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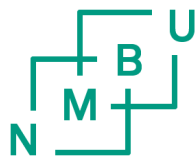
Vascular plant and lichen functional trait responses to warming in an alpine ecosystem

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Master of Science in Ecology

Preface

This master thesis is the final product of my MSc in Ecology at the Norwegian University of Life Sciences (NMBU). This has been a memorable year with new experiences, knowledge and acquaintances. A big highlight was visiting Finse for the first time, with fieldwork in beautiful surroundings at Sanddalsnuten. That said, I wish to thank my great supervisors at the FuncFinse project for the opportunity to do this thesis. In particular, a big thank you to my main supervisor Johan Asplund for all the valuable guidance and feedback throughout the entire process. Further, I wish to thank my co-supervisors Kristel van Zuijlen and Kari Klanderud for all help with planning this thesis and for advice and feedback along the way. Also, thanks to Ruben Erik Roos for his guidance at Finse this summer and during the lab work, and to the hosts at Finse Research Center for great accommodation during the fieldwork. Finally, a special thanks to my fellow MSc partner in crime, Åshild Hasvik for good teamwork in field and valuable conversations throughout this year.



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Abstract

Functional traits are recognized as potential predictors of plant community responses to climate change. In stressful alpine environments, temperature is a limiting factor and may select for resource conservative individuals. Increasing temperature may, therefore, cause a shift in alpine plant community-level traits towards levels associated with higher resource acquisition. This study addresses the functional trait responses of both vascular plants and lichens in an alpine community to climate change and attempts to assess the relative importance of species turnover vs. intraspecific variation in explaining the total community-level trait variation. Several recent studies have dealt with these responses in vascular plant communities but less is known of the community-level trait responses of lichens to climate change, despite their definite ecological importance in alpine ecosystems.

I conducted an open top chamber (OTC) experiment at 1500 m elevation at Finse, Western Norway. Along with coverage data for all species in all plots of both treatments (control and OTC), several functional traits of both vascular plants and lichens were measured. From this, community-weighted mean trait values were calculated and further used to study the responses at the whole community level to the increased warming in the OTC treatment.

Only vascular plant traits responded at the community level, for which specific leaf area (SLA) and nitrogen content (N) decreased and carbon to nitrogen ratio (C:N) increased with warming. In contrast with my expectations, these results indicate a shift in vascular plant traits towards levels associated with higher resource conservation. Lichen functional traits did not respond to warming at the whole community level. I, however, found variation between treatments in several traits in two of the lichen species, although with contrasting responses, implying intraspecific variation in the lichen community. By decomposing the total community-weighted trait variation, I showed that intraspecific variation was the single significant contributor to the changes observed for all three community-weighted traits that responded to the increased temperature in the OTCs. These results highlight the importance of taking intraspecific trait variation into account in order to reveal the community-level responses of vascular plants and lichens to climate change.

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1. Introduction

Environmental changes in temperatures are affecting ecosystems, communities and species in all parts of the world and are leading to severe consequences for biodiversity and ecosystem processes (McCarty 2001; Chapin 2003; Parmesan & Yohe 2003; Walther 2003). Alpine areas are expected to be particularly sensitive to these changes in climate, as they represent edges of biotic distribution where ecosystems are limited by low temperatures and extreme weather favoring species with specialized adaptations (Grabherr 1994; Callaghan & Jonasson 1995; Körner 2003; Normand et al. 2009). It is well acknowledged that individuals can adapt to changes in their surrounding environments, and how plants respond to environmental change is reflected in both their phenotypic plasticity and heritable genetics (MacArthur 1972; Bradshaw & Holzapfel 2006; Valladares et al. 2007; Williams et al. 2008). Recent studies substantiate that such adaptations alone may be inadequate in explaining the potential long-term effects of a changing climate for alpine plant communities. It is shown that changes in the environmental properties in alpine areas may make it possible for novel species to shift ranges upwards and create new interspecific competitive relationships between native specialists and novel species (Klanderud & Birks 2003; Walther 2003; Lenoir & Svenning 2013; Grytnes et al. 2014; Alexander et al. 2015).

