), Ingjaldssandur (I), Skálavík (S), and Thorgeirsfjördur (T). The three valleys on the left of each figure represent ungrazed, while the three on the right represent the grazed valleys.

Within habitats found on west-facing slopes there was a marginally significant difference in the model estimates of the mean number of hits per plot for pleurocarpous mosses based on a 10% level (Table 3.8). There were no significant differences detected within these habitats for any other growth forms (Table 3.8). Under growing conditions found on west-facing slopes, the back-transformed model estimates for number of hits to pleurocarpous

mosses was 1.1 $hits_p$ greater in grazed [2.2 $hits_p$] than in ungrazed [1.1 $hits_p$] valleys (Figure 3.10B, Table 3.8).
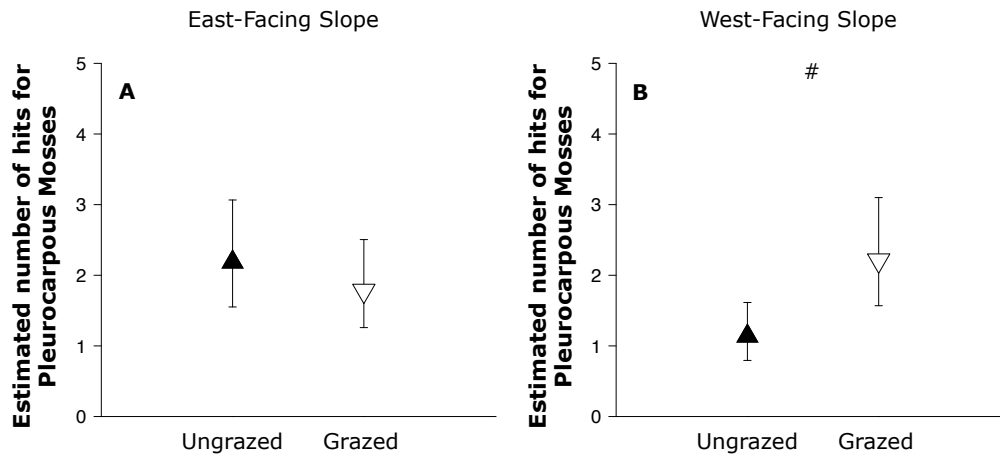
Figure 3.10. Back-transformed model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on pleurocarpous mosses in the valleys used in this study, located in Iceland. Illustrating differences found in different growing conditions based on exposure ('A' east; 'B' west-facing slope). The filled triangles are the estimated number of hits per plot of pleurocarpous mosses in ungrazed, and the open triangles are the estimated number of hits per plot for grazed valleys. Values are given as estimates from linear mixed effects models and "#" indicates marginally significant effects based on a 10% level.

There were no significant grazing effects detected on mean number of hits per plot for pleurocarpous or acrocarpous mosses between high and low elevation or between concave and convex landforms (Table 3.8).

Table 3.8 Log transformed differences in bryophyte growth forms between ungrazed and grazed valleys, and within each growing condition. All valleys used in this study, located in Iceland, are represented.

Response Variable	Growing Condition	Estimate Ungrazed	Estimate Grazed	Std. Error	df	t-value	p-value
Acrocarpous	All	-1.06	-1.15	0.33	4	-0.27	0.80
	East-Facing	-0.76	-1.08			0.85	0.44
	West-Facing	-1.36	-1.26			0.31	0.77
	High Elev.	-1.07	-1.17			-0.30	0.78
	Low Elev.	-1.05	-1.13			-0.24	0.82
	Concave	-0.84	-1.09			-0.73	0.50
	Convex	-1.28	-1.21			0.20	0.85
Pleurocarpous	All	0.52	0.73	0.22	4	0.99	0.38
	East-Facing	0.83	0.64			-0.83	0.45
	West-Facing	0.21	0.83			2.66	0.06
	High Elev.	0.56	0.59			0.11	0.92
	Low Elev.	0.48	0.88			1.73	0.16
	Concave	0.52	0.57			0.23	0.83
	Convex	0.52	0.90			1.62	0.18

3.5 Bryophyte life-history groups

Nesdalur valley had the highest abundance of colonist [0.2 hits$_p$], Ingjaldssandur valley had the highest abundance of colonist pioneer [0.7 hits$_p$], Grunnavík, Nesdalur, and Skálavík valleys had the highest abundances of long-lived shuttle [0.4, 0.4, 0.4 hits$_p$], Nesdalur valley had the highest abundance of perennial competitive [2.9 hits$_p$], and Thorgeirsfjördur valley had the highest abundance of perennial stress tolerant bryophytes [0.8 hits$_p$] (Figure 3.11). The perennial competitive (PEC) group was more abundant than any other life-history group, with 2.4 hits$_p$ (Table 3.9). The PEC group was hit over four times more per plot when compared to the second most abundant group, the perennial stress tolerant group [0.6 hits$_p$] (Table 3.9). The colonist pioneer group had 0.5 hits$_p$ and the long-lived shuttle group had 0.3 hits$_p$. The colonist group was the least abundant out of all the life-history groups, with a mean of 0.1 hits$_p$. There were not enough data to detect any significant differences for colonist pioneer and long-lived shuttle groups under any growing conditions.

Table 3.9 List of total number of hits to bryophyte life-history groups in the valleys used in this study, located in Iceland. The differences in total number of hits to bryophyte life-history groups are shown in ungrazed (U) and grazed (G) valleys, as well as, in these valleys and under different growing conditions based on east and west-facing slopes, high and low elevations, and concave and convex landforms. The life-history groups given in this table are: colonists (COL), colonist pioneer (COP), long-lived shuttle (LLS), perennial competitive (PEC), perennial stress tolerant (PST).

