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Long-term experimental warming in an alpine heath: decrease in cover of the most abundant bryophytes

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Preface

This master thesis concludes my master's degree in General Ecology at The Norwegian University of Life Science (NMBU). Most of all, I would like to thank my supervisor Kari Klanderud and my co-supervisor Johan Asplund at NMBU for good guidance, great comments on the text and quick replies. A special thanks to Kari Klanderud for good discussions and for letting me use the Open top chambers that she put up and maintained for 18 years, and a special thanks to Johan Asplund for great advice on the statistics. I have learned so much from both! Further, I would like to thank Hauk Liebe, Kelsey Barnhill and Sigrud Elsrud for feedback on the text! I would also like to thank Oda Sofie Dahle for cooperation and good company during field work and the writing process. The fieldwork would not have been as joyful without her company!

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Abstract

Alpine ecosystems have shown to be sensitive to climate warming. Bryophytes are particularly important in alpine ecosystems and are known to support ecosystem services such as water regulation, nitrogen fixation and carbon storage. However, few studies have investigated the effects of long-term warming on alpine bryophytes at species level or genus level. The aim of this thesis is to investigate how global warming will affect community structure for alpine bryophytes. I hypothesize that the consequences of climate warming will be: (I) A decrease in cover of bryophytes. (II) A shift towards decreased richness and decreased evenness of bryophytes – where a few species will increase their cover, and the majority will decrease in cover. (III) A stronger decrease in cover of acrocarpous mosses than in cover of pleurocarpous mosses. I also explore the role of water availability and competition with vascular plants. For this I collected data from an on-going, 18-year old, warming experiment that uses open top chambers, in an alpine heath at Finse. To test the effects of warming on cover, evenness and richness of bryophytes, I performed linear regression models. To test and visualize the effects of warming on species composition, I used non-metric multidimensional scaling (NMDS). To test if acrocarpous mosses decreased more in cover than pleurocarpous mosses, I used linear regression models including an interaction between growth-form and warming.

Warming had a negative effect on cover of bryophytes and a positive effect on evenness and richness. Species composition was significantly changed – the abundant species decreased while the less abundant species showed an increasing trend. Acrocarpous mosses did not decrease more than pleurocarpous mosses. Increased competition with vascular plants and decreased moisture availability seemed to be important variables driving the change in the community structure of bryophytes. Different taxa were associated with different environmental variables, such as moisture and cover of litter. This study underlines that the effects of warming on bryophyte communities depend on the physical and biological environment and the species which make up the community. How global warming will affect community structure for alpine bryophytes remain an un answered question, as these results may not be applicable to other sites and because global warming is likely to be followed by changes in other aspects of the climate. Nevertheless, this thesis show how sensitive bryophyte communities can be to elevated temperatures. A potential decrease in cover of bryophytes and a shift in species composition may greatly impact the alpine ecosystems.

Contents

Introduction	1
Materials and methods	4
Study site	4
Measurement procedure	5
Statistics	6
Results	8
Discussion	17
Decrease in cover of bryophytes with experimental warming.....	17
Shift in species composition where abundant species decrease and less abundant species show a trend of increasing.....	18
Acrocarpous mosses did not decrease more than pleurocarpous mosses	21
The future of alpine bryophyte communities in a global warming perspective.....	21
Conclusions	22
References	24
Appendix	28

Introduction

Communities in extreme environments, such as alpine ecosystems, are expected to be particularly sensitive to climate warming (Root et al., 2003; Sala et al., 2000). On average, bryophytes contribute to 30% of the total vegetation cover in a broad range of alpine and arctic habitats (Wielgolaski et al., 1981, cited in Russel, 1990). Ecosystem services such as water regulation (Beringer et al., 2001), nitrogen fixation (Cornelissen et al., 2007; Solheim et al., 1996; Turetsky, 2003) and carbon storage (Rydin & Jeglum, 2013) are supported by bryophytes. Further, bryophytes can impact the microclimate in the soil by affecting the temperature- and moisture (Cornelissen et al., 2007), and have the potential to affect distribution of vascular plants by competing with or facilitating for them (Cornelissen et al., 2007; Gornall et al., 2011). Furthermore, bryophytes are a source of food for some groups of arthropods (Slansky, 1987) and are believed to be the main food source of lemming (*Lemmus lemmus*) during the winter (Soininen et al., 2013), both of which play key roles in alpine food webs (Høye & Culler, 2018; Ims & Fuglei, 2005). Despite this, bryophytes are probably the least explored functional group of the alpine vegetation, and only a few studies have examined the long-term effect of climate warming on bryophytes at species or genus level (but see Hollister et al., 2005; Lang et al., 2012). To predict the future of alpine ecosystems it is crucial to understand how bryophyte communities respond to a warmer climate.

Alpine and arctic bryophytes tend to have optima for photosynthesis at low temperatures, generally between 5-15 °C (He et al., 2016). In addition, the temperature range for net photosynthetic gain tend to be narrow (Dilks & Proctor, 1975; Fraham, 1990). Many bryophyte species growing in tundra vegetation exhibit a rapid decline in photosynthetic efficiency above 20 °C and net photosynthetic gain rarely exceeds 26 °C (Oechel & Sveinbjörnsson, 1978). In addition to the direct effect of elevated temperature on growth, elevated temperatures can also affect bryophytes through increased evaporation. The growth of a bryophyte is assumed to be directly proportional to the total duration in which the bryophyte is wet (Proctor, 1972). Bryophytes are also more sensitive to elevated temperature when dry conditions persist (Meyer & Santarius, 1998). The intimate dependence of bryophytes on water is believed to be reflected in their distribution, with high diversity and abundance where temperature and thus evaporation is low (He et al., 2016). A meta-analysis addressing experimental warming studies from tundra sites worldwide shows that the cover of bryophytes decrease in most alpine and arctic sites when the vegetation is exposed to warming (Elmendorf et al., 2012a). The authors suggest that

warming causes constrained seasonal water availability, which in turn causes the decrease in bryophyte cover.

Bryophytes lack roots and vascular tissue and are thus believed to be less efficient in utilizing resources efficiently and competing for light in productive habitats, compared to vascular plants (Grime et al., 1990). Hence, the low degree of competition in alpine and arctic regions may also explain why bryophytes are successful in such ecosystems. However, the vegetation in high elevations and latitudes is getting greener and more productive with anthropogenic warming (Elmendorf et al., 2012b; Jia et al., 2003; Pouliot et al., 2009). The competition regime that allows bryophytes to be successful in the alpine might thus be altered (Hollister et al., 2005; Klanderud & Totland, 2005). Nevertheless, evidence shows that cover of bryophytes are not necessarily negatively affected by experimental warming in all sites (Hudson & Henry, 2010). Furthermore, Elmendorf et al. (2012b) presents plot scale evidence indicating that cover of bryophytes was not affected by anthropogenic warming in the period between 1980 and 2010.

Bryophytes are hard to identify to species level, and sometimes even to genus level, particularly those growing in high latitudes and elevations because of their small size. Consequently, none of the big meta-analysis investigating the effects of warming on alpine and arctic vegetation have looked at bryophytes on genus or species level (Elmendorf et al., 2012a; Elmendorf et al., 2012b; Walker et al., 2006). Considerable evidence show that the effects of warming on plants are species specific (Dormann & Woodin, 2002; Klanderud, 2008; Lang et al., 2012; Little et al., 2015). Consequently, the effects of warming on bryophytes might become masked when they are treated as a broad group. Further, important information about the effects of warming on species diversity is lost when bryophytes are not included. For instance, the direction of the combined effects of warming and altered snow regimes may be positive or negative on overall species diversity in High Arctic tundra, depending on whether bryophytes are included or not (Mörsdorf & Cooper in prep.)