Functional traits are defined by Violle et al. (2007) as any trait, i.e. morphological, physiological or phenological properties measurable at the individual level, which indirectly impacts the fitness. Studies show that plant functional traits can vary consistently along climatic gradients and can thus potentially be used to predict plant community responses to climate change (Fortunel et al. 2009; Sundqvist et al. 2011; Guittar et al. 2016). The principle of using a trait-based approach is that the environmental conditions act as filters by constraining which individuals are able to persist in the community depending on their functional traits. Further, this approach can be used to predict the effects of climate change in a plant community by identifying which traits are emphasized under different types of environmental conditions (Keddy 1992b; Keddy 1992a). It is well established that the stressful alpine environments require species with traits associated with higher resource conservation, e.g. low nitrogen content, specific leaf/thallus area (SLA/STA) and water holding capacity (WHC), and high carbon to nitrogen ratio (C:N) and leaf dry matter content (LDMC) (Sundqvist et al. 2013). As temperature plays an important part in deciding the nutrient availability and decomposition rates in ecosystems, changes in temperature will likely be depicted in the chemical concentrations of plant tissue. Morphological traits can also indicate changes in temperature as they can describe

resource availability by depicting the trade-offs in the functional strategy of the plants (Chapin 2003; Sundqvist et al. 2013). Increased temperatures can therefore potentially cause a shift from resource conservative communities to communities with higher resource acquisition.

Recently, many studies have focused on examining the variation in functional traits at the community level (Sundqvist et al. 2013; Siefert et al. 2015; Mayor et al. 2017). Following the “biomass ratio hypothesis”, the individual level trait values should be weighted by each species’ contribution to the community, and this community-weighted trait value can be affected by both species turnover (across-species trait variation) and intraspecific trait variation (within-species trait variation) (Grime 1998; Garnier et al. 2004). The relative importance of species turnover and intraspecific variation in explaining the total community trait variation is the subject of many recent studies, and with increasing recognition for intraspecific variation as an important contributor. However, most studies still support species turnover to be the main driver of variation (Albert et al. 2010; Lepš et al. 2011; Kichenin et al. 2013; Kazakou et al. 2014; Siefert et al. 2015). Kichenin et al. (2013) showed that the relative contribution of species turnover and intraspecific variation in explaining total community variation can differ substantially among different traits. Further, it has been shown that the relative extent of intraspecific variation is greater for chemical traits than for morphological traits, implying that chemical traits are more labile than morphological traits within species (Kazakou et al. 2014; Siefert et al. 2015).

While this trait-based approach at the community level is well acknowledged for studies of vascular plants, this is not the case for non-vascular primary producers e.g. lichens and bryophytes (St Martin & Mallik 2017). This is despite their definite ecological importance, especially in alpine ecosystems where they contribute strongly to primary production and nutrient cycling and where the vascular plant cover is less dominant (Matveyeva & Chernov 2000; Cornelissen et al. 2007; Asplund & Wardle 2017). However, in their study of epiphytic lichens’ responses to changes in nutrient availability during ecosystem retrogression, Asplund and Wardle (2014) found that intraspecific variation contributed significantly more than species turnover to the total community trait variation. This is also substantiated by Gauslaa and Coxson (2011), who found high intraspecific variation in STA and WHC when addressing variation in water storage abilities in epiphytic lichens from xeric and mesic habitats. The functional trait responses of vascular plant and lichen communities to increased temperature and the relative importance of species turnover and intraspecific variation in driving variation at the community level for vascular plants and lichens simultaneously will be central issues in this paper. A recent study has addressed these questions using elevational gradients (van Zuijlen et al. 2018).

The aim of this study was to investigate the functional trait responses of an alpine community to increased temperature, and more specifically to identify the potential sources of variation in functional traits in an alpine community under increased temperature. The study was conducted using open top chambers (OTCs) allowing for precise manipulation of temperature, and further close observations of the community responses to the applied changes (Marion et al. 1997; Hudson et al. 2011). Functional traits were measured in both vascular plants and lichens, using morphological and chemical traits that are comparable between both functional groups. I sought to test the following two hypotheses: (i) functional traits in vascular plants and lichens will shift from levels characterizing conservation of resources to levels associated with higher resource acquisition. This implies e.g. higher nutrient concentrations and higher SLA/STA. This shift will be detected both at the whole community level and within individual species. Further, it is expected that (ii) variation in community-weighted traits in vascular plants is mainly due to species turnover, while variation in community-weighted traits in lichens is mainly due to intraspecific variation. Also, the relative extent of intraspecific variation is expected to be greater for the chemical traits than for the morphological traits. Knowledge of functional traits is important as these traits play a central role in driving how vascular plants and lichens impact ecosystem processes, including rates of production and decomposition, and hence the functioning of communities (Chapin 2003; Díaz et al. 2013).