Growing Condition	COL		COP		LLS		PEC		PST	
	G	U	G	U	G	U	G	U	G	U
All	7.2	37.8	125.5	133.1	64.9	82.0	720.3	660.3	200.2	135.1
East-Fac.	3.6	12.7	79.7	92.8	34.6	54.8	339.6	363.2	96.8	81.0
West-Fac.	3.6	25.1	45.8	40.3	30.3	27.2	380.7	297.1	103.4	54.1
High Elev.	5.6	22.9	80.9	94.3	18.0	29.0	321.0	265.8	95.3	72.0
Low Elev.	1.6	14.9	44.6	38.8	46.9	53.0	399.3	394.5	104.9	63.1
Concave	3.0	27.7	34.7	31.8	52.5	49.1	361.5	358.7	111.6	86.7
Convex	4.2	10.1	90.8	101.3	12.4	32.9	358.8	301.6	88.6	48.4
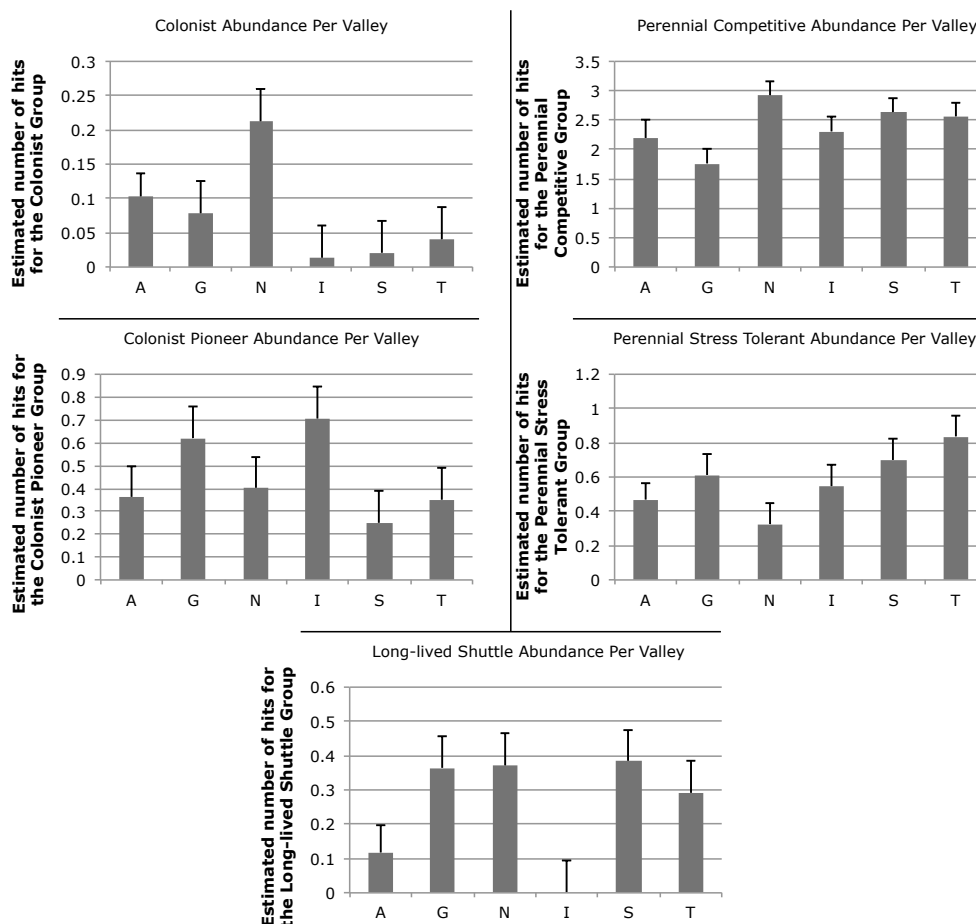
Figure 3.11. Model estimates (mean ± one standard error) representing number of hits to all bryophyte life-history groups per plot in all valleys used in this study, located in Iceland. The valleys shown in this figure are: Aðalvík (A), Grunnavík (G), Nesdalur (N), Ingjaldssandur (I), Skálavík (S), and Thorgeirsfjördur (T). The three valleys on the left of each figure represent ungrazed, while the three on the right represent the grazed valleys.

Within grazed valleys, the estimated mean number of hits per plot for the perennial stress tolerant (PST) group was greater when compared to ungrazed valleys, and this difference was marginally significant based on a 10% level (Table 3.10). There were no significant differences detected in grazed versus ungrazed valleys in general for any other life-history group (Table 3.10). The back-transformed model estimates for mean number of hits to the PST group was 0.1 $hits_p$ greater in grazed [0.3 $hits_p$] than ungrazed [0.2 $hits_p$] valleys (Figure 3.12). This difference becomes stronger when stratified by growing conditions.

Figure 3.12. Back-transformed model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on the perennial stress tolerant group in the valleys used in this study, located in Iceland. The filled triangle is the estimated number of hits per plot for the perennial stress tolerant group in ungrazed, and the open triangle is the estimated number of hits per plot for grazed valleys. Values are given as estimates from linear mixed effects models and are marginally significant based on a 10% level.

Within habitats found on west-facing slopes there was a statistically significant difference in the estimated mean number of hits per plot for the perennial stress tolerant (PST) group based on a 5% level (Table 3.10). Within these habitats there was a marginally significant difference in the estimated mean number of hits per plot for the perennial competitive (PEC) and colonist (COL) groups based on a 10% level (Table 3.10). The back-transformed model estimates on number of hits to the PST group was 0.2 $hits_p$ greater in grazed [0.3 $hits_p$] than ungrazed west-facing slopes [0.1 $hits_p$] (Figure 3.13B). The back-transformed model estimates on number of hits to the PEC group was 0.8 $hits_p$ greater in grazed [1.7 $hits_p$] than ungrazed west-facing slopes [0.9 $hits_p$] (Figure 3.13D). The back-transformed model estimates on number of hits to the COL group was 0.1 $hits_p$ less in grazed [0.01 $hits_p$] than ungrazed west-facing slopes [0.1 $hits_p$] (Figure 3.13F).

Figure 3.13. Back-transformed model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on the perennial stress tolerant (A, B), perennial competitive (C, D), and colonist groups (E, F) in the valleys used in this study, located in Iceland. Illustrating differences found in different growing conditions based on exposure. The filled triangles are estimated number of hits per plot for these groups found in ungrazed, and the open triangles are the estimates per plot found in grazed valleys. Values are given as estimates from linear mixed effects models. "*" indicates statistically significant effects based on a 5% level, and "#" indicates marginally significant effects based on a 10% level.

