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of Life Sciences

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# **Effects of long-term experimental warming on alpine bryophytes: trends in functional traits**

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Master of Science in Ecology



## Preface

This is the final product of my Master of Science in Ecology at the Norwegian University of Life Sciences (NMBU). I had the privilege to work in scenic surroundings at Sanddalsnuten, Finse. I wish to thank my patient, experienced and kind supervisors for always making time for guidance. Particularly a huge thank you to my main supervisor Johan Asplund for all the time, feedback and patient guidance. I also want to thank my co-supervisors Kari Klanderud for invaluable feedback and comments, and Kristel van Zuijlen for advice with R-programming and help in the field with species identification. I also wish to thank Marte Olsen for help with identification of species, and to the friendly hosts at Finse Alpine Research Center for comfortable accommodation during the field work. I want to thank Nathan H. Phinney for valuable conversations along the way and comments in the final phases of writing. My parents have given enthusiastic support, especially helping me push through the hard parts. Lastly, thank you to my fellow student collaborator Snorre Sundsbø for great teamwork and valuable conversations.



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## Abstract

Functional traits are becoming increasingly important tools to evaluate plant community response to climate change. Artificial warming treatments can shift community-level trait values as a consequence of intraspecific variation, species turnover and their covariation. These warming studies on vascular plants suggest that the shift is mostly caused by species turnover, while studies on lichens suggest that much of the shift in traits is explained by intraspecific variation. There is limited knowledge about how bryophytes respond under simulated warming and to what degree the response is a consequence of intraspecific variation. In contrast to vascular plants, they should respond strongly to their external environment, as they lack the physiological structures to maintain homeostasis. In order to evaluate the significance of intraspecific variation and species turnover for bryophytes, I assessed bryophyte cover and measured the functional traits: carbon concentration (C), nitrogen concentration (N), water holding capacity (WHC), shoot length, biomass, area and some of their ratios in warmed plots simulating climate change and control plots at Sanddalsnuten, Finse.

I found some support for my first hypothesis; shorter, lower biomass shoots with lower WHC in the warmed plots suggests higher competition from vascular plants in the warmed plots. My second hypothesis that most of the explained variation seen between plots would be accounted for by species turnover, was mostly supported. I found the growth form of the warmed bryophytes to shift towards growth forms associated with the lowland, giving support for my last hypothesis. My work in this thesis underline the importance of including the trait variation of non-vascular primary producers like bryophytes when predicting future environmental changes. To get a more complete picture environment change as a consequence of climate change phenomena, inclusion of species turnover as well as the within-species variation are paramount.

# Table of Contents

Preface.....	1
Abstract.....	2
Introduction.....	4
Methods.....	7
Study area.....	7
Study design of the OTC-experiment.....	8
Bryophyte cover estimates.....	9
Water holding capacity (WHC).....	10
Trait selection.....	11
Photograph analysis.....	12
C and N content.....	13
Trait by dominant species analysis.....	13
Life history traits.....	13
Statistics.....	13
Results.....	15
Community weighted means of traits.....	15
Trait by species analysis.....	19
Life history trait analysis.....	19
Discussion.....	20
The significance of intraspecific variation.....	21
Shifts in functional traits with warming.....	21
Conclusion.....	26
References.....	27
Appendix.....	32

## Introduction

A functional trait is a well-defined measurable characteristic of an organism that strongly influences its performance (McGill et al., 2006). These traits allow for easier generalization, as opposed to when individual species are used. Trait-based approaches are already helping us answer questions about community structure (Hudson & Henry, 2010; Keddy, 1992), climate change effects (Chapin, 2003; Sundqvist et al., 2011), how ecosystem services work (Lavorel, 2013), food production (Wood et al., 2015) and restoration ecology (Funk et al., 2008). The move from a species-based approach to a trait-based one has already been made to a large degree for vascular plants, but to a small degree for non-vascular primary producers. However, its slowly becoming more popular for groups like bryophytes (e.g. Cornelissen et al., 2007; Jägerbrand et al., 2003; Lang et al., 2012).

Common species contribute more to ecosystem functioning compared to the rarer species (Grime, 1998). Therefore, community-weighted means (CWM) are often used when it is necessary to prescribe a single trait value to a trait in a community. These values allow for easy comparisons between traits in contrasting ecosystems, or between different experimental treatments. For example, by analyzing the CWM of plant leaf and litter traits along an elevational gradient, Sundqvist et al (2011) found a significant relationship with elevation. Using CWMs, researchers have shown that available nutrients decrease with elevation (Huber et al., 2007), prompting a shift in CWM values towards those associated with resource conservation in vascular plants (Read et al., 2014; Sundqvist et al., 2013). A shift in CWM values can usually be explained by a combination of species turnover, intraspecific variation and their covariation (Lepš et al., 2011). Disentangling these elements is essential for predicting the impact on ecosystems. Failing to include intraspecific trait variability may underestimate community response (Lepš et al., 2011). There is limited knowledge about how some primary-producer groups like bryophytes respond, and to what degree the response is a consequence of intraspecific variation.

Alpine and arctic environments are some of the first to respond to climate warming phenomena (Theurillat & Guisan, 2001). Even minute temperature fluctuations in these environments can cause notable shifts in biodiversity and species composition (Sala et al., 2000). Bryophytes are among the most abundant primary producers in alpine ecosystems and can reach up to 100% cover in wetter and more protected areas (see figure 1) (Belnap & Lange, 2001; Russell, 2008; Wielgolaski & Kjelvik S, 1975). Alpine bryophytes are recognized as vital species that affect biogeochemistry (Cornelissen et al., 2007) by providing a major N

input by hosting N-fixing bacteria (During & Tooren, 2008) and playing a role in carbon and nutrient cycling (Belnap & Lange, 2001; Deyn et al., 2008; Longton, 1988; Smith, 1982). Bryophytes can either facilitate the establishment and growth of other plant species (Press et al., 1998) or impede their survival by competitive exclusion (Chernov, 1988). Additionally, they are food sources for arthropods and lemmings (Cornelissen et al., 2007; Soininen et al., 2013). These essential roles may change due to rapid changes as a consequence of global warming (e.g. Cornelissen et al., 2007; Hågvar & Klanderud, 2009; Lang et al., 2012), as one of the most severe responses to shifts in ecological communities occur when ecosystem processes change (Chapin, 2003).