2. Materials and methods

2.1. STUDY AREA

The study site is located at approximately 1500 m elevation in the southwest slope of the mountain Sanddalsnuten (60°36'N, 7°31'E), Finse, Western Norway. Climatic conditions at Finse are influenced by the relative proximity to the ocean at the west coast of Norway, contributing to mild winters and cool summers compared to equivalent alpine areas (Finse Alpine Research Center 2010). In 2017, the average summer temperatures (June to August) were approximately 6.3°C, while the average monthly summer precipitation was 97.8 mm (Yr 2018). The study site is situated on a heathland dominated by *Dryas octopetala*, and calcareous bedrock in the area provides conditions for a diversity of vascular plants and lichens (NGU).

2.2. DATA COLLECTION

Open top chambers (OTCs) were used to simulate environmental change by increasing the temperature in experimental plots. Open top chambers are on-ground passive systems, in this case made of polycarbonate, for increasing temperature *in situ* and can be used for simulating climate warming, as described by Marion et al. (1997). The open top minimizes secondary effects by allowing exchange of water, CO₂, light and for access of pollinators and herbivores (Molau & Mølgaard 1996). Several studies with OTCs have been conducted in this area and the experimental plots used in this study were established in 2000 (Klanderud & Totland 2005b). The effect on temperature in the summer is typically an increase of 1-3°C (Marion et al. 1997; Elmendorf et al. 2011), and Olsen and Klanderud (2014) found that the air temperature in the OTCs used in this study increased by 1.5°C and below ground (approx. 5 cm) temperature increased with 1°C.

A total of 20 plots were used for data collection, of which 10 ambient control plots and 10 experimental plots with OTCs. All plots with the measurements of 60 x 60 cm. To avoid edge effects, the OTCs had 1 m diameter. Ten OTCs were randomly selected in advance, and the selected control plots were the ones established closest to the selected OTCs. One of the plots had close to no representation of lichen and was therefore replaced with another random plot to ensure sufficient representation of both functional groups. Species composition was registered and the species coverage was estimated for lichen (Åshild Hasvik unpubl.). Each plot was divided into 10 x 10 cm squares to simplify the species recognition and estimating the

coverage. For vascular plants, this work was conducted for each plot using the same methodology in August 2016 (Siri Lie Olsen unpubl. data).

Samples of vascular plants were collected in all plots, following the protocol of Cornelissen et al. (2003). Preferably two leaves from 10 individual plants in each plot were collected, but more leaves per individual plant or per plot if a species was not sufficiently abundant. Within each plot, fully expanded, healthy, adult leaves from the most abundant species were collected, i.e. species with cumulated coverage of at least 80 % of the total vascular plant coverage in the plot. Collected samples of leaves were initially kept in plastic bags to stay fresh but stored in paper bags after measuring fresh weight and scanning. All lichen species were sampled, and the number of thalli sampled varied with the abundance in each plot. Several thalli from each species and from different parts of the plot were preferred. In some plots, the number of thalli and amount of mass of certain species were too small to be representative in the morphological trait analysis and not enough for the chemical trait analysis and were not included in the data material. Lichen thalli were collected and stored in paper bags.