Within habitats found on low elevations there was a marginally significant difference in the estimated mean number of hits per plot for the perennial stress tolerant (PST) group based on a 10% level (Table 3.10). There were no significant differences detected within these habitats for any other life-history group (Table 3.10). Under growing conditions found in low elevations, the back-transformed model estimates of number of hits to the PST group was 0.1 hits$_p$ greater in grazed [0.3 hits$_p$] than in ungrazed [0.2 hits$_p$] valleys (Figure 3.14B).
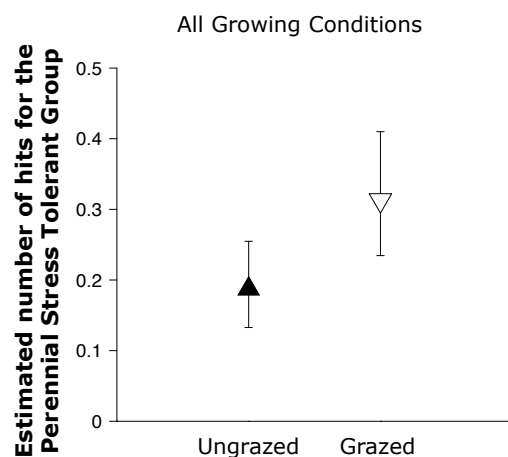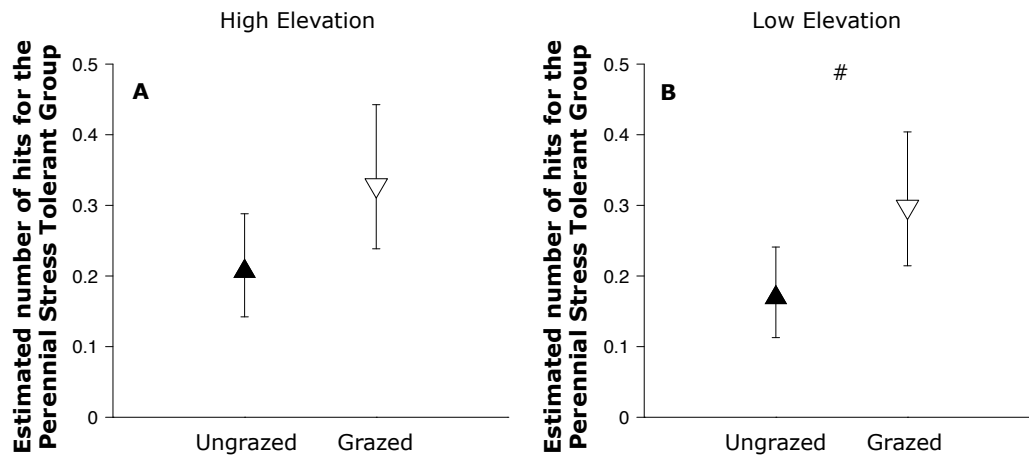

Figure 3.14. Back-transformed model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on the perennial stress tolerant group in the valleys used in this study, located in Iceland. Illustrating differences found in different growing conditions based on elevation ('A' high; 'B' low). The filled triangles are estimated number of hits per plot for this group found in ungrazed, and the open triangles are the estimates per plot found in grazed valleys. Values are given as estimates from linear mixed effects models and "#" indicates marginally significant effects based on a 10% level.