A respectable number of short-term (less than 5 years) experimental warming studies have included bryophytes at species/genus level, none of which found a significant effect of warming on diversity or species composition of bryophytes (Jägerbrand et al., 2009; Klanderud & Totland, 2005; Molau & Alatalo, 1998; Press et al., 1998). However, magnitude of the effect of warming is linearly correlated to the duration of the experiment (Elmendorf et al., 2012a). Lang et al. (2012) investigated alpine bryophyte communities exposed to long-term (9-16 years)

experimental warming by comparing community composition along natural temperature gradients, in Scandinavia and North America. Diversity of bryophytes decreased in one out of three sites with experimental warming. However, bryophyte diversity tended to decrease towards warmer climates along natural temperature gradients, on both continents (Lang et al., 2012). Overall, Lang et al. (2012) showed a trend where the majority of the alpine bryophytes decreased in abundance with warming while some common lowland bryophytes increased. *Hylocomium splendens* and *Pleurozium schreberi* constituted the lowland non-*Sphagnum* bryophytes that reacted positively to warming (Lang et al., 2012). Both species are believed to be shade tolerant, and both are pleurocarpous (Hallingbäck, 2016).

Mosses are the most abundant group of bryophytes in alpine ecosystems, followed by liverworts, while hornworts are insignificant. Further, mosses are divided into pleurocarpous and acrocarpous mosses, where acrocarpous mosses are more numerous in the alpine region (Robinson et al., 1989). While acrocarpous mosses grow sporophytes from the tip of their gametophyte, sporophytes develop on the sides of the branches on pleurocarpous mosses. Hence, acrocarpous mosses cannot continue growth during reproduction, while pleurocarpous mosses can (Vitt, 1991). Pleurocarpous mosses are thus believed to be better adapted to productive conditions where competition is relatively high (Robinson et al., 1989). This view is supported by the tendency for acrocarpous mosses to decrease more than pleurocarpous mosses with experimental warming (Elmendorf et al., 2012a).

In this thesis, I have investigated how the community structure of bryophytes is affected by experimental warming at Sanddalsnuten, an alpine heath in Finse, Norway. The experiment was initiated 18 years ago and has been running continuously since. The aim of the thesis is to investigate how global warming will affect community structure for alpine bryophytes. I hypothesize that the consequences of climate warming will be: (I) A decrease in cover of bryophytes. (II) A shift towards decreased richness and decreased evenness of bryophytes – where a few species will increase their cover, and the majority will decrease in cover (Lang et al., 2012). (III) A stronger decrease in cover of acrocarpous mosses than in cover of pleurocarpous mosses. In addition, I will explore whether potential changes in community composition of bryophytes subjected to warming is driven by a decrease in moisture availability and increased competition with vascular plants.

Materials and methods

Study site

This study was conducted on Sanddalsnuten at Finse, Norway (60° 36' 59.0" N, 7° 31' 31.6" E), from July 17 to August 10, 2018. Sanddalsnuten is a mountain in the northern part of Hardangervidda with base-rich bedrock and hence a rich community of calciophile species (Klanderud & Totland, 2005). The experimental plots are located in a *Dryas octopetala* heath on a south-west facing slope close to the top of Sanddalsnuten – approximately 1520 m above sea level. At Finse, the mean normal temperature at 1210 meters above sea level from June to August is 6.3 °C and the mean precipitation in the same three months is 86 mm (Meteorologisk institutt, 2018).

In this study, I used open top chambers (OTC) to simulate global warming (Figure 1). OTCs act as greenhouses and for the particular OTCs at Sanddalsnuten, the temperature is on average 1.5 °C higher than ambient temperatures (Klanderud & Totland, 2005). At the location there are 80 plots, 40 OTCs plots and 40 control plots, which have been operating since 2000. The OTCs and the control plots were installed as a part of the International Tundra Experiment (ITEX). Each plot (60x60 cm) contains two frames (30x60 cm) that include 18 subplots each (10x10 cm). For more details on the experimental setup, see Klanderud & Totland (2007). In 2017, cover and diversity of vascular plants and lichens were investigated in 10 of the warmed plots and 10 control plots (Hasvik, 2018). I used the same plots in this study. Warmed plots and controls were chosen in pairs: Warmed plots were randomly selected and each was further matched with a nearby control plot where the physical environment was similar.



Figure 1. Open Top Chambers (OTC) at the study site on Sanddalsnuten, a mountain in Finse, Norway. June 2018.

Measurement procedure

I recorded cover for each taxon on subplot level. I then calculated whole-plot cover from the average cover of each taxon across all the subplots in each plot. If I was uncertain about a identification, a sample was identified in the laboratory. If species could not be identified to species level, taxon were combined and grouped at the genus level. These genera were: *Dicranum*, *Racomitrium*, *Polytrichum*, *Hypnum*, *Bryum*, *Pohlia*, *Syntricia*, *Myurella*, *Dicranella*, *Fissidens* and *Grimmia*. Combining unidentified species into their genus groups underestimates species richness and is a potential source of error when comparing evenness, richness and species composition in warmed plots and controls. Due to the small size and low abundance of the liverworts at our site, I excluded all except *Ptilidium ciliare*. This species was the only liverwort with noteworthy abundance at the site. Knowing that species identification skills would improve during field work, I surveyed warmed plots and control plots alternately to avoid skewed amount of sampling errors between treatments.

Soil moisture was measured at 6 cm depth and was used as a proxy for bryophyte moisture availability, as there is a strong correlation between the two (Raabe et al., 2010). I did ten measurements randomly placed in each plot by using a Delta-T SM150 soil moisture kit, with mineral soil settings. This procedure was repeated on three different days (July 27, August 6, and August 9), with different weather conditions.

Litter was recorded visually in each subplot, and whole-plot cover was calculated from the average cover across all the subplots in each plot. To measure vegetation height, I pushed a ruler into the vegetation and noted the measurement when sufficient resistance was met. Vegetation height was then measured as the average height of the vegetation surrounding the ruler within a 1 cm radius. Such measures were done in the upper right corner of 12 pre-chosen subplots in each plot. Data with cover of the vascular plants was provided by Hasvik (2018).

Statistics

I conducted statistics and data management in R-studio (R Core, 2018) with the R stats-package (R Core & Contributors, 2015), if not otherwise specified. To calculate species richness, I summed the number of species recorded in each plot. Evenness (E) was calculated from Shannon's diversity index (S), $E = \frac{S}{\ln(S)}$. Shannon's diversity index is defined as $S = -\sum p_i \ln p_i$, where p is the proportion of individuals belonging to the i th species (Shannon & Weaver, 1949). Shannon's diversity was calculated by using the diversity-function in the vegan package (Oksanen, 2015).

To test the effects of warming on cover, evenness and richness of bryophytes, I used multiple linear regression models including the variables that were kept after correlation analysis and model selection. To detect correlating variables, I made a correlation matrix with the correlation-function in the package PerformanceAnalytics (Peterson et al., 2015), with Spearman's rank correlation coefficients. The environmental variables I included in the correlation analysis were soil moisture, cover of litter, vegetation height and cover of vascular plants. If two environmental variables correlated ($p < 0.05$), the variable that correlated most with the response variables was kept in the model. Further, environmental variables that were affected by warming were detected by performing two sample T-tests (two tailed), and removed if significantly affected ($p < 0.05$). These measures were done to prevent multicollinearity. When

performing the two sample T-test, height of vegetation was transformed by natural logarithm to meet the model assumptions of normally distributed residuals. Moisture, cover of litter and height of the vegetation correlated significantly. Because cover of litter and height of vegetation also were significantly affected by warming both were removed. Hence, the environmental variables that were kept for the stepwise model selection were soil moisture and cover of vascular plants. In addition, I included interaction between the environmental variables and warming in the model selection. Stepwise model selection was performed by using the step-function in the stats package with backward-forward stepwise model selection (default settings). The step-function is used to find the model with the lowest AIC value. First, it removes the variables that explains the least amount of the variation in the model and repeats this procedure until AIC stops decreasing (*backward*). Further, if any of the variables that were excluded in the backwards procedure contributes to a further decrease in AIC when reintroduced to the model, they are now reintroduced (*forward*). The warming variable was kept in the model, regardless of contribution to decrease in AIC. To test if the model meet the assumption of normally distributed residuals, I performed Shapiro-tests.