2.3. TRAIT MEASUREMENTS

2.3.1. MORPHOLOGICAL TRAIT ANALYSIS

Vascular plant leaves were weighed to the nearest 0.1 mg using a digital weighing scale, model Sartorius Extend ED224S (Sartorius AG, Germany), and scanned in fresh condition at the field station within 24 hours after collection, according to Cornelissen et al. (2003). Images of fresh leaves were retrieved using a color image document scanner, model Canon CanoScan LiDE 220 with jpeg resolution at 600 dpi. All scans included a measuring tape of known scale. Samples were processed consecutively and, in the meantime, stored in a refrigerator at 4°C. The stem of the vascular plants was cut at the basis of the leaf before weighing and scanning. Lichen thalli were repeatedly sprayed with distilled water to fully hydrate, and excess water was removed by careful shaking and wiping with paper, then photographed. Each lichen sample was photographed on top of a light table and with additional light from two sides using a Nikon D5500 with a Sigma 105mm F2.8 EX DG HSM Macro lens at 300 dpi jpeg resolution. A glass pane was added to level the thalli surface. The camera was mounted at a fixed distance during the photographing of all samples, and a measuring tape of known scale was included in all images. Leaf and thallus area was determined by analyzing the images from scans and photographs and accounting for the scale, using the software ImageJ (Schneider et al. 2012). The area was calculated by adjusting the threshold value to cover the plant or lichen mass as precisely as possible. Any shadows in the images affecting the area were excluded from the

threshold range by refining the leaf or thallus area with white lines. Finally, thalli were weighed using the same method as for vascular plants. As described by Cornelissen et al. (2003), both vascular plant leaves and lichen thalli were oven-dried for 72 hours at 60°C and kept dry in a desiccator with silica gel until weighed for dry mass (same method as for fresh/wet weight).

For vascular plants, the data on fresh and dry weight and area were used to calculate specific leaf area (SLA) and leaf dry matter content (LDMC). For the lichens, the equivalent thallus functional traits were specific thallus area (STA) and water holding capacity (WHC). Specific leaf area and STA ($\text{mm}^2\text{mg}^{-1}$) were calculated by dividing the area of one side of a fresh leaf or wet thallus by the weight of its oven-dry mass. Leaf dry matter content (mg g^{-1}) is depicting the tissue density of the leaf and was calculated by dividing the oven-dry mass of the leaf by its fresh mass (Cornelissen et al. 2003). Since lichen has no active water uptake, their ability to hold water, their WHC, is an important trait for measuring their metabolic activity. Water holding capacity (mg cm^{-2}) was calculated by dividing their water content (wet mass subtracted by dry mass) with the thallus area, as described by Gauslaa and Coxson (2011).

2.3.2. CHEMICAL TRAIT ANALYSIS

The tissue samples of both vascular plants and lichens were analyzed for carbon and nitrogen content. This analysis resulted in the traits carbon content (C), nitrogen content (N) and carbon to nitrogen ratio (C:N). Oven-dried tissue from all species sampled in all plots was ground in a ball mill and approximately 5 mg powder from each sample was packed in thin foil as preparation for the chemical analysis. Carbon and nitrogen content were quantified by combustion analysis using the CHN analyzer Vario MICRO cube (Elementar Company, Germany).

2.4. STATISTICAL ANALYSIS

Trait values of the collected species were weighted according to the species' relative abundance in each plot. From the weighted mean trait values, a community-weighted mean trait value for each plot was calculated as described by Garnier et al. (2004) and Fortunel et al. (2009):

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

Where p_i is the cover of species i as a proportion of the total cover of vascular plant or lichen species registered in the plot. The trait value of the species is given as $trait_i$. As described by Lepš et al. (2011), three community parameters can be calculated from this equation: (1) The community-weighted *specific mean* is the sum of the trait values recorded in each plot for each species in a community, weighted according to their relative abundance. (2) The community-weighted *fixed mean* is the sum of the averaged trait values of each species in a community, weighted according to their relative abundance. (3) *Intraspecific variation* is the difference between the specific and fixed mean (= specific mean - fixed mean). Differences in the *fixed mean* between treatments imply that the trait variation is the result of a change in species composition (species turnover), while differences in the *specific mean* between treatments can be caused by both species turnover and/or intraspecific variation. *Intraspecific variation* is established if there is a difference between specific and fixed mean trait values.

Following these principles, the relative contribution of respectively species turnover and intraspecific variation (and their covariation) in explaining changes in the specific community-weighted traits between treatments (control and OTC) was assessed using analysis of variance (ANOVA). According to Lepš et al. (2011), we can assume that the community mean trait data is normally distributed and combined with independence of observations and homogeneity of variances, the criteria for using a parametric approach are met. Three parallel one-way ANOVAs were conducted per trait, one for each of the community parameters acting as the response variables and with treatment (control and OTC) acting as the explanatory variable. The method is based on sum of squares (SS) decomposition, where the relative contribution of each of the three community parameters corresponds to the total SS found in their respective ANOVAs. The specific means depicts the total variation and comprises the variation explained by species turnover, intraspecific variation and their covariation, e.g. $SS_{specific} = SS_{fixed} + SS_{intraspecific} + SS_{covariation}$. Covariation is found by subtracting SS_{fixed} and $SS_{intraspecific}$ from $SS_{specific}$. The SS in each ANOVA is further decomposed into the amount of variation explained