Within habitats found in convex landforms there was a marginally significant difference in the estimated mean number of hits per plot for the perennial stress tolerant (PST) group based on a 10% level (Table 3.10). Under growing conditions found in convex landforms, the back-transformed model estimates of number of hits to the PST group was 0.1 hits$_p$ greater in grazed [0.3 hits$_p$] than in ungrazed [0.1 hits$_p$] valleys (Figure 3.15B). Within habitats found in concave landforms there was a marginally significant difference in the estimated mean number of hits per plot for the colonist (COL) group based on a 10% level (Table 3.10). There were no significant differences detected within these habitats for any other life-history group (Table 3.10). Under growing conditions found in concave landforms, the back-transformed model estimates of number of hits to the COL group was 0.02 hits$_p$ less in grazed [0.01 hits$_p$] than in ungrazed [0.03 hits$_p$] valleys (Figure 3.15C).
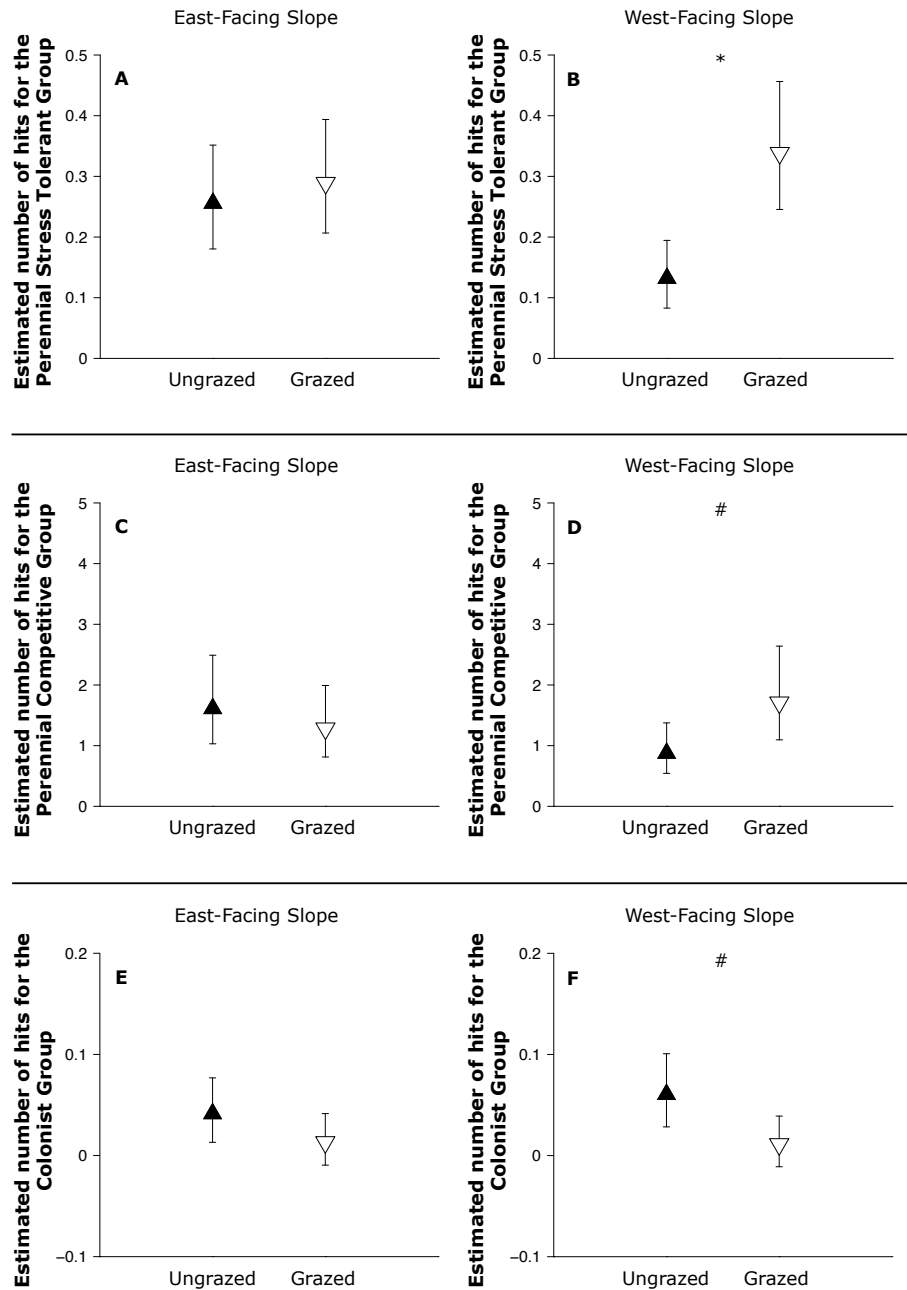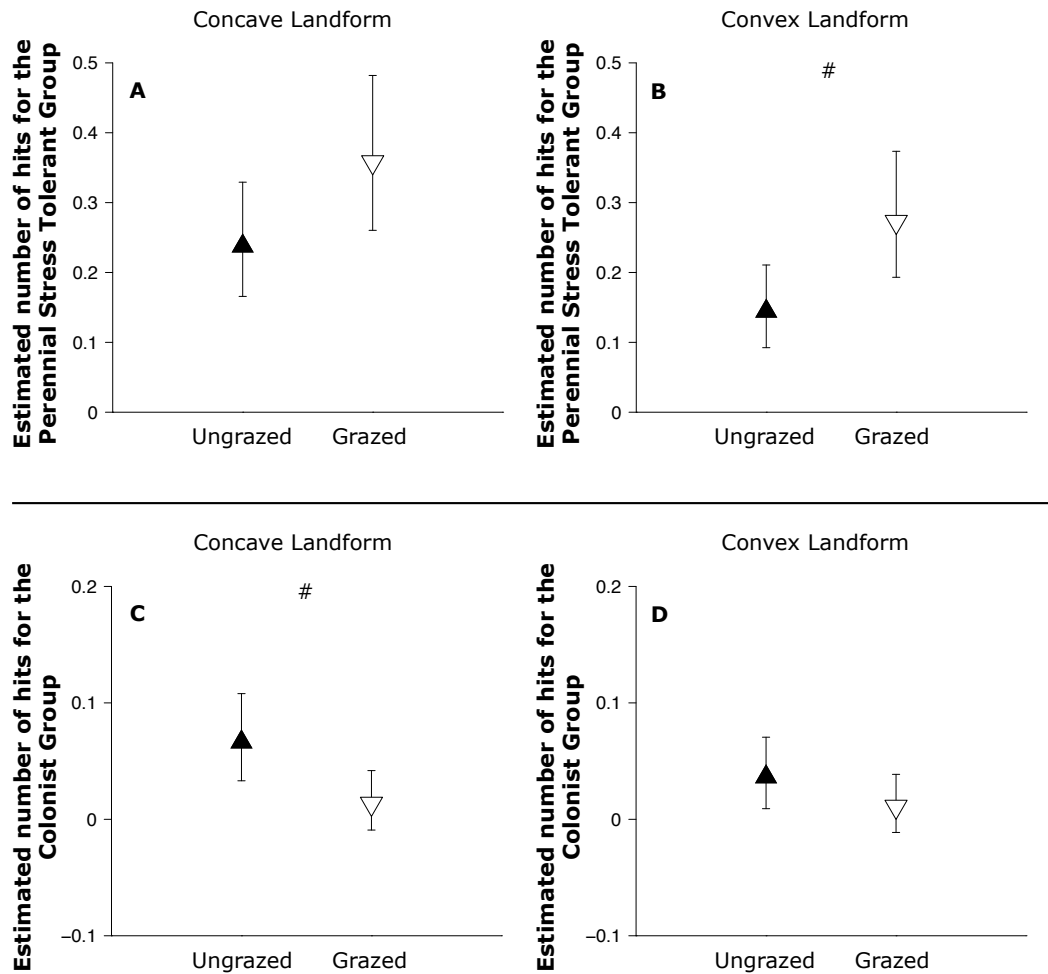
Figure 3.15. Back-transformed model estimates (mean ± 95% confidence intervals) representing the impacts of grazing on the perennial stress tolerant (A, B) and colonist groups (C, D) in the valleys used in this study, located in Iceland. Illustrating differences found in different growing conditions based on landform. The filled triangles are estimated number of hits per plot for these groups found in ungrazed, and the open triangles are the estimates per plot found in grazed valleys. Values are given as estimates from linear mixed effects models and "#" indicates marginally significant effects based on a 10% level.

Table 3.10 Log transformed differences in bryophyte life-history groups between ungrazed and grazed valleys, and within each growing condition. All valleys used in this study, located in Iceland, are represented.

Response Variable	Growing Condition	Estimate Ungrazed	Estimate Grazed	Std. Error	df	t-value	p-value
Colonists	All	-1.89	-2.18	0.16	4	-1.90	0.13
	East-Facing	-1.96	-2.18			-1.39	0.24
	West-Facing	-1.83	-2.20			-2.28	0.08
	High Elev.	-1.85	-2.12			-1.68	0.17
	Low Elev.	-1.94	-2.26			-1.99	0.12
	Concave	-1.79	-2.17			-2.38	0.08
	Convex	-1.99	-2.19			-1.29	0.27
Colonists Pioneer	All	-1.56	-1.59	0.19	4	-0.24	0.83
	East-Facing	-1.38	-1.49			-0.53	0.63
	West-Facing	-1.74	-1.72			0.10	0.93
	High Elev.	-1.26	-1.37			-0.53	0.62
	Low Elev.	-1.86	-1.84			0.10	0.93
	Concave	-1.85	-1.80			0.23	0.83
	Convex	-1.27	-1.41			-0.66	0.55
Long-lived Shuttle	All	-1.67	-1.85	0.26	4	-0.69	0.53
	East-Facing	-1.54	-1.81			-1.01	0.37
	West-Facing	-1.80	-1.88			-0.32	0.77
	High Elev.	-1.77	-1.97			-0.73	0.50
	Low Elev.	-1.56	-1.72			-0.60	0.58
	Concave	-1.63	-1.66			-0.11	0.92
	Convex	-1.70	-2.03			-1.23	0.29
Perennial Competitive	All	0.26	0.47	0.28	4	0.71	0.52
	East-Facing	0.54	0.33			-0.72	0.51
	West-Facing	-0.03	0.59			2.07	0.10
	High Elev.	0.06	0.28			0.74	0.50
	Low Elev.	0.45	0.63			0.62	0.57
	Concave	0.43	0.53			0.35	0.75
	Convex	0.08	0.38			1.03	0.36
Perennial Stress Tolerant	All	-1.25	-0.89	0.15	4	2.39	0.08
	East-Facing	-1.03	-0.94			0.52	0.63
	West-Facing	-1.46	-0.82			3.71	0.02
	High Elev.	-1.18	-0.85			1.97	0.12
	Low Elev.	-0.92	-1.31			-2.30	0.08
	Concave	-1.09	-0.79			1.76	0.15
	Convex	-1.41	-.99			2.44	0.07