To test if species composition has significantly changed with experimental warming, I performed a permutational multivariate analysis of variance (PERMANOVA) using distance matrices with the adonis-function in the vegan package (Oksanen, 2015). Further, I performed a non-metric multidimensional scaling (NMDS) to compress the information in the species-cover data (multiple response variables) into two dimensions, allowing interpretable visualizing and statistical analysis. NMDS is an ordination technique that uses ranked orders (Oksanen, 2015). To do this, I used the metaMDS-function in the vegan package with two dimensions. The stress value for the model was 0.19. To visually compare species composition between warmed plots and controls I plotted the NMDS including a 95% confidence interval for warming plots and control plots. To test if any of the environmental variables were significantly correlated to species composition I used the envfit-function in the vegan package (Oksanen, 2015). In addition, each species was represented by a dot, where the size corresponded to the relative abundance of the species. To do this, I plotted a bubble chart by using the GG-plots package (Wickham, 2016) with cover of each species located at their respective coordinates from the NMDS. To collect the coordinates, I used the scores-function from the vegan package.

The most abundant taxa collectively covering more than 80% of the area were further investigated. These were: *Dicranum* spp., *Hylocomium splendens*, *Racomitrium* spp., *Ptilidium ciliare* and *Polytrichum* spp. I performed linear models for each taxon following the same procedure as when investigating the effects of warming on cover, evenness and richness of bryophytes. I removed plots where the respective species were not observed from the data. To meet the assumptions of normally distributed residuals, cover data was transformed by natural logarithm for *Dicranum* spp., *Hylocomium splendens* and *Racomitrium* spp. To further investigate the relation between the specific taxa and the environmental variables I conducted T-tests with the environmental variables that were not included in the main model (Vegetation height and cover of litter). However, because these variables were strongly correlated, I only performed T-tests with the variable that was most correlated to overall cover of bryophytes – cover of litter.

To test if there was a stronger decrease in acrocarpous mosses than pleurocarpous mosses with warming, I performed a linear mixed effect model (LME), with plot pairs as random effect. Interaction between warming and growth form was included. Liverworts (*Ptilidium ciliare*), were excluded from the data. Cover of bryophytes was transformed by natural logarithm to meet the model assumptions of normally distributed residuals. Figures not already mentioned, were made by using GG-plots in R-studio, and the layout was further edited in Inkscape (0.92.4).

Results

I identified 24 taxa of bryophytes in total. All of the 24 taxa observed were found in the warmed plots, while *Blindia acuta*, *Campyliadelphus chrysophyllus*, *Grimmia* sp. and *Saelania glaucescens* were not found in the controls. None of the taxa unique to warmed plots were found in more than two plots (Table 1).

Table 1. List of all taxa observed in the experiment, sorted abundance in control plots, decreasing from the most abundant. Table including explanations of the abbreviations used in Fig. 3 and growth form (GF). Further, mean cover of each species in the control plots (C), warming plots (W) in percentage, the direction of change and standard error (SE). Finally, frequency of plots each species is observed.

SPECIES INFORMATION			COVER (%)			COUNTS	
Abbreviation	Scientific name	GF	C	W	Change	C	W
Dicranu.spp	<i>Dicranum spp.</i>	A	7.110±0.954	1.890±0.411	↓	10	10
Hyl.sple	<i>Hylocomium splendens</i>	P	3.402±2.131	0.100±0.059	↓	7	5
Rac.spp	<i>Racomitrium spp.</i>	P	2.118±1.022	0.110±0.045	↓	9	7
Pti.cil	<i>Ptilidium ciliare</i>	L	1.204±0.255	0.262±0.063	↓	10	9
Poly.spp	<i>Polytrichum spp.</i>	A	0.926±0.166	0.251±0.052	↓	10	8
Dis.cap	<i>Distichium capillaceum</i>	A	0.631±0.163	0.457±0.161	↓	9	9
Rhy.rug	<i>Rhytidium rugosum</i>	P	0.6±0.236	0.024±0.008	↓	8	5
Sani.unc	<i>Sanionia uncinata</i>	P	0.589±0.316	0.093±0.030	↓	7	8
Brac.alb	<i>Brachythecium albicans</i>	P	0.440±0.149	0.063±0.012	↓	10	8
Hyp.spp	<i>Hypnum spp.</i>	P	0.432±0.106	0.446±0.160	↑	10	10
Isopt.pul	<i>Isopterygiopsis pulchella</i>	P	0.407±0.204	0.162±0.045	↓	8	8
Bry.spp	<i>Bryum spp.</i>	A	0.197±0.058	0.214±0.059	↑	8	9
Poh.spp	<i>Pohlia spp.</i>	A	0.130±0.028	0.251±0.086	↑	7	9
Syn.spp	<i>Syntricia spp.</i>	A	0.050±0.028	0.004±0.002	↓	4	2
Myu.sp	<i>Myurella sp.</i>	P	0.047±0.023	0.019±0.001	↓	3	5
Dit.flex	<i>Ditrichum flexicaule</i>	A	0.035±0.014	0.031±0.019	↓	3	3
Dicrane.spp	<i>Dicranella spp.</i>	A	0.029±0.020	0.060±0.035	↑	1	5
Tort.tor	<i>Tortella tortuosa</i>	A	0.007±0.003	0.097±0.039	↑	3	4
Fis.sp	<i>Fissidens sp.</i>	A	0.001±0.001	0.003±0.001	↑	1	2
Mee.uli	<i>Meesia uliginosa</i>	A	0.001±0.001	0.003±0.001	↑	1	2
Bli.acu	<i>Blindia acuta</i>	A	-	0.007±0.003	*	0	2
Camp.chry	<i>Campyliadelphus chrysophyllus</i>	P	-	0.0403±0.02	*	0	1
Grim.sp	<i>Grimmia sp.</i>	A	-	0.003±0.002	*	0	1
Sae.gleu	<i>Saelania glaucescens</i>	A	-	0.001±0.001	*	0	1

Degrees of freedom: Intercept $F_{(1,18)}$, Warming $F_{(1,9)}$, Growth form $F_{(1,18)}$, Warming:Growth form $F_{(1,18)}$

Growthform (GF): P = pleurocarpous mosses, A = acrocarpous mosses, L = liverworts

Change: ↓ = Less abundant in warmed plots, ↑ = more abundant in warmed plots, * = only present in warmed plots,

The following results are from linear regression models including the explanatory variables selected through correlation analysis and stepwise model selection, if not otherwise specified. Cover of bryophytes decreased by 75% with warming (Fig. 2A, Table 2) and was positively correlated with moisture (Table 2). Degree of moisture did not affect the effect of warming on cover of bryophytes, as indicated by the non-significant interaction between moisture and warming. Evenness was positively affected by warming (Fig. 2B, Table 2). None of the environmental variables correlated significantly with evenness (Fig. 2C). A two sample T-test showed that mean richness of bryophytes did not change with warming ($T_{18} = 0.32$, $P = 0.754$) (Fig. 2C). However, the linear model revealed that richness was positively affected by warming when moisture was taken to account (Fig. 2D, Table 2). Moisture and richness were positively correlated, but there was no significant interaction between moisture and warming (Fig. 2D, Table 2).

The correlation analysis showed that cover of bryophytes was negatively associated to cover of litter and height of vegetation (Appendix 1). Further, cover of litter and height of vegetation were positively correlated to each other (Appendix 1). There was a negative association between evenness and cover of bryophytes (Appendix 1). Richness was negatively associated to height of vegetation (Appendix 1).