Graminoids, shrubs and lowland species are becoming more frequent, while bryophytes and lichens are declining in warming alpine environments (Elmendorf et al., 2012a; Elmendorf et al., 2012b; Klanderud & Birks, 2003; Walker et al., 2006). This is consistent with paleoecological findings that describe temperature and vegetation fluctuations similar to the ones we are seeing today (Hu et al., 2002). Herb dominated tundra was overtaken by shrubs and evidence suggested transition to a more productive system (Hu et al., 2002). There are however notable exceptions to this pattern, where some organisms resist long-term warming (Grime et al., 2008; Hudson & Henry, 2010; Lamb et al., 2011; Van Wijk et al., 2004).



*Figure 1: An example of how bryophytes can dominate the tundra vegetation. Pictures are from Finse. (Hoy, 2016)*

Like vascular plants, bryophytes are migrating upwards in elevation when the climate gets warmer (Bergamini et al., 2009). Vascular plants have been shown to partially out-compete bryophytes under experimental warming treatments (e.g. Elmendorf et al., 2012a; Jägerbrand et al., 2003). Bryophytes have also been shown to respond strongly to simulated warming (Elmendorf et al., 2012b; Klanderud & Totland, 2005), which translates to a more stressful environment for the bryophytes (Furness & Grime, 1982; Jägerbrand et al., 2003). After a warming treatment, the bryophyte species in the Furness & Grime (1982) experiment had a lower growth rate and lower shoot length than control. This is despite moving closer to bryophytes temperature optima (Furness & Grime, 1982; Proctor, 1982). This indicates that increased temperature did not cause the stunted growth of the bryophytes. Interactions with vascular plants in the form of competition may be the most important challenge for bryophytes exposed to warming (Jägerbrand et al., 2003). In cold environments, bryophytes have been shown to change the frequency and manner of reproduction by, for instance, altering sporophyte frequency (Casanova-Katny et al., 2016). This was thought to be solely an effect of adaption, but it may in part be caused by competition with vascular plants. The growth form itself has also been shown to change with abiotic factors alone (Sandvik & Heegaard, 2003). Under changes in snowmelt and moisture patterns, one bryophyte species changed growth form with simulated climate warming (Sandvik & Heegaard, 2003). Little is currently known about how bryophyte growth form and life-history traits varies with changes in the environment.

There is limited knowledge about how bryophytes respond under simulated warming and to what degree the response is a consequence of intraspecific variation. In contrast to vascular plants, they should respond strongly to their external environment, as they lack the physiological structures to maintain homeostasis (Proctor, 1982). Studies on vascular plants suggest that community-level shift in traits is mostly caused by species turnover (Kichenin et al., 2013; Lepš et al., 2011; Siefert et al., 2015), while in lichens, much of the shift in traits can be explained by intraspecific variation (Asplund & Wardle, 2014). Less is known about bryophytes, but they have been shown to respond to a warming treatment with within-species variation (Jägerbrand et al., 2003).

With this thesis, I aim to investigate the relative importance of intraspecific variation and species turnover as drivers of community-level functional trait change through an experimental setup using open top chambers (OTCs). I looked at how the functional traits of an alpine bryophyte community is affected by a long-term warming treatment. I recorded the bryophyte species composition in experimentally warmed plots and in control plots with ambient temperature. In addition, I sampled the dominating species in each plot and measured several functional traits (i.e. water holding capacity (WHC) and C content). From these measurements I calculated community weighted means. I used this experimental set-up to test the



following hypothesis: (I) With warming there is a shift in bryophyte functional traits towards those associated with higher competition with vascular plants. (II) Interspecific variability will account for most of the explained variation between plots. (III) There is a change towards life-history traits associated with more effective reproduction with warming and a change in growth form (as seen in (Casanova-Katny et al., 2016)).

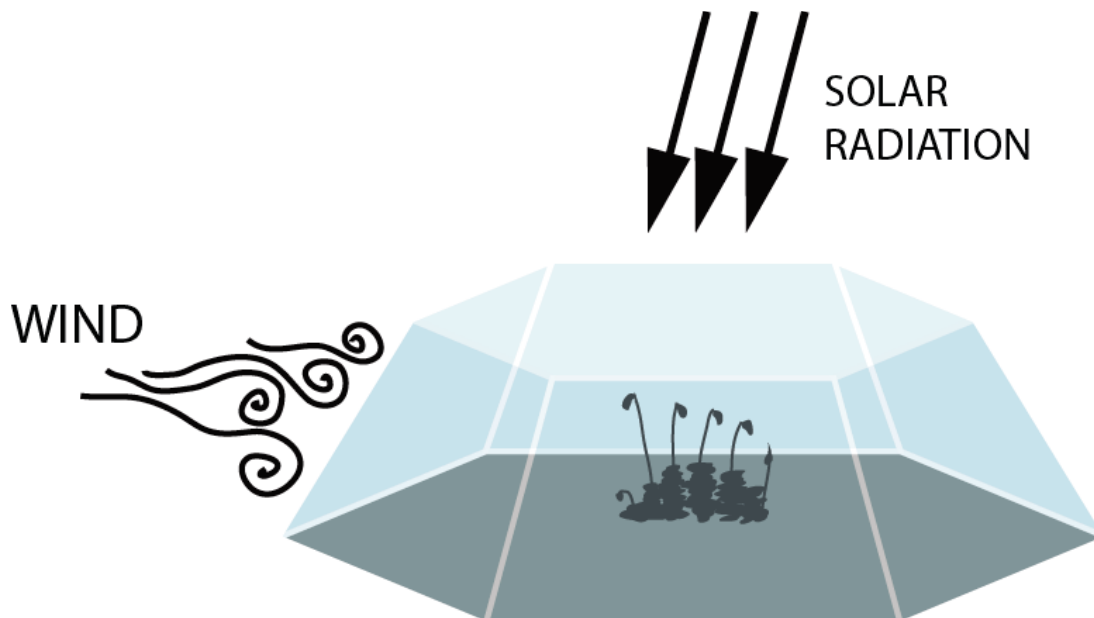
## Methods

### Study area

The study area is at Finse in Ulvik municipality located in Hordaland county. The site is on a calcareous alpine ridge called Sanddalsnuten (60° 36' 59.0" N, 7° 31' 31.6" E). Sanddalsnuten is at an altitude of 1545 meters above sea level with total precipitation from September last year to September this year at 688.1mm (*Annual Weather Averages in Finse*, 2018). Temperature and precipitation information is from the closest climate station which is located approximately 2 kilometers away. Sanddalsnuten, is in Hallingskarvet National Park and it's registered as a nature type described as a "calcareous alpine area" and is a *Dryas* heath. (Miljødirektoratet, 2005; Miljødirektoratet, 2006).