by treatment and variation that is not explained by treatment (residual values). This process was conducted for all traits: SLA, LDMC, C, N and C:N for vascular plants and STA, WHC, C, N and C:N for lichens. The methodology was carried out using the function `traitflex.anova`, which is a part of package “`cati`” from CRAN R project (Taudiere & Violle 2016). This function provides a script for decomposing the variation of the community-weighted trait values and running the parallel ANOVAs as described above.

Considering the results from the community-level ANOVAs, the intraspecific variation was further explored at the species level. T-tests were conducted separately for all species represented in a minimum of five plots of each treatment (5 controls + 5 OTCs). The assumptions of normality and homogeneity of variances were checked and each trait was tested separately for differences between treatments (control and OTC). Wilcoxon signed rank test was used if the data were not normally distributed, giving a W-value as output instead of a T-value. Paired t-tests were conducted if all samples of a species were represented in plots of pairs. All statistical analyzes were performed using R version 3.4.3 (R Core Team 2013).

3. Results

3.1. VARIATION IN COMMUNITY-WEIGHTED MEAN TRAITS

The ANOVA tests showed significant differences between treatments for SLA in vascular plants, with 7.9 % lower SLA in the OTCs compared to the control plots (Table 1, Fig. 1a). Nitrogen content was also significantly lower in the OTCs, with a decrease of 18.0 % from control plots (Table 1, Fig. 1c). The C:N ratio increased significantly in the OTCs and was 28.3 % higher than in the control plots (Table 1, Fig. 1e). By decomposing the total variation between treatments it was shown that differences in all of these traits were explained exclusively by intraspecific variation: Fixed trait values, representing species turnover and ignoring intraspecific variation, were virtually unaffected by treatment and differed considerably from the specific trait values for SLA, N content and C:N ratio. Differences in N content and C:N ratio were significant to such an extent that it was reflected in the total variation between treatments. No significant differences were found between treatments for traits LDMC and C content for vascular plants (Table 1, Fig. 1b and 1d). The ANOVAs showed no significant differences between treatments in any of the lichen traits (Table 1), although the p-values for intraspecific variation explaining differences in STA and N content were relatively low and therefore interesting to explore further at the species level.

Table 1. Relative contribution (%) of species turnover and intraspecific variation in explaining differences in traits SLA/STA (specific leaf/thallus area), LDMC (leaf dry matter content), WHC (water holding capacity), N (nitrogen content), C (carbon content) and C:N (carbon to nitrogen ratio) between treatments. For both vascular plants and lichens. The p-value for each response is given within brackets, and significant values at $p < 0.05$ are highlighted.

	Relative contribution of			
	Species turnover	Intraspecific variation	Covariation	Total
<i>Vascular plants</i>				
SLA	0.0 (0.972)	10.0 (0.008)	-0.4	9.6 (0.184)
LDMC	0.1 (0.879)	0.1 (0.849)	0.2	0.5 (0.775)
N	0.0 (0.816)	51.5 (< 0.001)	-2.9	48.7 (< 0.001)
C	0.0 (0.974)	6.9 (0.125)	-0.4	6.6 (0.274)
C:N	0.4 (0.569)	29.3 (< 0.001)	7.0	36.7 (0.005)
<i>Lichens</i>				
STA	0.5 (0.716)	4.0 (0.092)	-2.8	1.7 (0.586)
WHC	0.0 (0.901)	0.9 (0.456)	0.4	1.3 (0.627)
N	5.8 (0.312)	0.3 (0.064)	-2.8	3.4 (0.440)
C	0.0 (0.896)	3.7 (0.422)	0.6	4.3 (0.381)
C:N	1.8 (0.398)	3.8 (0.172)	-5.1	0.4 (0.796)