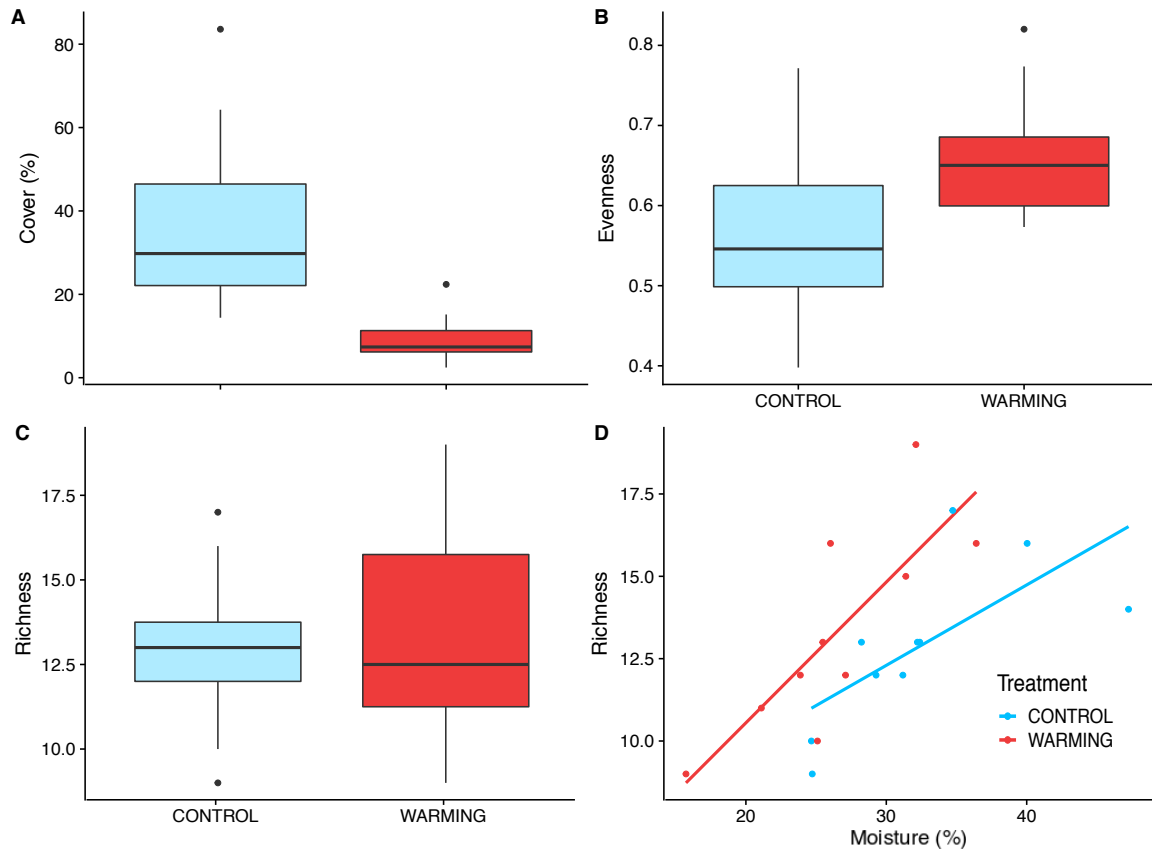


Figure 2. The effects of experimental warming on bryophyte cover (A), evenness (B) and species richness (C). The boxes represent control plots (blue) and plots that have been warmed with open top chambers (red). Figure D exhibits the effects of warming on soil moisture (%) and richness, as well as illustrating the correlation between moisture and richness. The top and the bottom of the boxes in figure A, B and C represent the first and the third quartiles (the 25th and 75th percentiles). The whisker extends from the top and the bottom of the box to the largest or smallest value no further than $1.5 * IQR$ from the hinge ($IQR = Q3 - Q1$). Any observation less than $Q1 - 1.5 * IQR$ or greater than $Q3 + 1.5 * IQR$ are plotted as individual dots. The black line that intersects the boxes are the median values.

Table 2. Results from linear models (LM) with cover, richness and evenness of bryophytes as response variables. The models contain warming treatment and other explanatory variables selected through model selection. Tests are based on twenty observations, ten in warmed plots and ten in control plots.

	Estimate	Std. Error	T value	P
Cover				
(Intercept)	-7.99	17.35	-0.46	0.651
Warming	-19.10	7.11	-2.68	0.016
Moisture	1.40	0.52	2.67	0.016
Evenness				
(Intercept)	0.57	0.03	18.65	<0.001
Warming	0.10	0.043	2.36	0.030
Richness				
(Intercept)	2.64	2.38	1.11	0.282
Warming	2.34	0.97	2.39	0.028
Moisture	0.32	0.07	4.46	<0.001

Bold P-values are <0.05 .

Warming had a positive effect on vegetation height and cover of litter, while it did not affect cover of vascular plants or soil moisture significantly (Fig. 3, Table 3). However, soil moisture was 30% lower in warmed plots compared to controls and the two sample T-tests showed that the effect of warming on moisture was close to significant ($P=0.05$).

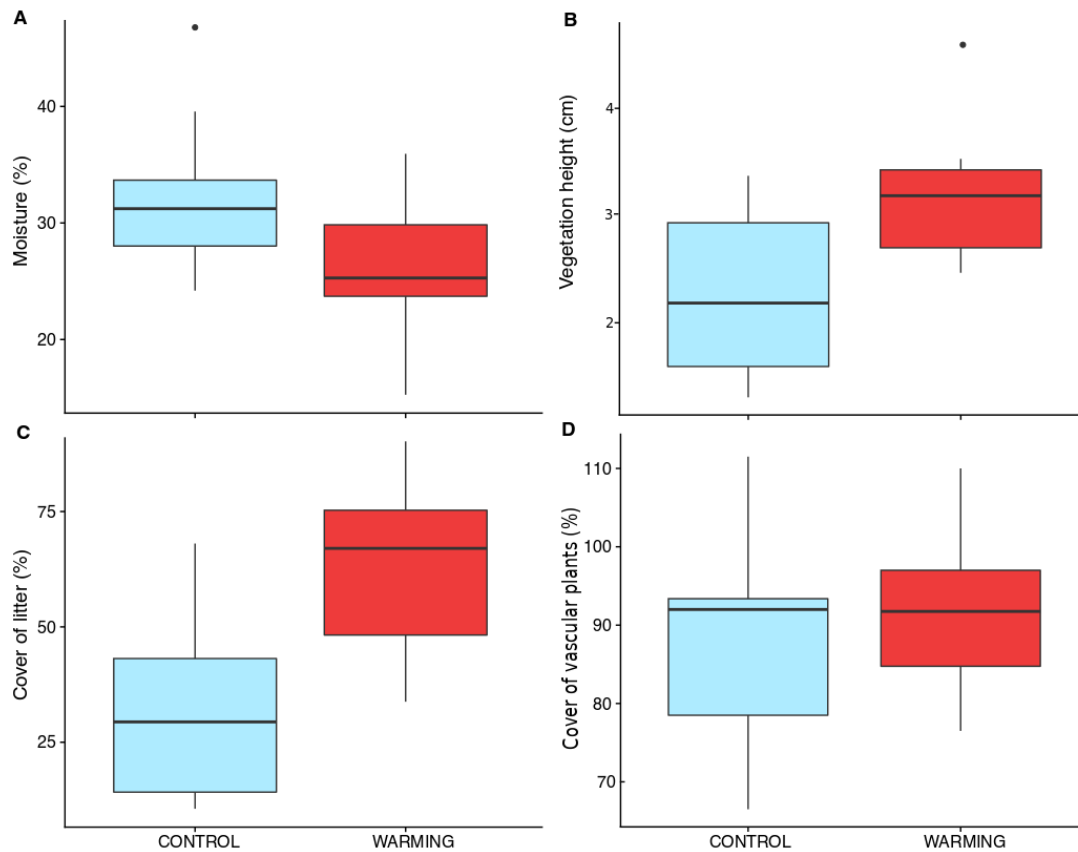


Figure 3. Effects of warming treatment on (A) moisture (%), (B) vegetation height (cm), (C) cover of litter (%) and (D) cover of vascular plants (%). The boxes represent control plots (blue) and plots that have been warmed with open top chambers (red) The top and the bottom of the boxes represent the first and the third quartiles (the 25th and 75th percentiles). The whisker extends from the top and the bottom of the box to the largest or smallest value no further than $1.5 * IQR$ from the hinge ($IQR = Q3-Q1$). Any observation less than $Q1 - 1.5*IQR$ or greater than $Q3 + 1.5*IQR$ are plotted as individual dots. The black line that intersects the boxes are the median values.

Table 3. Results from two sample T-tests testing the effects of warming on cover of litter, soil moisture, vegetation height and cover of vascular plants.

	Df	T value	P
<i>Moisture</i>	17.52	-2.10	0.050
<i>Vegetation height</i>	16.72	2.78	0.013
<i>Cover of litter</i>	17.94	3.70	0.002
<i>Cover of vascular plants</i>	16.91	0.64	0.531

Bold P-values are <0.05 .