## Study design of the OTC-experiment

OTCs are a widely used and effective form of manipulative experiment (figure 2). The main effects of the chambers are to increase inside air temperature by approximately 1.5°C, the soil temperature with 1°C and reduce the effect of wind. Some side effects may include change in some of the snowmelt patterns, change in soil conditions and possibly change in air humidity (Marion et al., 1997). They can be used in quite inaccessible locations, which makes them a widely used tool for climate effects research. The OTC site in this study is also a part of a larger international research network called ITEX (International Tundra Experiment). The OTCs at Sanddalsnuten have been on location since 2000 (figure 3). They were going on the 18<sup>th</sup> year when the study was conducted. For my study I used 10 plots in OTCs and 10 control plots located close to the OTCs.



*Figure 2: OTC of ITEX (International Tundra Experiment) design. The chambers passively warm the vegetation inside and reduces temperature extremes. Illustration by N. H. Phinney.*



Figure 3: Open-top chambers in the field at the study site Sanddalsnuten, Finse.

### Bryophyte cover estimates

The species I worked on are a group of mosses and one particularly abundant species of liverwort. Some groups of bryophytes are particularly species-rich and challenging to identify. For practical reasons, some of the species were only determined to genus. These genus groups were: *Dicranum*, *Polytrichum*, *Hypnum*, *Dicranella*, *Tortella*, *Racomitrium*, *Bryum* and *Pohlia*.

To estimate species-cover, we used a 60×30cm metal frame divided with wire into 18 10×10 cm squares (figure 4). Each plot was split into two parts, each the size of one frame. The frame was therefore used twice in each plot. I estimated cover individually for the small squares in the field and later calculated the total cover. I measured functional traits on samples taken from the most dominating species in each plot (which together made up at least 80% of the biomass per plot). I then separated out approximately 10 living shoots per sample and proceeded to analyze functional traits.



*Figure 4: The metal frame that was used in the cover estimates*

### Water holding capacity (WHC)

WHC was measured for each species for each plot. I used a method described by Zuijlen where she used a combination of other protocols (Zuijlen, 2018b). For each species per plot, 10 living shoots (including the brown and green part) were separated out. These were put in a Petri dish and submerged in demineralized water for 30 minutes (figure 5). They were then incubated in new Petri dishes with a moistened filter paper for 24 hours. The lid was sealed with parafilm to prevent evaporation. After the incubation, the shoots were blotted dry on tissue paper and water saturated mass was recorded (Sartorius Extend EDS2245 (std.  $\pm 0.1$ mg)). The shoots were then air-dried for at least 24 h and weighed again. To control for variations in air moisture, I made 5 weighed control samples that were made up from approximately 15 shoots of different moss species. These were weighed every time I would weight air-dried samples. After all the air-dried samples were weighed, I oven-dried the weight control samples at 70°C for 24 h and

weighed them again. From this I calculated a conversion factor for air-dried mass to oven-dried mass. WHC expressed in  $\text{g g}^{-1}$  was calculated as:

$$WHC = \frac{(\text{wet mass} - \text{dry mass})}{\text{dry mass}}$$



*Figure 5: In the process of measuring water holding capacity (WHC). Sampled shoots in the process of soaking before 24h incubation and weighing.*

## Trait selection

I selected the traits for this thesis based on what was easy to measure and often found in other studies (e.g. Asplund & Wardle, 2014; Sundqvist et al., 2011; Zuijlen, 2018a). These traits are important for the cycling of N and C (Pérez-Harguindeguy et al., 2013). The traits I chose were C and N concentrations and the ratio between them, water holding capacity (WHC), shoot length, biomass and the ratio between shoot length and biomass.

I also looked at some life history traits which have been shown to change with the environment of the bryophyte eg. (McLetchie & Stark, 2006; Proctor et al., 2007; Sandvik & Heegaard, 2003). I chose the life history traits based on what was available on the Bryoatt (Hill et al., 2007) database, and what is commonly used in other studies (e.g. Sandvik & Heegaard, 2003).

## Photograph analysis

The 10 shoots from the WHC measurements were used in this procedure. The brown part of the shoot was removed with a scalpel before a picture was taken. “The brown part” was consequently defined as the brown part of the longest branch. If this brown part had branches which were green further up, these were also cut away. The green part was placed on a projector and photographed with a Nikon D5500 in combination with a Sigma 105mm f2.8 DG macro HSM lens at maximum jpeg resolution (300 dpi) (figure 6). A millimeter paper for scale and sample ID were placed in each photograph. Shoot area was estimated from the photographs, using the software ImageJ (Rueden et al., 2017).



*Figure 6: One of the pictures used in analyzing shoot length*

## C and N content

The samples were ground to a powder in a ball mill (model MM400, Retsch GmbH & Co, Haan, Germany). Carbon and nitrogen concentration were analyzed from approximately 5 mg sub-samples of the ground powder on a Vario MICRO cube (Elementar Analysensysteme GmbH, Hanau, Germany). Some of my samples were too small, which gave me no measurement. In these cases, I used the average trait value of the species.

## Trait by dominant species analysis

I wanted to investigate whether any of the dominant species played a larger part in any of the measured traits. I chose species that appeared in at least 4 warmed and 4 control plots. The species were *Dicranum spp.*, *Distichium capillaceum*, *Polytrichum spp.* and *Ptilidium ciliare*.

## Life history traits

I used the life history trait database Bryoatt (Hill et al., 2007) to make my dataset. The database is for British and Irish bryophytes with Information on Native Status, Size, Life Form, Life History, Geography and Habitat. Norwegian and British habitats are comparable enough that many of the same species thrive in both regions. I chose to look at the life history traits spore size, growth form and sporophyte frequency. As I only recorded genus for some species, I had to decide on one value for every trait. I did this by using the most common trait in the species that were likely to occur in the region I worked in. I used the species distribution maps from Nationalnyckeln (Hallingbäck et al., 2006; Hallingbäck, 2008) when writing up an approximate species list.