4 Discussion

In this study, the bryophyte communities are clearly patterned by growing conditions, and within certain conditions herbivory has a detectable impact. Findings show that to some extent, disturbance caused by sheep grazing impacts bryophyte layer depth, species diversity, and causes variation in the composition of bryophyte communities based on growth forms and life-history groups.

Grazing activity had more pronounced effects on the bryophyte communities in the west than the east-facing slopes. There are some possible explanations for this pattern. The soil variables measured in this study were unable to detect differences between topographical units based on exposure, in regards to soil C and N concentrations, as well as, soil pH. There were significant differences in the soil variables in regards to elevation and landform curvature. Whereas other studies have found that the probability of bryophytes being present on a plot increases with increasing soil pH (Virtanen et al., 2000), this is not necessarily observed in this study, however, this is most likely due to the pH range found here being to narrow to base findings on this variable. Previous research has shown that due to the prevailing wind direction from the east and northeast, there will be more accumulation of snow and longer duration of snow cover on west-facing slopes (Evans et al., 1989). Because of this, one can assume that the west will be moister than the east-facing slopes and it has been shown that moisture is among the most important environmental variables when considering good habitat for bryophytes (Fenton & Bergeron, 2006). Thus, it seems when other soil characteristics are similar, moisture may play an important role in determining the suitability of habitat for bryophytes. If we assume that the west-facing slopes are more advantageous for bryophytes due to higher moisture, it is interesting to find that those same communities are the ones to show the most responses to grazing pressure. In general, there are most likely other factors that influence these communities, such as exposure to solar radiation and vascular plant communities that may be competing with the bryophyte communities in these habitats (Van der Wal, Pearce, & Brooker, 2004). Further comparisons between this study and that of Mörsdorf, (2015b), will be needed to help determine if there is strong interplay between bryophytes and vascular plants in these habitats, interplay like what has been observed in previous studies (e.g., Gornall et al., 2011; Jónsdóttir, 1991). These comparisons might ultimately reveal what causes these strong connections between bryophyte communities and slope exposure.

Bryophyte communities found under low elevation growing conditions showed more differences between ungrazed and grazed valleys, when compared to high elevation communities. This may also be related to soil fertility as the soil variables measured in this study show that low elevation has higher soil C and N concentrations. Elevation is also correlated with soil moisture, and lower elevations within a slope are characterized has having higher soil moisture (Evans et al., 1989; Parker, 1982; Swanson, Kratz, Caine, & Woodmansee, 1988). Thus, it is clear that the low elevation growing conditions are more favorable for bryophytes, in regards to soil moisture and nutrients, and also this was one of the communities where a detectable impact from grazing was seen. Mörsdorf, (2015b),

also presented interesting findings pertaining to differences between elevations within these valleys. It was found that graminoids were more abundant in these low elevation conditions and probably cause some degree of competitive exclusion of other plant species, it will be important to make comparisons between the vascular plant and bryophyte communities within these habitats to get a better picture of all the interactions at play (Mörsdorf, 2015b).

The perennial bryophyte groups showed differences in ungrazed and grazed valleys depending on landform curvature, and analysis of soil C and N concentrations in this study showed that concave was more fertile when compare to convex landforms. Concave, with its high concentrations of soil C and N, as well as, higher moisture content due to the snow-bed like features, suggest it is a more wet growing condition for bryophytes when compared to convex landforms (Evans et al., 1989; Parker, 1982; Swanson et al., 1988). Mörsdorf, (2015b), presented that forbs were more common in concave when compared to convex landforms, which suggests that these communities have faster rates of nutrient cycling when compared to other communities with less abundance of forbs (Eskelinen, Stark, & Männistö, 2009). Since concave landforms seem to be more advantageous for bryophytes and forbs, it might be the case that these habitats have a relatively fast nutrient recycling rate when compared to other habitats due to both of these groups being important components of nutrient cycles (Eskelinen et al., 2009; Gornall et al., 2007).

Based on data presented in this study, bryophyte communities that are occurring in growing conditions that are more favorable, in regards to soil moisture and nutrients, seem to have more detectable levels of disturbance by sheep grazing.

4.1 Impacts to the depth of the bryophyte layer

It was predicted that sheep would decrease the depth of the bryophyte layer, either by grazing, or more likely trampling while grazing. The average depth of the bryophyte layer varied throughout the different valleys with the largest difference occurring between Nesdalur and Ingjaldssandur valley. There was a 3.7cm difference in the average depth of the bryophyte layer between these two valleys. With an average of 7.3cm, the bryophyte mats found in Nesdalur can be characterized as deep. In one study it was shown that deep (6cm) moss mats will significantly reduce soil temperature and nitrogen availability and this is directly related to a reduction of graminoid productivity (Gornall et al., 2011). In Grunnavík valley the deepest bryophyte layer was recorded at 23.8cm, and in the other ungrazed valleys there were numerous recordings of similarly thick bryophyte layers. The bryophyte layer depths observed in this study suggest that within these valleys there are substantial bryophyte mats when compared to observations in other studies (e.g., Gornall et al., 2007). Within this study, *Racomitrium lanuginosum*, *Pleurozium schreberi*, and *Hylocomium splendens* accounted for the thickest bryophyte mats and more petite species like those found in *Dicranum spp* accounted for some of the thinner bryophyte mats.