Warming affected species composition ($F_{1, 18} = 4.99$, $P < 0.001$, PERMANOVA) (Fig. 3). Abundant taxa tended to be more common in the control plots than in the warmed plots, as

shown by the distribution pattern of big and small dots in the NMDS ordination plot (Fig 4). Conversely, taxa that were less abundant tended to be proportionally more common in the warmed plots (Fig. 4). Dot size corresponds to the relative abundance of the taxa it represents. Correspondingly, the nine most abundant taxa in the control plots were less abundant in warm plots than in control plots, while the eight least abundant taxa in the controls were more abundant in the warm plots (see the distribution of arrows, representing the direction of change, in the species inventory list that is ordered by abundance, Table 1). None of the environmental variables were significantly correlated with the species composition.

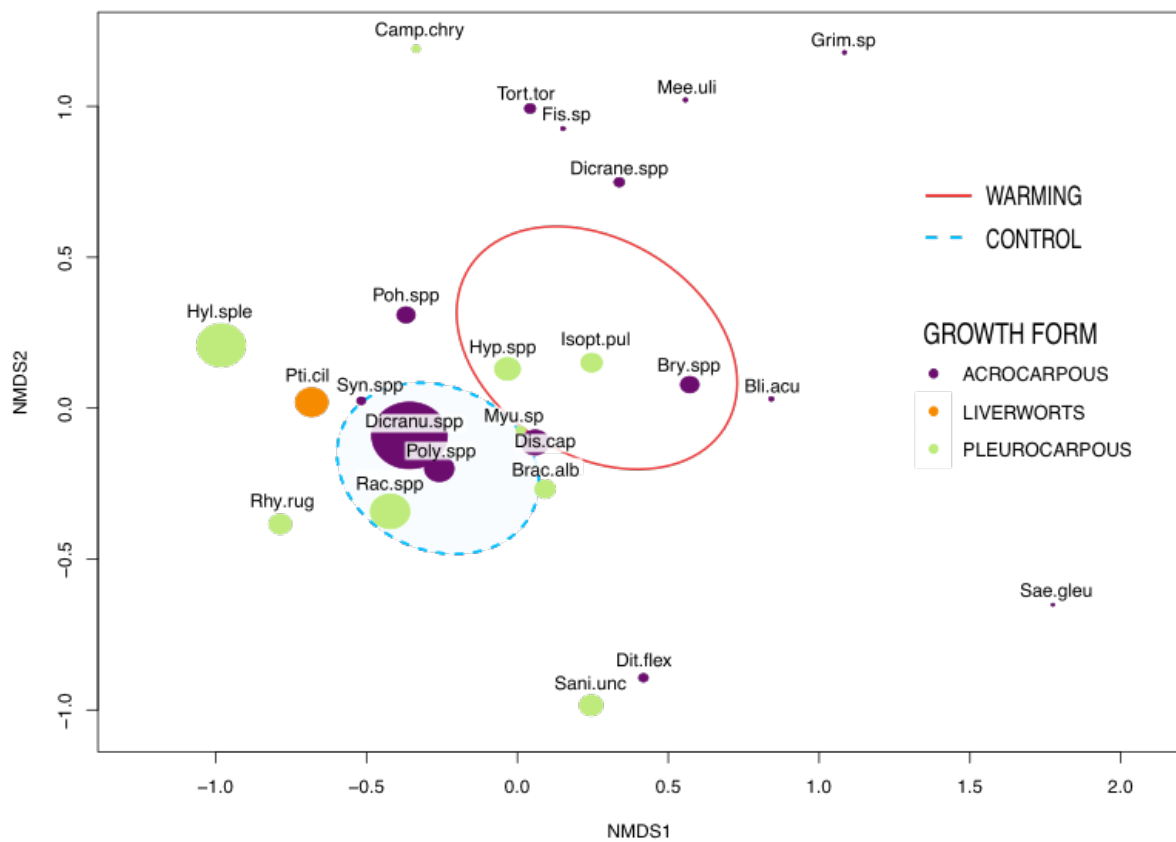


Figure 4. Non-metric multidimensional scaling (NMDS) ordination plot of the bryophyte community investigated in both warming and control plots. Dot size correspond to the overall relative abundance and dot color indicates the growth form of the taxa. The ellipse are 95% confidence intervals of warmed plots and control plots, based on SE-values.

The five most abundant taxa (*Dicranum* spp., *Hylocomium splendens*, *Racomitrium* spp., *Ptilidium ciliare* and *Polytrichum* spp.) collectively constituted 83% of the total bryophyte cover. Linear regression models with the most abundant bryophyte taxa as response variables and explanatory variables selected through correlation analysis and model selection revealed that except for *H. splendens*, warming had a significantly negative effect on cover of the four remaining taxa (Table 4). *H. splendens* covered 97% less in warmed plots than in control plots,

however with great variation and few observations, the difference was not significant (Table 4). Further, *H. splendens* was positively correlated to moisture, while the remaining four did not correlate with moisture (Table 5, Fig. 4B).

Table 4. Results from linear models (LM) with the effect of warming on cover of the five most common bryophyte species/genera at the study site. The models contain warming treatment and other explanatory variables selected through model selection.

	Estimate	Std. Error	T value	P
<i>Dicranum</i> spp. (N= 10+10) †				
(Intercept)	1.80	0.30	5.85	<0.001
Warming	-1.68	0.40	-3.87	0.001
<i>Hylocomium splendens</i> (N= 7+5) †				
(Intercept)	-10.66	3.46	-3.08	0.012
Warming	-0.22	1.30	-0.17	0.800
Moisture	0.27	0.10	2.71	0.024
<i>Racomitrium</i> spp. (N= 9+7) †				
(Intercept)	-0.53	0.58	-0.92	0.372
Warming	-2.13	0.88	-2.42	0.030
<i>Ptilidium ciliare</i> (N= 10+9)				
(Intercept)	1.20	0.27	4.45	<0.001
Warming	-0.91	0.39	-2.33	0.033
<i>Polytrichum</i> spp. (N= 10+8)				
(Intercept)	0.92	0.18	5.01	<0.001
Warming	-0.61	0.27	-2.24	0.040

Bold P-values are <0.05.

N= number of observations in control plots + number of observations in warmed plots

† = transformed by natural logarithm

The following results are from the additional linear regression model, with the five most abundant species as response variables and cover of litter as explanatory variable. *Dicranum* spp., *Racomitrium* spp., and *P. ciliare* were negatively associated to cover of litter, while cover of *H. splendens* and *Polytrichum* spp. were not correlated to cover of litter (Fig. 4A, 4C, 4D, Appendix 2).