## Statistics

The values of the measured traits were weighted by their relative abundance per plot. From this, a community-weighted mean was calculated by weighting each trait value by its relative abundance (Garnier et al., 2004).

$$trait_{weighted} = \sum_{i=1}^n p_i \times trait_i$$

$p_i$  is the relative cover of species  $i$  as a part of the total cover of all bryophyte species.  $Trait_i$  is the trait value for species  $i$ . It's possible to calculate the fixed mean, the specific mean and the intraspecific variation from this equation (Lepš et al., 2011). The community-fixed mean value is the average sum of a trait value for a single species, weighted by its relative abundance. The specific mean is the sum of the measured trait value per plot per species, weighted by relative abundance. The value for intraspecific species variation can be disentangled from these two values by finding the difference between the specific mean and the fixed mean. This is done by subtracting specific mean value from the fixed mean value. Any measured change in the specific mean value of a trait must be due to species turnover. Any measured change in specific mean trait value can either be due to species turnover or due to intraspecific variation. Intraspecific variation occurs, when fixed and specific trait means differ:

$$Intraspecific\ variation = specific\ mean - fixed\ mean$$

Building on these assumptions, I performed three separate analyses of variance (ANOVAs) on each response variable to evaluate the potential difference between bryophytes in the warmed plots and in the control plots. ANOVA analysis requires the data to be normally distributed, have independent observations and homogeneous variance. These requirements are all met in my data.

The ANOVA analysis on traits was executed using the R function `traitflex.anova`, which is a part of the package “`cati`” from CRAN R project (Taudiere & Violle, 2016). The `traitflex.anova` function contains a script for disentangling the different kinds of community-weighted means as described above. It carries out three parallel one-way ANOVA analysis per trait, teasing apart the three different community responses. The community parameters were the response variable and the treatment along with the effect of “pairs” were the explanatory variables. One control and one warmed plot were designated into pairs based on similar environmental conditions in the plots. This was done to eliminate noise in the data.

The ANOVA analysis method gives a value called sum of squares (SS). The SS is made up of the sum of squared residual differences from the total mean, divided by  $n-1$ . These ANOVA analysis were executed for all traits; WHC, C, N, C:N, shoot length, area, biomass, biomass to shoot length ratio and area to biomass ratio. I also conducted ANOVA analysis for the life history traits, where I used the life history traits as the dependant variables and the treatment



I wanted to further explore which species significantly affected either trait. I performed another set of ANOVA analysis, one for each species, for four of the most common species for all traits. These were namely the species *Dicranum spp.*, *D. capillaceum*, *Polytrichum spp.* and *P.ciliare*. I selected only species that were present in both warmed and control plots.

## Results

### Community weighted means of traits

I found that tissue C concentration and shoot biomass decreased, while shoot length:biomass increased with warming at the whole community level (Table 1). The communities in the warming treatment were dominated by shorter species with lower WHC compared with the control plots, but this effect was not significant when I accounted for differences within species. The negative change in C concentration with warming could not be explained by a change in species composition (Figure 7). There are not more species that generally have a lower C concentration. Instead, the shift in C concentration largely reflect intraspecific variation. Except for C content, the shift in traits caused by warming was almost completely explained by species turnover. Species turnover is represented by fixed trait values which is the mean of all measurements for that individual species. Changes in fixed trait values thereby reflect a change in species composition. Intraspecific variation on the other hand reflects a change within an individual species itself.

*Table 1: ANOVA tests comparing the warming treatment to control. Significant results are bold. P-value is given in parenthesis. All calculations have one degree of freedom.*

	<b>F- and P-value for species turnover only</b>	<b>F-value for species turnover and intraspecific variability</b>	<b>F-value for intraspecific variability alone</b>
<b>WHC</b>	<b>6.63 (0.030)</b>	4.03 (0.076)	0.60 (0.459)
<b>Length/biomass</b>	4.37 (0.066)	<b>6.01 (0.036)</b>	0.41 (0.537)
<b>N</b>	2.54 (0.146)	1.13 (0.315)	0.35 (0.568)
<b>C:N</b>	3.04 (0.115)	0.94 (0.357)	0.23 (0.647)
<b>C</b>	0.21 (0.661)	<b>5.81 (0.039)</b>	<b>8.93 (0.015)</b>
<b>Area/biomass</b>	2.70 (0.135)	3.71 (0.086)	0.23 (0.645)
<b>Length</b>	<b>9.50 (0.013)</b>	2.00 (0.191)	0.05 (0.834)
<b>Biomass</b>	<b>9.67 (0.012)</b>	<b>7.42 (0.023)</b>	0.01 (0.936)