This study found that sheep, most likely from trampling done while grazing, can have impacts on the depth of the bryophyte layer. These impacts were observed under all growing conditions, with the largest differences occurring between east-facing slopes in grazed and ungrazed valleys. In general, there was a difference of 1.95cm in the depth of the bryophyte layer between grazed and ungrazed valleys. Because sheep decrease the depth of the bryophyte layer, it can be assumed that this will increase the temperature and

nutrient availability of the soil, as well as, influence vascular plant growth and microbial activity (Gornall et al., 2007; 2011; Jónsdóttir, 1991; Van der Wal & Brooker, 2004). Warmer soil will directly impact vascular plants, and could potentially benefit their growth. It might also influence vascular plant abundance and community composition. In another study conducted in Iceland, it was found that sheep are likely to trample bryophyte mats and decrease their depth, this in turn played a role in the interaction between certain bryophytes and vascular plants (Jónsdóttir, 1991). It was shown that through the act of grazing, the trampling impact caused a decrease in depth of *Racomitrium lanuginosum*, which lead to a decrease in the tiller size but an increase in tiller density of *Carex bigelowii*. It will be an important next step to compare what was found in this study with those findings in the partner study that was addressing issues dealing with vascular plants (Mörsdorf, 2015b).

With a difference of over three centimeters, the most significant difference in depth was found on east-facing slopes, between ungrazed and grazed valleys. This is interesting because west-facing slopes are believed to be more advantageous for bryophytes due to the idea that they tend to have higher moisture (Evans et al., 1989). However, there are some possible explanations for this pattern. Maybe within east-facing slopes there is less competition between bryophytes and vascular plants, and the depth of the layer might be greater, thus when a disturbance like trampling occurs, it is more detectable under these growing conditions. Or perhaps due to the fact that east-facing slopes have less duration of snow cover (Evans et al., 1989), the bryophyte communities there are more accessible to be trampled during the early parts of the summer grazing season of Icelandic sheep (Thórhallsdóttir, 2002). Ultimately there are many factors at play, and further research will be necessary to determine what other factors might be influencing bryophyte communities within different exposures.

Another difference was found in low elevation growing conditions. Within these conditions the bryophyte layer that was found in grazed was 2.6cm less when compared to ungrazed valleys. This follows the overall observation that the impacts of sheep grazing are more detectable in more favorable bryophyte habitats, in regards to soil moisture and nutrients.

4.2 Impacts to bryophyte community diversity

It was predicted that bryophyte species diversity would be higher in medium to slightly heavy grazed when compared to ungrazed locations and that this grazing effect would be dependent on the growing conditions. Nesdalur valley had the highest species richness out of any valley in this study, as well as, recording some of the highest values of both Gini-Simpson and Shannon indexes of diversity. The species richness in Nesdalur is particularly high, especially when comparing it to other studies from tundra areas (e.g., Jägerbrand, Lindblad, Björk, Alatalo, & Molau, 2006). Gini-Simpson recordings in this study were similar but slightly lower when compared to another study in the tundra that was addressing questions on simulated environmental change (Jägerbrand et al., 2006). The highest recorded value of Shannon index [1.89] was on the low end of the diversity spectrum, and typical values are generally between 1.5 and 3.5 in most ecological studies (Magurran, 2013). Shannon index incorporates both richness and evenness in its calculations, and this can be a strength but also a weakness because it makes it difficult to

compare communities that vary greatly in richness. The unique species found in ungrazed and grazed valleys where numerous, however, there were no obvious patterns and this was most likely due to some other environmental factors.

It was shown that under west-facing growing conditions, Gini-Simpson diversity was higher in grazed than in ungrazed valleys. There was an 11% greater probability of interspecific encounter (PIE) within grazed west-facing slopes than in the comparable ungrazed sites. The slight differences that were detected occurred on west-facing slopes, which again leads to the notion of bryophyte communities found in more moist habitats showing impacts from sheep grazing. This was the only detected difference in any diversity measure that was assessed. However, this difference was only marginally significant and it is hardly enough evidence to make strong conclusions.

Unlike other studies addressing grazing and bryophyte diversity (e.g., Eskelinen & Oksanen, 2006; Jasmin et al., 2008; Olofsson et al., 2001), the differences in diversity between these grazing regimes in Iceland were only slightly noticeable. This is somewhat surprising because the valleys selected for this study represented the strongest contrasts in sheep grazing, with respect to similar environmental conditions. One explanation for this could be the notion that the ungrazed valleys used in this study are still showing signs of persistent grazing impact from the grazing that was conducted there many years ago. It could be that the ungrazed valleys used in this study are still recovering from this historical grazing pressure. One explanation for this increase in diversity could be due to the general increase in availability of patches caused when sheep remove plant material (Augustine & McNaughton, 1998). When sheep graze vascular plants it could happen that they expose patches, in turn, bryophyte species may be able to migrate there. If the disturbance observed in this study were greater, i.e., higher density of sheep, then the diversity should be less in grazed valleys. Following the relationships described in the IDM, one can assume that the valleys in this study are on one of the ends of the spectrum. Having a better picture of historical grazing activity would hopefully shine some light on this subject but it should be noted here that this study was not specifically designed to try and capture historical grazing impacts. Previous research supports the idea that heavy and high density grazing will reduce bryophyte species diversity (Eskelinen & Oksanen, 2006; Olofsson et al., 2001), and one can assume similar results to happen in Iceland should the grazing densities increase. There will need to be further research to try and capture these impacts on a large scale here in Iceland.

4.3 Impacts to bryophyte growth forms and life-history groups

It was predicted that sheep grazing and trampling would alter the growth form composition of bryophyte communities. Previous research suggested that the abundance of acrocarpous mosses will decrease and pleurocarpous mosses will increase under the pressures caused from herbivory due to the trampling effect (Jägerbrand & Alatalo, 2015). Based on the characteristics of certain life-history groups and the limited previous research on this subject, it was predicted that early successional groups, like the colonist group, would be more abundant in ungrazed than grazed locations (Austrheim et al., 2007).