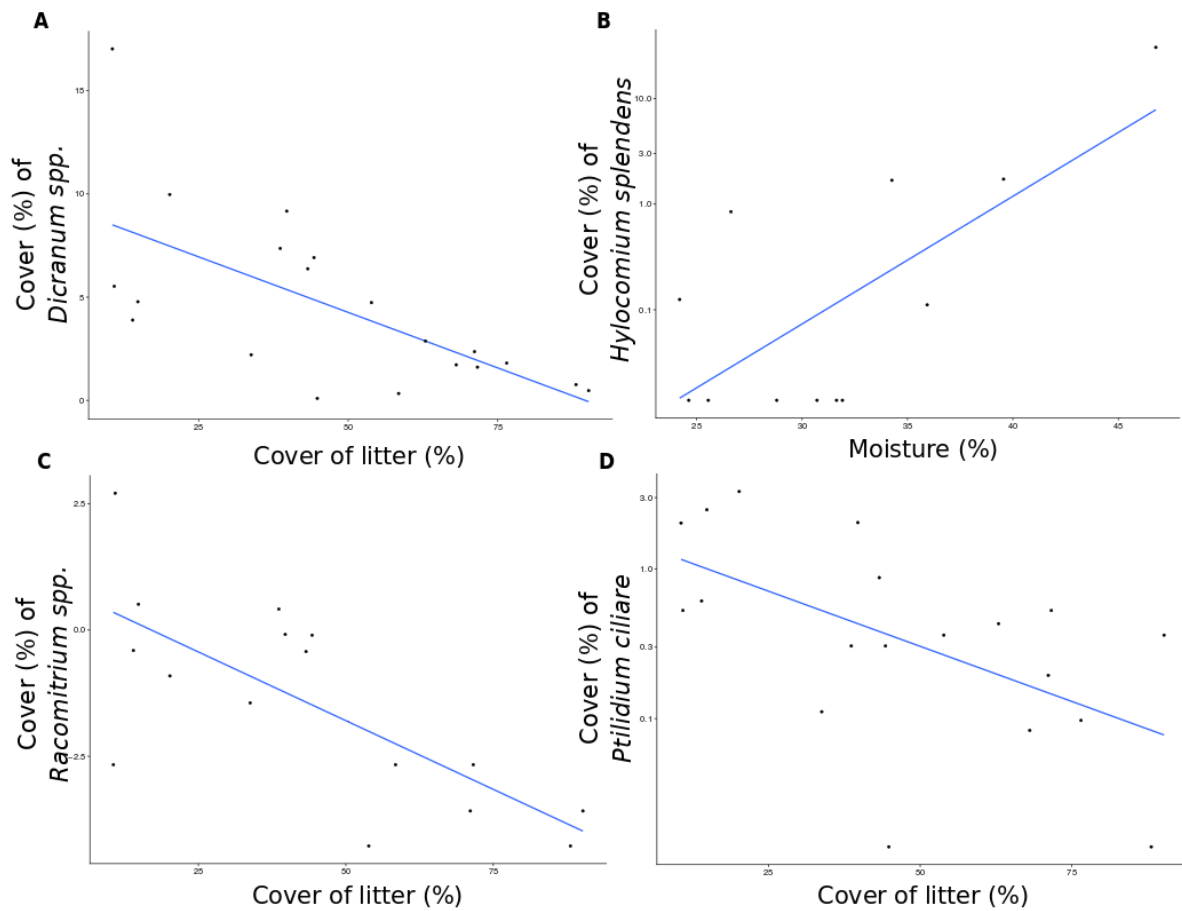


Figure 5. Scatterplots with cover data for (A) *Dicranum spp.*, (B) *Hylocomium splendens*, (C) *Racomitrium spp.*, (D) *Ptilidium ciliare* on the Y-axis, and the environmental variable that each species is most associated with on the x-axis. Linear least squares regression lines are included. Cover data for *H. splendens* (B) and *P. ciliare* (D) is log transformed, but values showed on the Y-axis are untransformed.

On average, acrocarpous mosses amounted for 36% more cover than pleurocarpous mosses. Cover of acrocarpous mosses did not decrease more than cover of pleurocarpous mosses, as shown by non-significant interaction between growth form and treatment (Fig. 6, Table 5). On the contrary, when comparing number of taxa that decreased with warming a tendency of the opposite trend was observed. While 36% of the acrocarpous taxa decreased in cover with warming (5 out of 14 taxa), 78% of the pleurocarpous taxa decreased (7 out of 9 taxa) (Fig 4, Table 1).

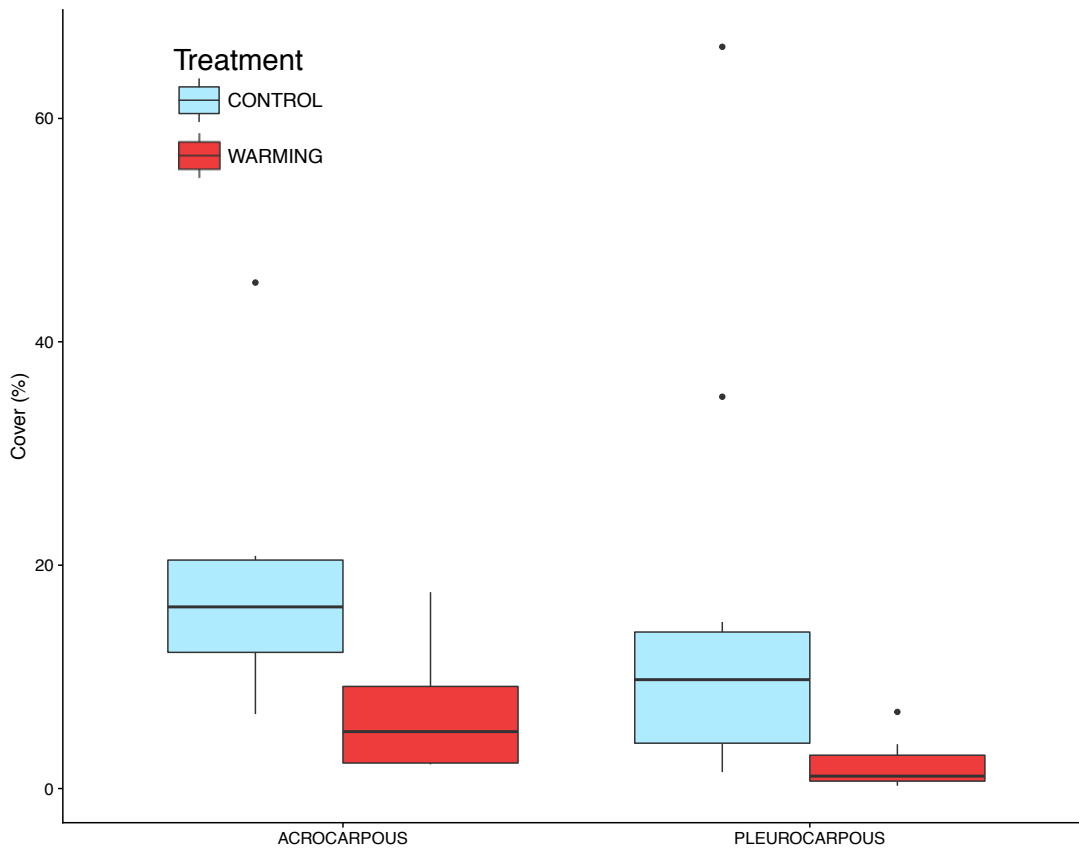


Figure 6. The effect of warming on cover (%) of acrocarpous and pleurocarpous mosses. The top and the bottom of the boxes represent the first and the third quartiles (the 25th and 75th percentiles). The whisker extends from the top and the bottom of the box to the largest or smallest value no further than $1.5 * IQR$ from the hinge ($IQR = Q3 - Q1$). Any observation less than $Q1 - 1.5 * IQR$ or greater than $Q3 + 1.5 * IQR$ are plotted as individual dots. The black line that intersects the boxes are the median values.

Table 5. ANOVA-table with results from a linear mixed effects model, where cover of bryophytes is the response variable, while warming and relative abundance of different growth forms (pleurocarpous and acrocarpous) were explanatory variables. Plot pairs was included as random factor.

	F-value	p-value
<i>(Intercept)</i>	113.76	<.001
<i>Warming</i>	32.43	0.001
<i>Growth form</i>	12.34	0.003
<i>Treatment:Growth form</i>	1.77	0.200

Discussion

Decrease in cover of bryophytes with experimental warming

Eighteen years of warming had a negative effect on cover of bryophytes in the alpine heath in Finse, which supports my first hypothesis. This result corroborates the findings of most experimental warming studies (Elmendorf et al., 2012a). However the opposite trend has also been observed at some sites (Hudson & Henry, 2010).

Warming did not affect soil moisture significantly. However, considering the low P-value (Table 3) and because warming under normal circumstances increases evaporation (Wetherald & Manabe, 1999), warming is likely to have affected moisture availability of bryophytes negatively. Further, cover of bryophytes and soil moisture had a significant positive association. Hence, my results indicate that decreased moisture availability likely contributes as a driver of the decline in bryophyte cover with warming. Regardless of statistical significance, the results alone could not prove causality between soil moisture and bryophyte cover – warming could be, or have triggered, a confounding factor. However, in one of the few, if not the only, experimental warming study where overall bryophyte abundance significantly increased with warming, soil moisture remained constant (Hudson & Henry, 2010). Warming alone is thus not necessarily detrimental to bryophyte cover when moisture remained unchanged. Further, the strong dependence of moisture availability for growth and distribution of bryophytes (He et al., 2016; Proctor, 1972; Sun et al., 2013) suggests that the positive correlation between moisture and cover of bryophytes could be causal. Bryophytes forming dense and thick layers have the potential of decreasing evaporation from the soil (Gornall et al., 2011). However, in my study bryophytes rarely grew densely, and the layer was never deep. It is thus reasonable to believe that decreased moisture availability caused the decrease in bryophyte cover, and not the other way around. Further, based on data from 61 sites worldwide, Elmendorf et al. (2012a) concludes that moisture is the main driver of decreases in bryophyte cover with experimental warming. Elmendorf et al. (2012a) does not discuss other potential explanations for the decrease in bryophyte cover, such as increased competition with vascular plants, despite their results also showing a significant increase in canopy height and increased accumulation of litter with warming. Walker et al. (2006) who performed a similar meta-analysis as Elmendorf et al. (2012a) analyzing data from some of the same experiments, but with shorter duration of the

warming, concludes that the decline of bryophyte cover is probably due to increased competition with vascular plants.