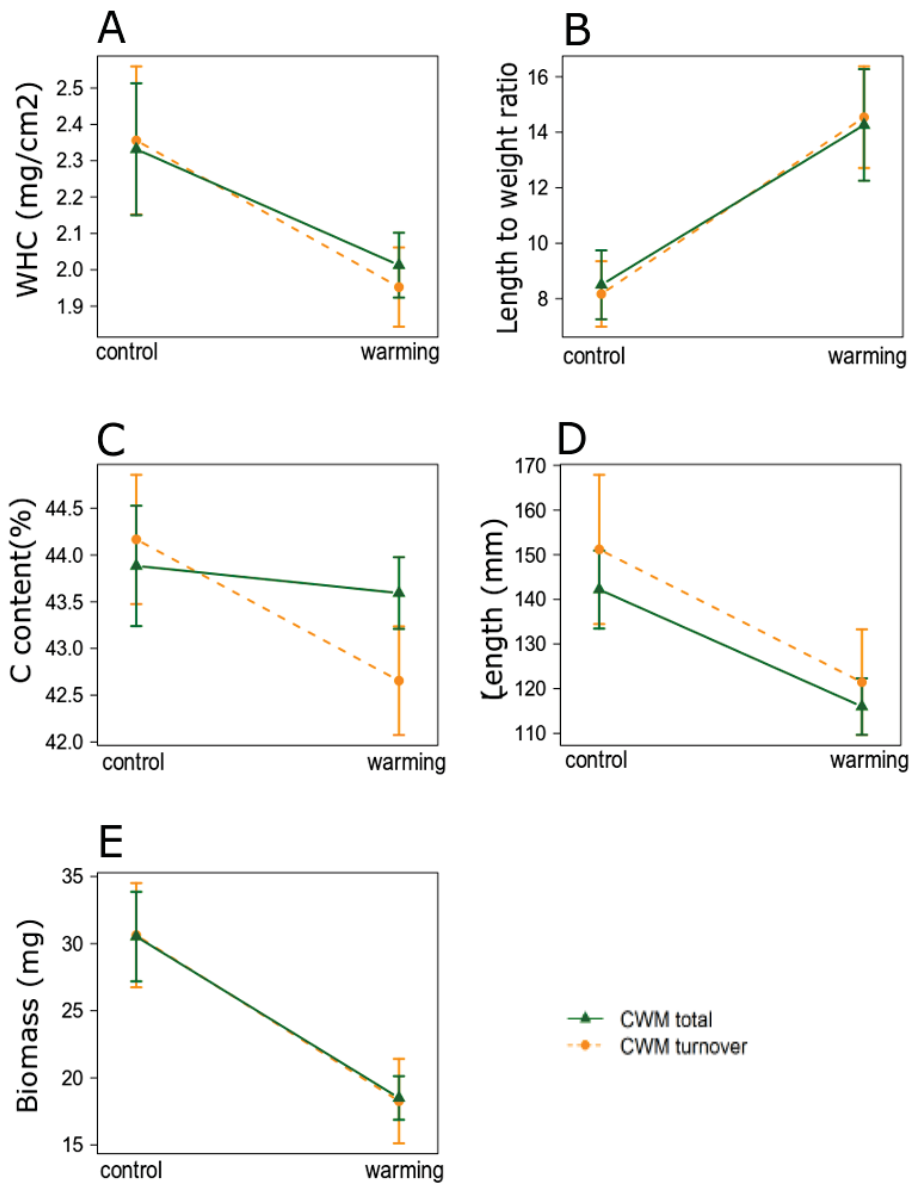


Figure 7: Community weighted mean (CWM) for A: water holding capacity, B: length/biomass ratio, C: C content, D: shoot length and E: biomass. Error bars indicate 95% confidence interval. Where the lines indicating CWM turnover and CWM total diverge, it is an indication of intraspecific variation.

The explained variation in shoot length and biomass, area : biomass ratio, length : biomass ratio and WHC were mostly explained by species turnover (Figure 8). Of these, the effect was significant for WHC, shoot length and biomass. Carbon concentration was largely explained by intraspecific variation. Variation in C:N ratio and N concentration were not significantly explained by species turnover or intraspecific variation. There was always a positive covariation between species turnover and intraspecific variation, as the black bars were always to the right of the grey and white boxes.

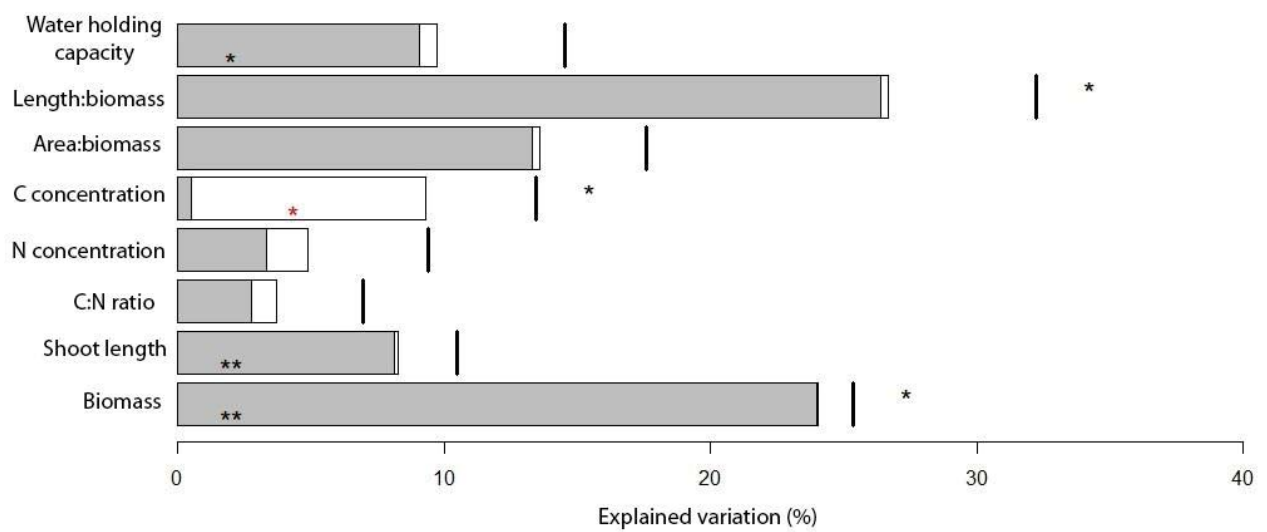


Figure 8: Grey indicates species turnover, white indicated intraspecific variation and the black bars indicate total variation. Asterix indicate significance, red asterisk indicate significance in intraspecific variation, black asterisk indicates species turnover.