Pleurocarpous mosses were by far the most common growth form encountered in this study and Ingjaldssandur and Nesdalur valleys had the highest abundance of this group. Alternately, these two valleys had the lowest abundances of acrocarpous mosses when compared to the other valleys in this study. It is unclear what might explain this and it certainly poses some interesting questions. The analysis of this study indicated that pleurocarpous mosses were more abundant in grazed than in ungrazed valleys, when looking under the more moist west-facing growing conditions. Pleurocarpous mosses might tolerate disturbance caused by sheep grazing relatively well. Generally speaking, they more commonly form spreading carpets with branches extending laterally outwards, usually fixed to the substrate (LaFargeEngland 1996). This could mean that when a sheep causes a disturbance to an individual they will still have unaffected sections that are unharmed and can continue to grow. Pleurocarpous mosses tend to live longer than acrocarpous mosses and are consider more durable when compared to the more fragile acrocarpous species (Atherton, Bosanquet, & Lawley, 2010). This difference is only marginally significant and should be treated carefully, however, it does fall in line with previous studies and the prediction of this study. Further research would be necessary to determine if pleurocarpous mosses are truly better adapted at dealing with disturbance caused by trampling.

There were three life-history groups that showed some degree of differences under the different grazing regimes. The perennial stress tolerant (PST) life-history group showed the strongest differences amongst the other groups. The PST group was more abundant in grazed than ungrazed valleys and this evidence was stronger when looking at growing conditions based on west-facing slopes, under low elevation, and in convex landforms. Considering the west-facing slope and low elevation habitats, these tend to be more favorable for bryophytes, in regards to soil moisture and nutrients, as mentioned before, which follows previous patterns. The perennial competitive (PEC) group also showed strong differences based on grazing regime. Both the PST and PEC groups were more abundant in grazed than ungrazed valleys. Similar to other research in suitable habitats, the PST and PEC groups are usually the most abundant life-history group (Austrheim et al., 2005). Showing opposite responses to grazing regime, under the more moist west-facing growing conditions, the colonist group was less abundant in grazed than in ungrazed valleys. This follows the prediction of this study, however, it should be noted that this is only a marginally significant difference and not a biologically significant one.

The unique species found in ungrazed and grazed valleys were numerous, however, there were no obvious patterns and this was most likely due to some other environmental factors. However, colonists did tend to be more unique to grazed and ungrazed valleys, as well as, acrocarpous mosses. This poses some questions that can be addressed in future investigations.

There is limited research dealing with sheep grazing and the various groups of bryophytes, which made it hard to make strong predictions or to compare results with other studies. When there were studies available, comparisons were made. However, this is not viewed as a limitation but rather an opportunity to add some information to the knowledge pool.

4.4 Limitations and final conclusions

4.4.1 Limitations of this study

To address some limitations of this study, a brief discussion of some methodical issues. Quite possibly the largest limitation of this study was the inability of being able to assess a range of grazing densities or intensities. This was simply not possible, as the most suitable valleys in Iceland were chosen and there was limited information available pertaining to historical grazing practices in these areas. It has been shown in previous research that analyzing a spectrum of grazing densities would allow for more robust comparisons (Austrheim et al., 2008). However, this was not possible in Iceland, and since there are many questions surrounding the impacts of sheep on the Icelandic tundra, it was important to devise a best suitable design for the study area. The strategy used to assess bryophyte frequencies and relative abundances, the point intercept method, is a respected way of assessing plant communities. The adaptation suggested by Bråthen, (2004), has been shown to work for vascular plants, but there is still debate on its effectiveness with bryophytes. This is due to the fact that when using this method it is only possible to record one hit per point. In this study, using five pins, it was only possible to record five hits (plus 0.1 for each extra species present within the plot). Another limitation was the determination of favorable habitat for bryophytes, unless a proper experiment is conducted it is hard to determine what the most favorable environmental characteristics are for bryophytes. But all assumptions were based on some form of previous knowledge.

4.4.2 Final conclusions

An investigation into the richness of a plant community based on taxonomic classification is perhaps the most common strategy when looking at diversity studies on plant ecology, and this is even more apparent when reviewing literature on bryophytes (Bates, 1998; A. J. Shaw et al., 2011; Söderström & During, 2005). Most research on plant communities has been conducted on vascular species, however, since bryophytes comprise a significant portion of the plant species pool in tundra ecosystems, a study of how sheep grazing shapes bryophyte communities is important. Iceland offered a unique opportunity to investigate this issue because bryophytes comprise a particularly significant portion of the species pool and sheep are the dominating large herbivore.

This study showed that sheep in Iceland cause impacts to bryophyte communities. These impacts can affect both the structure and composition of these communities. This in turn can have impacts on numerous ecosystem functions, impacting both biotic and abiotic factors. These patterns are shaped by the growing conditions and impacts seem to be more detectable in more favorable habitats, in regards to soil moisture and nutrients. The most impacted habitats are those found on west-facing slopes, and under low elevation conditions.

A shift in the plant community is likely when a tundra ecosystem is grazed. This is a two-step process: 1) grazers trample and reduce the bryophyte layer depth, increasing the soil temperature; 2) grasses benefit from nutrients from feces and urine, and have a higher tolerance to grazing (Van der Wal & Brooker, 2004). The essential notion of this concept is that, as grazing increases in tundra habitats, a transition from a lichen-dominated habitat to a moss-dominated one will occur. Further, this habitat will transition to a graminoid-

dominated one under heavy grazing densities. This transition is one that occurs due to natural populations of herbivores, for example reindeer. However, if this process is allowed to continue with livestock grazing, the concept of extreme community transition has been called habitat degradation (Van der Wal, 2006). It has been shown that sheep grazing can lead to damages to the ecosystem in terms of soil erosion and habitat degradation has occurred in certain regions of Iceland (Arnalds & Barkarson, 2003). It would seem that the impact to the bryophyte layer observed in this study are suggesting that sheep can impact ecosystem function in terms of bryophyte communities.

In Iceland, sheep grazing is a common land use form, and it is important both economically and culturally. Most research on the ecological impacts of sheep in Iceland has focused on the impacts on vascular plants, and bryophyte community research is still very limited. Only a few studies are available on how sheep grazing affects bryophyte communities in Iceland (e.g., Jónsdóttir 1984; Jónsdóttir, 1991; Magnusson & Magnússon, 1990). I hope this study is able to fill in some of the knowledge gaps that exist pertaining to the impacts of sheep on bryophyte communities in Iceland.

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Appendix

Table 5.1. List of all bryophyte species encountered in this study, their life-history classification, and their growth form classification.