Warming increased vegetation height and cover of litter in my study, which corroborates the findings of Elmendorf et al. (2012a). Further, both vegetation height and cover of litter was negatively correlated to bryophyte cover, indicating that increased competition with vascular plants is a driving factor for the changes in community composition of bryophytes. However, the problem of distinguishing between correlation and causation arises once more, as there could be confounding factors. Nevertheless, abundant cover of litter has the potential of reducing bryophyte growth by blocking light and changing the physical environment (Xiong & Nilsson, 1999). In plots with dense layers of litter, bryophytes seemed to be almost entirely excluded (personal observation). It is therefore reasonable to believe that the strong negative correlation between cover of litter and cover of bryophytes appears because litter affects cover negatively. Lang et al. (2012) also provides evidence indicating that cover of litter can be a driver of decreasing cover of bryophytes with warming (Lang et al., 2012). Further, tall-growing vegetation block more light than short-growing vegetation (Kotowski & van Diggelen, 2004), which suggests a causal relation between height of the vegetation and cover of bryophytes. However, in my study vegetation height was more strongly correlated to cover of litter than to bryophyte cover. My results may thus indicate that taller growing vegetation produce more litter – which in turn reduces cover of bryophytes. The direct effect of increased shade with higher vegetation is thus not necessarily strong in my experiment, but it cannot be excluded.

Shift in species composition where abundant species decrease and less abundant species show a trend of increasing

Warming had a positive effect on evenness. Correspondingly, cover of the most abundant species decreased when subjected to warming and cover of the least abundant species increased. In addition, a few taxa were only observed in warmed plots (4 out of 24). These results contrast the findings of Lang et al. (2012) who found a significant increase in cover of a few species, while the great majority decreased.

Evenness did not correlate to any of the environmental variables, but it was positively correlated to bryophyte cover. Hence, evenness of bryophytes is high where bryophytes are scarce, and vice versa. Vegetation studies on higher order plant communities show an almost persistent negative correlation between evenness and biomass (Drobner et al., 1998; Mulder et al., 2004). Evidence indicates that the community organization and the relative abundance distribution of bryophytes are remarkably similar to those of higher order plants, despite some differences (Steel et al., 2004). The relation between evenness and biomass for higher order plant communities is explained by the approximately geometric distribution of abundances that is found in plant communities (Drobner et al., 1998). The largest species tend to be bigger in high productivity communities, compared to communities with low productivity. Thus, the gap between the biggest and the smallest species increases with increased productivity – which gives lower evenness (Drobner et al., 1998; Mulder et al., 2004). Accordingly, Dahle (2019) shows a decrease in relative abundance of the longest and heaviest bryophytes with warming in the same plots as I examine in this study. Increased evenness with warming could therefore possibly be explained by a smaller gap between the biggest and the smallest bryophytes in the warm plots compared to the controls. Even though productivity of the ground layer decreases with warming, increased height of the vegetation and cover of litter indicate that productivity of the overall plant community increases with warming, which is in line with the literature (Elmendorf et al., 2012a). Following the logic of Drobner et al. (1998) and Mulder et al. (2004), evenness should therefore decrease with warming when including all species groups in the calculation. Such negative relations between evenness and productivity can occur in absence of biological interactions (Mulder et al., 2004). However, increased cover of the least abundant bryophytes with warming (not only relative cover), indicates that geometric distribution of abundances is at least not the only explanation of the increase in evenness with warming.

Warming had a positive effect on richness of bryophytes, which also contrasts my second hypothesis and the findings of Lang et al. (2012). However, the positive effect seems to be offset by decreased moisture availability – the effect was only observed when moisture was included in the model. Warmed and wet plots had the highest bryophyte richness, while warmed and dry plots had the lowest bryophyte richness. This is in line with the findings of Mörsdorf & Cooper (in prep.) who found that bryophyte abundances increase in combination with enhanced snow regimes (and thus high moisture availability) and warming within moist meadows on Svalbard. The beneficial environment created in the warmed and wet plots could possibly explain the pattern where cover of the least abundant bryophytes increased with

warming, and that a few taxa were only observed in the warmed plots. A negative correlation between vegetation height and bryophyte richness suggests that the positive effect of warming on bryophyte richness is further offset by increased height of the vegetation. Bryophyte richness was not associated with cover of litter. This is surprising, considering that cover of litter was strongly correlated to height of the vegetation and that there was a strong negative association between cover of litter and cover of bryophytes. One possible explanation is that litter may have excluded all bryophytes in the areas where it was sufficiently abundant, while shade from vegetation may only have affected a selection of shade intolerant bryophyte species, but in a larger area. Because of the small scale-nature of the bryophyte community at the study site (personal observation), all the normal bryophyte taxa could have possibly been present in the area that was not affected by litter. If for instance 65% of a plot was covered by litter and all bryophytes were excluded from this area the remaining 35% could possibly still host all normal variation in microhabitats, and thus all the most common bryophytes. This explanation could be tested if data was collected on a smaller scale.

Warming had a negative effect on cover of four out of the five most abundant taxa. Among these taxa, *Polytrichum* spp. was the only that was not negatively associated to cover of litter. *Hylocomium splendens* was not significantly affected by warming or association to cover of litter. Further, *Hylocomium splendens* differed from the other four taxa by being positively associated to moisture. None of the other most abundant taxa showed any associated to moisture. My results thus indicate that different taxa of bryophytes react differently to warming and that they are affected differently by changes in different environmental variables. This makes sense, considering that bryophytes in general are assumed to have narrow niches and are often specific to certain microhabitats (Tuba et al., 2011). *Hylocomium splendens* is widespread in the lowland and it is often growing on the forest floor (Hallingbäck, 2016). One would therefore expect *H. splendens* to be adapted to more shade and higher ambient temperatures than what is found at the study site. This could explain why warming did not affect cover of *H. splendens*. Nevertheless, *H. splendens* covered 97% less in warmed plots than in controls, but with high variation and few observations, the difference was not significant. By contrast, Lange et al. (2012) showed that long-term warming had a positive effect on cover of *H. splendens*. Hence, if moisture availability did not decrease in warmed plots, cover of *H. splendens* may have been positively affected by warming.

Acrocarpous mosses did not decrease more than pleurocarpous mosses

Cover of acrocarpous mosses did not decrease more than cover of pleurocarpous mosses when subjected to warming. On the contrary, cover of most pleurocarpous taxa decreased when subjected to warming and cover of a minority of the acrocarpous taxa decreased. However, this pattern was not tested statistically, and it is not unlikely that it appeared by chance. In contrast to this pattern, Elmendorf et al. (2012a) found a stronger overall decrease in cover of acrocarpous mosses than in cover of pleurocarpous mosses with warming.

Vegetation grew higher in the warmed plots compared to the controls. Pleurocarpous mosses are believed to be better adapted to shade than acrocarpous mosses (Robinson et al., 1989). One would therefore expect acrocarpous mosses to decrease more than pleurocarpous mosses. However, pleurocarpous mosses are also believed to be less adapted to drought compared to acrocarpous mosses (Robinson et al., 1989) that are known to possess more advanced water conducting structures (Glime, 2007). One possible explanation for the unexpected results could thus be that acrocarpous mosses tolerate decreased water availability better than pleurocarpous mosses. The positive correlation between moisture and cover of the pleurocarpous bryophyte *H. splendens* supports this explanation. However, the insignificant interaction between growth-form and warming may also simply reflect the large variation of responses to warming among species that show the same growth form. Hence, my results stress the importance of high taxonomic resolution when investigating the effects of warming on bryophytes.