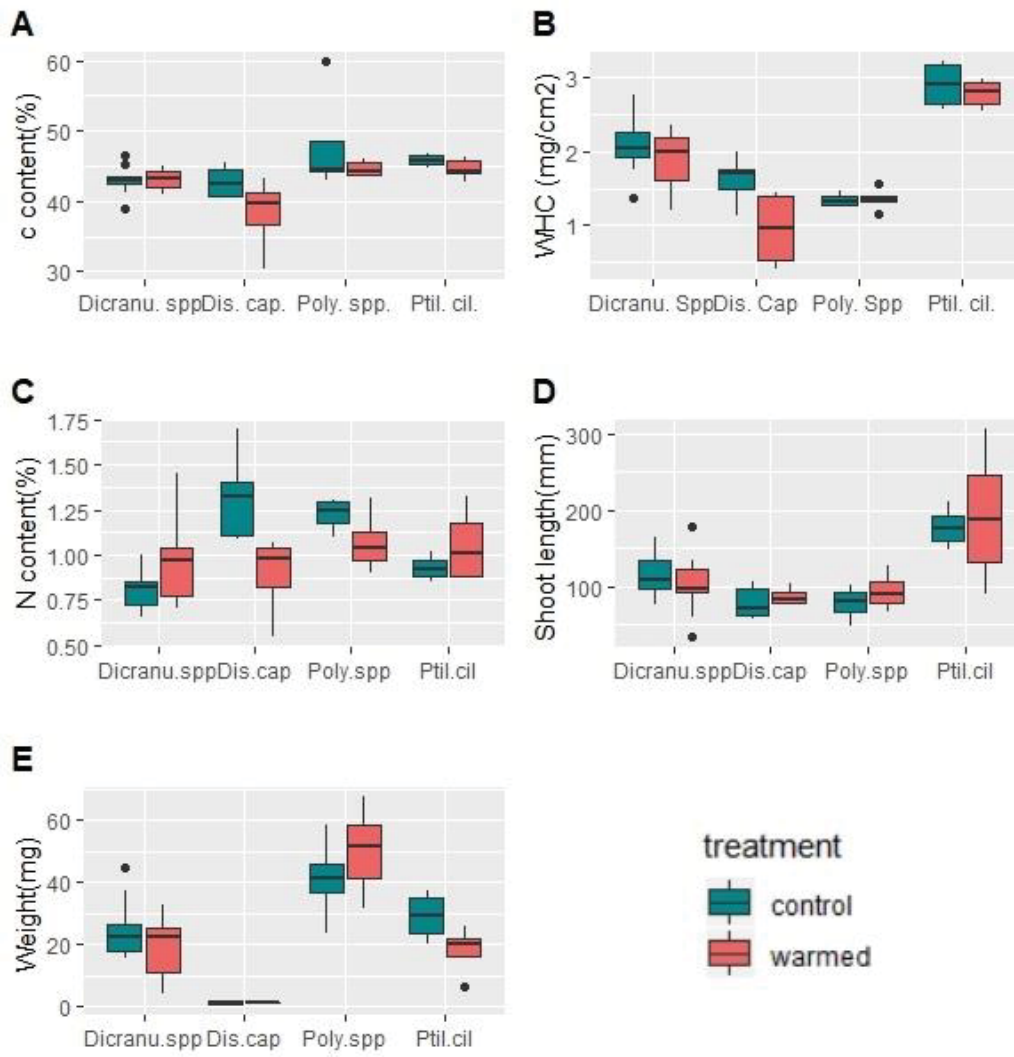


Figure 9: Boxplots for A) C concentration, B) water holding capacity, C) N concentration, D) shoot length and E) shoot biomass of individual bryophyte species in control(blue) and warmed plots(red).

Table 2: ANOVA analysis comparing the trait-responses of four common species to the warming treatment. Values are F-values with P-values in parenthesis. Significant results are bold. Borderline (below 0.1) results are indicated by a full-stop.

	<i>Dicranum</i> spp.	<i>D. capillaceum</i>	<i>Polytrichum</i> spp.	<i>P. ciliare</i>
<b>C concentration</b>	0.0 (0.970)	2.9 (0.132)	0.9 (0.373)	2.5 (0.149)
<b>N concentration</b>	4.0 (0.060) .	<b>7.0 (0.033)</b>	2.9 (0.133)	1.1 (0.333)
<b>Shoot length</b>	0.7 (0.400)	0.4 (0.541)	1.0 (0.359)	0.1 (0.770)
<b>Shoot biomass</b>	1.9 (0.185)	0.1 (0.772)	0.9 (0.375)	3.6 (0.105)
<b>WHC</b>	1.4 (0.254)	5.2 (0.056) .	0.0 (0.884)	0.3 (579)

### Trait by species analysis

*D. capillaceum* had a 33% lower N concentration in warmed plots (figure 9). The rest of the species were non-significantly different. However, two species were borderline significant. *D. capillaceum* almost had a 41% lower WHC in warmed plots, and *Dicranum* spp. almost had a 21% higher N concentration in warmed plots (Table 2).

### Life history trait analysis

None of the life history traits I looked at had been significantly changed by the warming treatment. Weft growing mosses were found slightly more often in the warmed chambers. Sporophyte presence was almost significant with an increase in sporophytes with the warming treatment, when excluding the effect of plot pair in the ANOVA model.

Table 3: Results from ANOVA analysis with one degree of freedom(df) of the effect of warming with the effect of pairs as error on life history traits. Borderline value (p-value between 0.05 and 0.1) indicated with a full-stop.

Trait	F-value	P-value
<b>Turf</b>	0.17	0.689
<b>Tuft</b>	0.84	0.384
<b>Weft</b>	3.89	0.080 .
<b>Cushion</b>	1.00	0.341
<b>Mat rough</b>	0.08	0.784
<b>Mat smooth</b>	2.12	0.180
<b>Minimum spore size</b>	1.91	0.199
<b>Maximum spore size</b>	2.19	0.173
<b>Sporophyte presence</b>	2.34	0.161

## Discussion

I found shorter and lighter bryophytes with a lower WHC and C content in warmed plots, giving support for my first hypothesis that there is a shift in bryophyte traits towards those associated with higher competition with vascular plants in the warmed plots. The OTCs are in some ways simulating lowland conditions by being warmer, more sheltered and containing more plants characteristic of lowland flora. Community-level WHC of bryophytes has been shown to drop with increasing elevation, which would give the expectation of seeing higher WHC inside the warmed plots (Roos et al., *In review*). This is not in line with my findings, suggesting interference from competition with vascular plants. Intraspecific variation accounted for almost all the explained variation in C concentration between warmed and control plots. Stunted growth, dry, low-light conditions may have caused lower photosynthetic rates and lower C concentration. The explained variation in the other traits were almost entirely accounted for by species turnover. This gives support for my second hypothesis that interspecific variability will account for most of the explained variation between plots. These results are in line with some recent studies on the relative importance of interspecific variation and intraspecific variation in vascular plants (Kazakou et al., 2014; Kichenin et al., 2013; Lepš et al., 2011; Siefert et al., 2015). I discovered that the growth form of the bryophytes exposed to the warming treatment is more often weft growth form. I also found a trend towards more frequent sporophyte production in the warmed plots, giving partial support for my

hypothesis that that life-history traits would shift towards those associated with lowland growth forms and more effective reproduction (Casanova-Katny et al., 2016; Mägdefrau, 1982). I will further discuss my findings and some broader implications.