Bryophyte Species (Authority)	Life-history	Growth Form
Andreaea rupestris (Hedw.)	Colonists	Acrocarpous
Aneura pinguis (L.) Dumort	Colonists	Liverwort
Antitrichia curtipendula (Hedw.) Brid.	Perennial competitive	Pleurocarpous
Aulacomnium palustre (Hedw.) Schwägr.	Perennial competitive	Acrocarpous
Barbilophozia floerkei (F.Weber & D.Mohr) Loeske	Perennial stress tolerant	Liverwort
Barbilophozia lycopodioides (Wallr.) Loeske	Perennial competitive	Liverwort
Brachythecium reflexum / starkei (Starke) Schimp.	Perennial stress tolerant	Pleurocarpous
Bryum pseudotriquetrum (Hedw.) Gaertn.et al	Perennial competitive	Acrocarpous
Calliergonella cuspidata (Hedw.) Loeske	Perennial competitive	Pleurocarpous
Calliergon giganteum (Schimp.) Kindb.	Perennial competitive	Pleurocarpous
Chiloscyphus polyanthos (L.) Corda	Perennial competitive	Liverwort
Climacium dendroides (Hedw.) F.Web. & D.Mohr	Perennial competitive	Pleurocarpous
Conostomum tetragonum (Hedw.) Lindb.	Colonists	Acrocarpous
Cratoneuron filicinum (Hedw.) Spruce	Perennial competitive	Pleurocarpous
Dicranum bonjeanii (DeNot.)	Perennial stress tolerant	Acrocarpous
Dicranoweisia crispula (Hedw.) Milde	Colonists	Acrocarpous
Dicranum laevidens (R.S.Williams)	Perennial competitive	Acrocarpous
Dicranum majus (Sm.)	Perennial competitive	Acrocarpous
Dichodontium palustre (Dicks.) M.Stech	Colonists	Acrocarpous
Dicranum scoparium (Hedw.)	Perennial stress tolerant	Acrocarpous
Dicranum spadiceum (J.E.Zetterst.)	Perennial stress tolerant	Acrocarpous
Ditrichum flexicaule (Schwaegr.) Hampe	Colonists	Acrocarpous
Fissidens adianthoides (Hedw.)	Perennial competitive	Acrocarpous

Fissidens osmundoides (Hedw.)	Perennial competitive	Acrocarpous
Grimmia longirostris (Hook.)	Colonists	Acrocarpous
Hylocomium splendens (Hedw.) Schimp.	Perennial competitive	Pleurocarpous
Hypnum cupressiforme (Hedw.)	Perennial stress tolerant	Pleurocarpous
Jungermannia exsertifolia (Steph.)	Colonists	Liverwort
Kiaeria starkei (F.Weber & D.Mohr) I.Hagen	Colonists Pioneer	Acrocarpous
Lescuraea incurvata (Hedw.) E.Lawton	Perennial stress tolerant	Pleurocarpous
Marchantia polymorpha (L.)	Long-lived Shuttle	Liverwort
Mnium spinosum (Voit) Schwägr.	Long-lived Shuttle	Acrocarpous
Oncophorus virens (Hedw.) Brid.	Long-lived Shuttle	Acrocarpous
Pellia neesiana (Gottsche) Limpr.	Colonists	Liverwort
Philonotis fontana (Hedw.) Brid.	Perennial competitive	Acrocarpous
Philonotis seriata (Mitt.)	Perennial competitive	Acrocarpous
Philonotis tomentella (Molendo)	Perennial competitive	Acrocarpous
Plagiomnium ellipticum (Brid.) T.J.Kop.	Perennial competitive	Acrocarpous
Plagiomnium medium (Bruch & Schimp.) T.J.Kop.	Perennial competitive	Acrocarpous
Pleurozium schreberi (Brid.) Mitt.	Perennial competitive	Pleurocarpous
Pogonatum urnigerum (Hedw.) P.Beauv.	Colonists	Acrocarpous
Pohlia nutans (Hedw.) Lindb.	Colonists	Acrocarpous
Polytrichastrum alpinum (Hedw.)	Perennial stress tolerant	Acrocarpous
Polytrichum commune (Hedw.)	Perennial competitive	Acrocarpous
Ptilidium ciliare (L.) Hampe	Long-lived Shuttle	Liverwort
Racomitrium aciculare (Hedw.) Brid.	Colonists Pioneer	Pleurocarpous
Racomitrium ericoides (Brid.) Brid.	Colonists Pioneer	Pleurocarpous
Racomitrium fasciculare (Hedw.) Brid.	Colonists Pioneer	Pleurocarpous
Racomitrium lanuginosum (Hedw.) Brid.	Colonists Pioneer	Pleurocarpous
Racomitrium macounii (Kindb.)	Colonists Pioneer	Pleurocarpous
Racomitrium sudeticum (Funck) Bruch. & Schimp.	Colonists Pioneer	Pleurocarpous
Rhizomnium magnifolium (Horik.) T.J.Kop.	Perennial competitive	Acrocarpous

Rhizomnium pseudopunctatum (Bruch & Schimp.)T.J.Kop.	Perennial competitive	Acrocarpous
Rhytidiadelphus loreus (Hedw.) Warnst.	Perennial competitive	Pleurocarpous
Rhytidium rugosum (Hedw.) Kindb.	Perennial competitive	Pleurocarpous
Rhytidiadelphus squarrosus (Hedw.) Warnst.	Perennial competitive	Pleurocarpous
Sanionia uncinata (Hedw.) Loeske	Perennial stress tolerant	Pleurocarpous
Sarmentypnum sarmentosum (Wahlenb.) Tuom. & T.J.Kop.	Perennial competitive	Pleurocarpous
Scapania undulata (L.) Dumort.	Colonists	Liverwort
Schistidium papillosum (Culm.)	Colonists	Acrocarpous
Schistidium strictum (Turner) Loeske ex Mårtensson	Colonists	Acrocarpous
Scorpidium revolvens (Sw.) Rubers	Perennial competitive	Pleurocarpous
Sphagnum girgensohnii (Russow.)	Long-lived Shuttle	*Sphagnum*
Sphagnum squarrosum (Crome)	Long-lived Shuttle	*Sphagnum*
Sphagnum subnitens (Russow &. Warnst.)	Long-lived Shuttle	*Sphagnum*
Sphagnum warnstorfii (Russow)	Long-lived Shuttle	*Sphagnum*
Timmia austriaca (Hedw.)	Perennial competitive	Acrocarpous
Tomentypum nitens (Hedw.) Loeske	Perennial competitive	Pleurocarpous