The future of alpine bryophyte communities in a global warming perspective

The results of this study indicate that different taxa of bryophytes can react differently to elevated temperatures and to the changes that follow in the physical and biological environment. Further, the environment surrounding a bryophyte community differs between sites, and different sites host different bryophyte taxa (Hallingbäck, 2016). Thus, it is logical that the effects of warming on bryophyte diversity (Lang et al., 2012) and bryophyte abundance (Elmendorf et al., 2012a) differs between sites. The results of this thesis can therefore not be used to project the effects of warming on all alpine bryophyte communities. However, it outlines some trends that one could expect to observe with elevated temperatures in similar sites as the study location (Sanddalsnuten). As discussed previously, my results indicate that

the effects of warming on cover and especially richness of bryophytes depends on water availability. Global warming is likely to be followed by changes in other aspects of the climate, such as precipitation patterns (Trenberth, 2011). The effects of global warming on community structure of bryophytes will thus depend on how precipitation patterns are affected by elevated temperatures. Meanwhile, the warmed plots in this study (Open top chambers) primarily manipulate temperature (Hollister & Webber, 2000). Great caution must therefore be taken when interpreting the results and transferring them to a future global warming scenario. Nevertheless, this thesis presents an example showing how sensitive alpine bryophyte communities can be to elevated temperatures. To be able to draw broader conclusions on how alpine bryophytes will be affected by global warming, more long-term experimental warming studies including high taxonomic resolution on bryophytes in different sites are required.

Conclusions

This thesis highlights the sensitivity of bryophyte communities to increased temperatures. Total cover of bryophytes showed a strong decrease with long-term experimental warming, which supports the first hypothesis. Hence, my results indicate that bryophyte communities in similar environments are likely to experience a decrease in cover with elevated temperatures. In contrast to the second hypothesis, warming had a positive effect on richness and evenness of bryophytes. However, the positive effect seemed to be offset by decreased water availability and possibly increased height of the vegetation. Different taxa reacted differently to warming and were associated to different environmental variables. A trend was observed where the most abundant species tended to decrease in cover while less abundant species tended to increase in cover. Acrocarpous mosses did not decrease more than pleurocarpous mosses, which could be due to the decrease in moisture. These findings underline the importance of high taxonomic resolution when investigating the effects of warming on bryophytes. Increased competition with vascular plants (cover of litter and height of vegetation) and decreased availability of moisture seem to be important drivers of change in different aspects of the community structure of alpine bryophytes. Overall, this study shows that the effects of warming on bryophyte communities depends on the physical and biological environment and the species composition of the community. General conclusions on how global warming will affect the community structure of alpine bryophytes can thus not be made based on this study. Nevertheless, this study presents

an example showing how fragile and sensitive a bryophyte community can be to elevated temperatures.

Bryophytes are known to affect water regulation, nitrogen fixation and carbon storage in the soil. Further, bryophytes are believed to be the most important source of food for lemming (*Lemmus lemmus*) during the winter and a source of food for some arthropods. A potential decrease in cover of bryophytes and a shift in species composition may therefore greatly impact alpine ecosystems.

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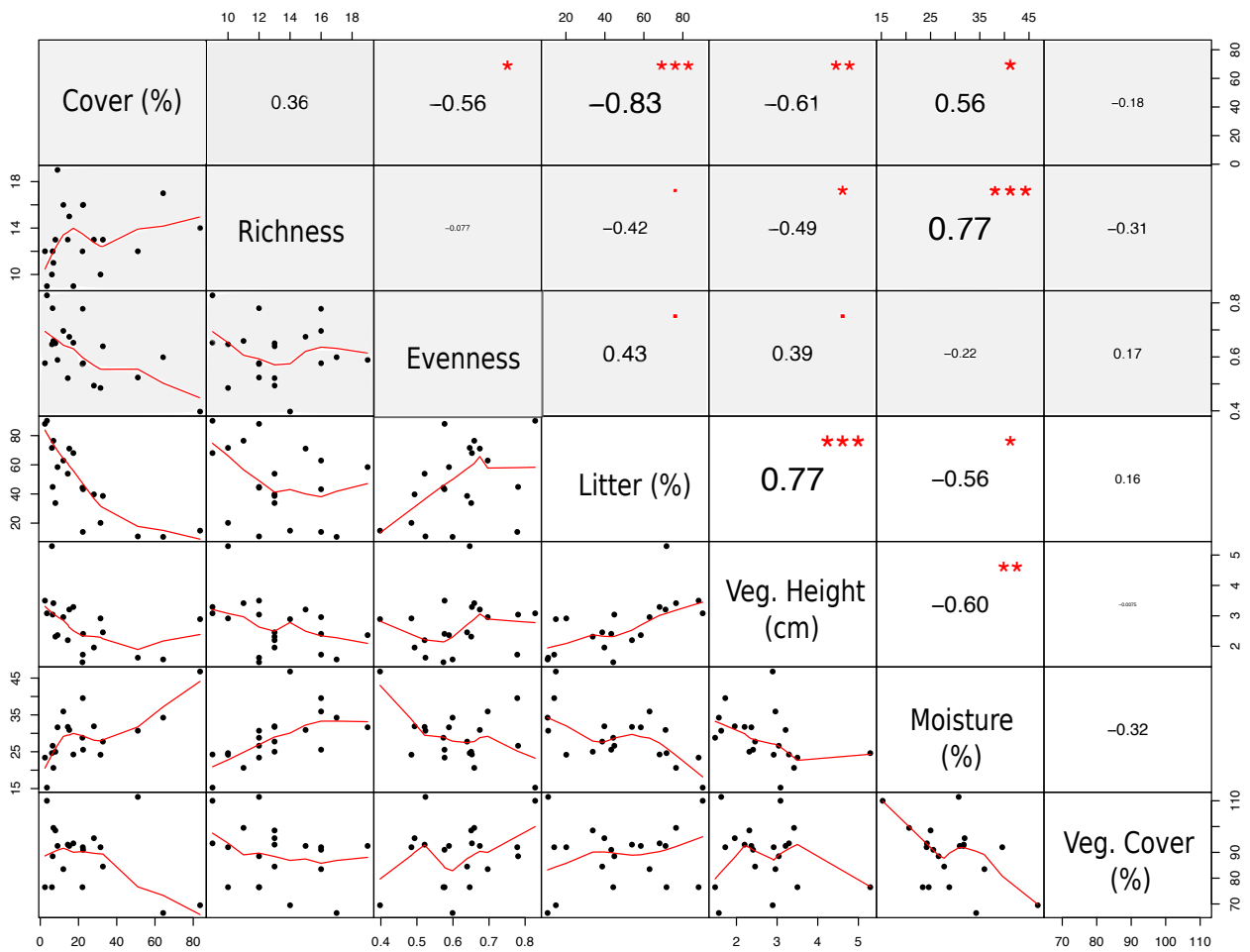
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Appendix



Appendix 1: Correlation matrix including the response variables (shaded in gray) and environmental variables. The lower left triangle of the matrix exhibits scatterplots with non-linear trend lines, while the upper right triangle exhibits spearman correlation coefficients. $P < 0.001 = ***$, $P < 0.01 = **$ and $P < 0.05 = *$, $P < 0.1 = \cdot$.

Appendix 2. Results from linear regression model (LM) showing the association between cover of litter and the five most common bryophyte species/genera at the study site.

Estimate	Std. Error		T- value	P
<i>Dicranum spp.</i> (N= 10+10)				
<i>(Intercept)</i>	9.6	1.57	6.13	<0.001
<i>Cover of litter</i>	-0.1	0.03	-3.70	0.002
<i>Hylocomium splendens</i> (N= 7+5) †				
<i>(Intercept)</i>	0.26	1.35	0.19	0.85
<i>Cover of litter</i>	-0.07	0.03	-2.04	0.068
<i>Racomitrium spp.</i> (N= 9+7) †				
<i>(Intercept)</i>	1.20	0.27	4.46	<0.001
<i>Cover of litter</i>	-0.91	0.39	-2.32	0.033
<i>Ptilidium ciliare</i> (N= 10+9)				
<i>(Intercept)</i>	1.78	0.39	4.60	<0.001
<i>Cover of litter</i>	-0.02	>0.01	-2.96	<0.001
<i>Polytrichum spp.</i> (N= 10+8)				
<i>(Intercept)</i>	1.10	0.30	3.62	0.002
<i>Cover of litter</i>	-0.01	>0.01	-1.70	0.111



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