## The significance of intraspecific variation

I found the explained variation between warmed and control plots to be mostly a consequence of species turnover, not intraspecific variation. The explained variation in N concentration was partially explained by intraspecific variation. However, only species turnover came out as significant for N concentration. Vascular plants and lichens display higher intraspecific variation in N concentration than what I found in this thesis (Asplund & Wardle, 2014; Siefert et al., 2015). This was unexpected, as bryophytes, unlike vascular plants, are mostly dependent on their local environment for nutrient availability (Chapin et al., 1990; Siefert et al., 2015). Carbon concentration was the only trait largely explained by intraspecific variation. Ferns show the opposite trend in an elevational gradient (Wegner et al., 2003), which may indicate stunted growth as a consequence of increased competition with vascular plants.

## Shifts in functional traits with warming

I found a decreased shoot length and a lower biomass in the warmed plots. This is in line with my hypothesis that I expected to find traits that are associated with adaption to a higher competition environment. I think these traits are associated with higher competition, because the already small-statured, low biomass alpine version of these bryophyte species become even shorter and less massive with the warming treatment. Decreased shoot length and lower biomass as a result of warming are patterns sometimes seen in similar studies to mine (e.g. Jägerbrand et al., 2003). Vascular plants also become shorter with increasing elevation, possibly in response to increasing stress with increasing elevation (Körner, 2003; Sundqvist et al., 2013). The stress from increasing elevation may come from an increase in radiation, rougher weather conditions and colder temperatures.

In the warmed plots I found a shift towards weft-growing bryophytes driven by species turnover. Examples of species with this growth form are *P. schreberi*, *H. splendens* and *T. tamariscinum* (the latter not found in my plots) (figure 10). The warmed plots had taller vegetation and more litter, and by proxy also more shadow (Sundsbo, 2019). Weft-growing bryophytes are often more shadow-tolerant and they are therefore more associated with the lowland and more shadowy habitats (Mägdefrau, 1982). This is

consistent with how lowland vegetation is creeping upwards as temperature rises (Elmendorf et al., 2012a; Elmendorf et al., 2012b). With weft-growing bryophytes being better adapted to shadowy habitats, their increase may be due to an increase in shadow from the taller vegetation and the increase in litter. Thus, they seem to out-compete the more light-dependant bryophytes.

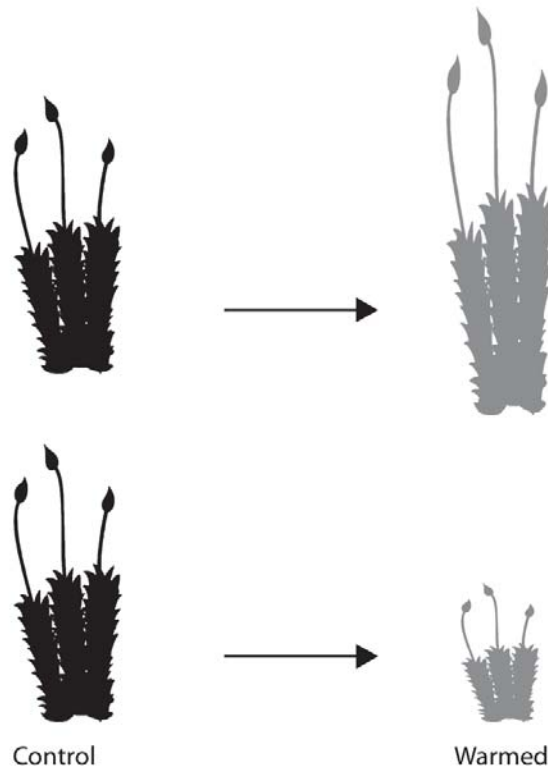


*Figure 10: Thuidium tamariscinum as an example of a weft-growing moss.*

I found a significantly lower C concentration in the bryophytes exposed to the warming treatment. With warming, vegetation becomes taller, the shrub canopy denser and their litter increases (Sundsbo, 2019; Walker, 2000; Walker et al., 2005). It is possible that the taller vascular plants compete more efficiently for sunlight and moisture compared to bryophytes. This would explain the lower carbon concentration as a symptom of lower photosynthetic rates. This is in line with my hypothesis that the warmed bryophytes move towards traits associated with adaption to higher competition. I assume this because the bryophytes in the control plots are exposed to lower stress levels than in the drier, high-competition OTC plots



(Elmendorf et al., 2012b; Sundsbø, 2019). I see two possible explanations for the drop in C concentration; it could be due to a higher growth rate and unchanged or lower C fixation rate, subsequently diluting the C molecules in the shoots. This would mean tall/regular shoot length with low C concentration compared to control plots. The other explanation could be retarded growth rate and a lower C fixation rate. This would mean shorter, lighter shoots with lower C concentration. The last explanation for low C concentration fits my findings that shoots become shorter, lighter and have a lower C concentration (figure 11). I assume the abiotic factors in the OTCs to favor bryophyte growth, especially with increasing moisture. I make this assumption, because many of my species have a higher temperature optimum than control plots and would benefit from temperature increase (Proctor, 1982). When looking at the whole picture including competition from vascular plants, I found that growth becomes stunted, probably because of increased competition with vascular plants (Lang et al., 2012). Ferns show a drop in C concentration with increasing elevation (Wegner et al., 2003). Bryophytes and ferns show the opposite trend, which may be in support of my hypothesis that bryophytes are stunted by an increase in competition with vascular plants. Lower carbon gain in *S. uncinata* (a species also present in my research plots) was found in an experiment measuring how photosynthesis was affected by increased temperature (Nakatsubo, 2002). This also lends supports to my hypothesis.



*Figure 11: Illustration of two possible explanations for low C concentration in bryophyte shoots after warming treatment. Top: Bryophyte stretches for light, producing tall shoots but diluting the C concentration. Bottom: Bryophyte experiences growth restrictions and produces short, light shoots with low C concentration. The latter fits my data better. Black indicates high C concentration.*

I found WHC to be lower in the bryophytes in the warmed plots. That could either be a consequence of stress or it could be a result of adaption. Depending on whether it is an adaption or a maldevelopment, it may or may not be in line with my hypothesis. The opposite response pattern was found in a water economy experiment looking at bryophyte traits associated with water conservation (Henriques et al., 2017). The traits associated with water conservation decreased with increasing elevation. They also found precipitation to increase with increasing elevation, as is analogous to my warmed plots being drier than the control plots. Lower evapotranspiration due to low temperature with increasing elevation is likely the mechanism behind the decrease in WHC with increasing elevation. Their results contrast my findings that WHC drops with the warming treatment, while moisture availability apparently follows the same pattern. I think that the bryophytes in my study experienced stressful conditions and were not able to develop

properly, thus malfunctioning in holding water per individual shoot. Some studies also concluded along the lines of moisture being important to community composition and the direction of trait change in bryophytes (Furness & Grime, 1982; Hudson & Henry, 2010; Sandvik & Heegaard, 2003). In the following study, wet sites where the water loving genus *Sphagnum* was present, bryophytes increased in cover with a warming treatment (Lang et al., 2012). This may indicate at least a partial dependence on moisture availability and may be explained further by species specific ecology. The reason for bryophytes being strongly affected by the presence of water may be due to their poikilohydric nature where unlike vascular plants, they are able to desiccate completely (Tuba et al., 2011).

An experiment looking at water conservation in mixed and single species bryophyte cushions found that mixed species cushions dried out slower with a non-additive effect (Michel et al., 2012). The species in the cushion were even able work together and adapt to form more coherent and denser cushions to conserve water more efficiently than single shoots. In my plots, species richness went up with the warming treatment when taking moisture into account (Sundsbo, 2019). Even though there are more species in the warmed plots, they may not be able to form healthy well-developed cushions in the warmed plots as they do in the control plots (personal observation). I suspect bryophyte water availability is heavily dependent on the micro-climate of its cushion, the water holding capacity of individual shoots, local soil moisture, cover of other bryophyte species and precipitation. This may obstruct their ability to hold water on a community scale. Cushions are important for water economy in lichens (N. H. Phinney 2019, personal communication, 19<sup>th</sup> of April) and they are probably very important for bryophytes too. I did not test WHC on a cushion level, but future researchers may want to look closer at intraspecific variation in water economics in cushion-forming bryophytes, as opposed to only in isolated shoots.

I did not find significant support for my hypothesis of altered reproductive patterns in bryophytes with the warming treatment. However, when I excluded the effect of plot pairs in the ANOVA analysis, sporophyte presence was borderline significantly affected by the warming treatment. Species with a higher frequency of sporophyte presence were found more often in the warmed plots, when ignoring the effect of plot pairs. In a study looking at within-species variation in sporophyte presence, they found that species produced more frequent and larger sporophytes than the control (Casanova-Katny et al., 2016). They concluded that the altered patterns of reproduction were caused by environmental restriction rather than it being an adaptation. I did not investigate the possible within-species variation of sporophyte presence, but it would have been interesting to look at. In bryophytes, sporophytes are more sensitive to drought than the gametophyte (Proctor et al., 2007). Either because the sporophyte has an inherently lower heat tolerance

or because stress in the gametophyte affects sporophyte vitality. (McLetchie & Stark, 2006) All the sporophytes may die if exposed to enough drought cycles while the gametophytes persist. Sporophyte presence depends on among other factors, how often drought cycles occur. The warmed plots were somewhat drier and warmer, but it seems they were not dry and warm enough to discourage the presence of species that usually have higher sporophyte production. However, if the trend that Casanova-Katny (2016) found is also true for my plots, it means that warmed plots will have more sporophytes than control plots for two reasons. Intraspecific variation causes a shift towards larger and more frequent sporophytes, and there is a species-turnover towards species that on average produce sporophytes. Altered reproductive patterns in bryophytes may have large consequences on a large scale, effecting both genetics and dispersal patterns (Casanova-Katny et al., 2016).

## Conclusion

My findings in this thesis underline that the contribution of intraspecific contra species turnover to community-level changes differs greatly from that vascular plants and lichens. Most of the research in functional traits on primary producers has revolved around vascular plants, while other ecologically essential primary producers like bryophytes have been left out, despite producing different responses to the same environmental stimuli. Bryophytes are one of the largest primary producers in high elevation, high latitude environments, and in these narrow niches they are some of the first to respond to consequences of global warming like temperature increase and increased competition with vascular plants and their litter (Jägerbrand et al., 2003; Lang et al., 2012). When predicting how future environmental changes will affect ecosystem processes, traits of important primary producers like bryophytes and their within-species variation must be taken into account where they are abundant.

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## Appendix

Table 4: List of all species present in the experiment. “Control” and “warmed” columns indicate the mean cover percentage of the listed species in its respective plot and standard error(SE).

Scientific name	Control (%)	Warmed (%)
<i>Dicranum spp.</i>	7.110±0.954	1.890±0.411
<i>Hylocomium splendens</i>	3.402±2.131	0.100±0.059
<i>Racomitrium spp.</i>	2.118±1.022	0.110±0.045
<i>Ptilidium ciliare</i>	1.204±0.255	0.262±0.063
<i>Polytrichum spp.</i>	0.926±0.166	0.251±0.052
<i>Distichium capillaceum</i>	0.631±0.163	0.457±0.161
<i>Rhytidium rugosum</i>	0.6±0.236	0.024±0.008
<i>Sanionia uncinata</i>	0.589±0.316	0.093±0.030
<i>Brachythecium albicans</i>	0.440±0.149	0.063±0.012
<i>Hypnum spp.</i>	0.432±0.106	0.446±0.160
<i>Isopterygiopsis pulchella</i>	0.407±0.204	0.162±0.045
<i>Bryum spp.</i>	0.197±0.058	0.214±0.059
<i>Pohlia spp.</i>	0.130±0.028	0.251±0.086
<i>Syntricia spp.</i>	0.050±0.028	0.004±0.002
<i>Myurella sp.</i>	0.047±0.023	0.019±0.001
<i>Ditrichum flexicaule</i>	0.035±0.014	0.031±0.019
<i>Dicranella spp.</i>	0.029±0.020	0.060±0.035
<i>Tortella tortuosa</i>	0.007±0.003	0.097±0.039
<i>Fissidens sp.</i>	0.001±0.001	0.003±0.001
<i>Meesia uliginosa</i>	0.001±0.001	0.003±0.001
<i>Blindia acuta</i>	-	0.007±0.003
<i>Campyliadelphus chrysophyllus</i>	-	0.0403±0.02
<i>Grimmia sp.</i>	-	0.003±0.002
<i>Saelania glaucescens</i>	-	0.001±0.001



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