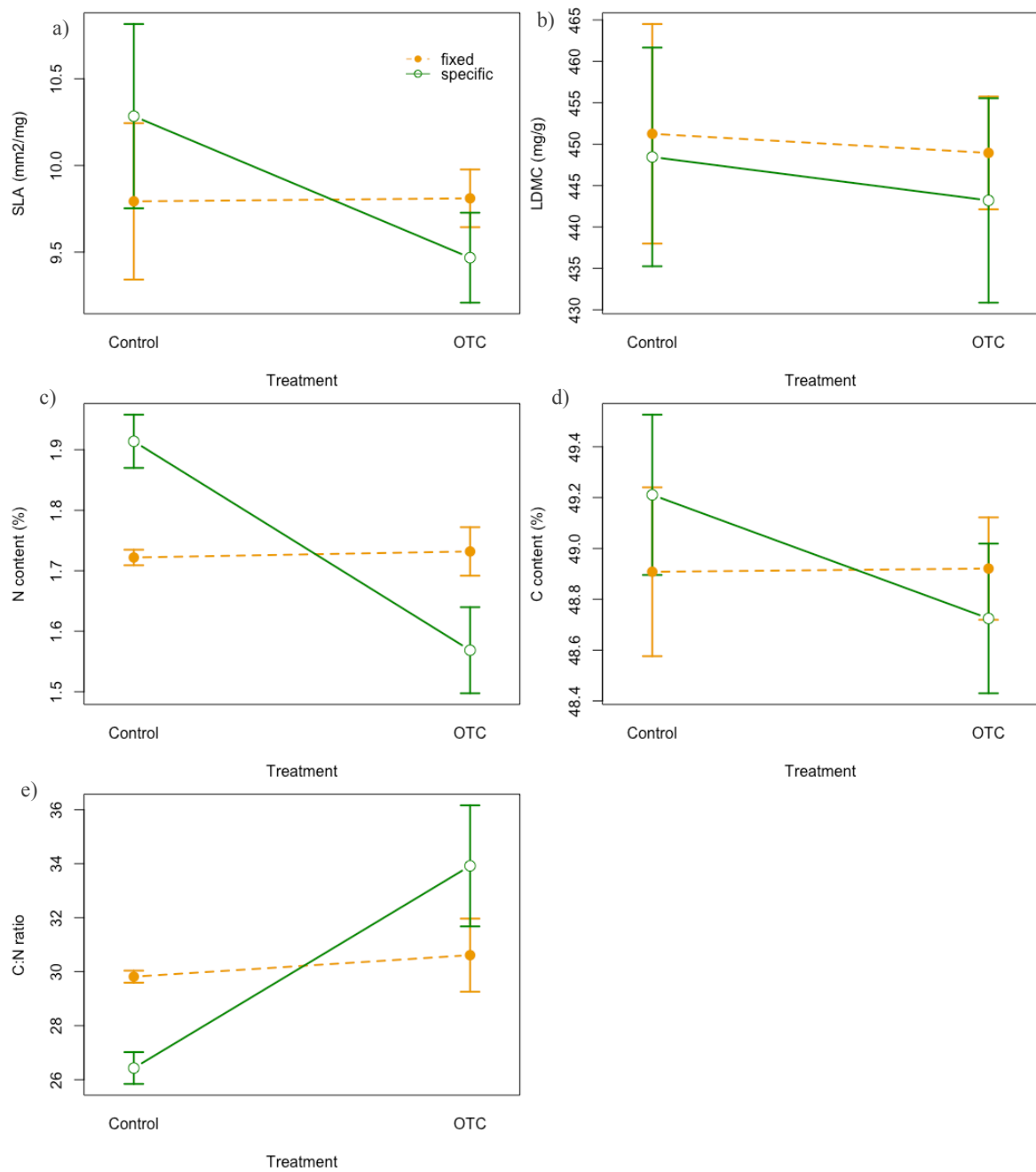


Figure 1. Community-weighted mean values of traits (a) SLA (specific leaf area), (b) LDMC (leaf dry matter content), (c) N (nitrogen content), (d) C (carbon content) and (e) C:N (carbon to nitrogen ratio) for vascular plants in the two treatments control and OTC (open top chamber). The community-weighted *specific mean* was calculated from the trait values recorded in each plot for each species in a community. The community-weighted *fixed mean* was calculated from the averaged trait values of each species in a community. Error bars indicate confidence intervals (95 %). Table 1 shows the results of the corresponding ANOVA tests.

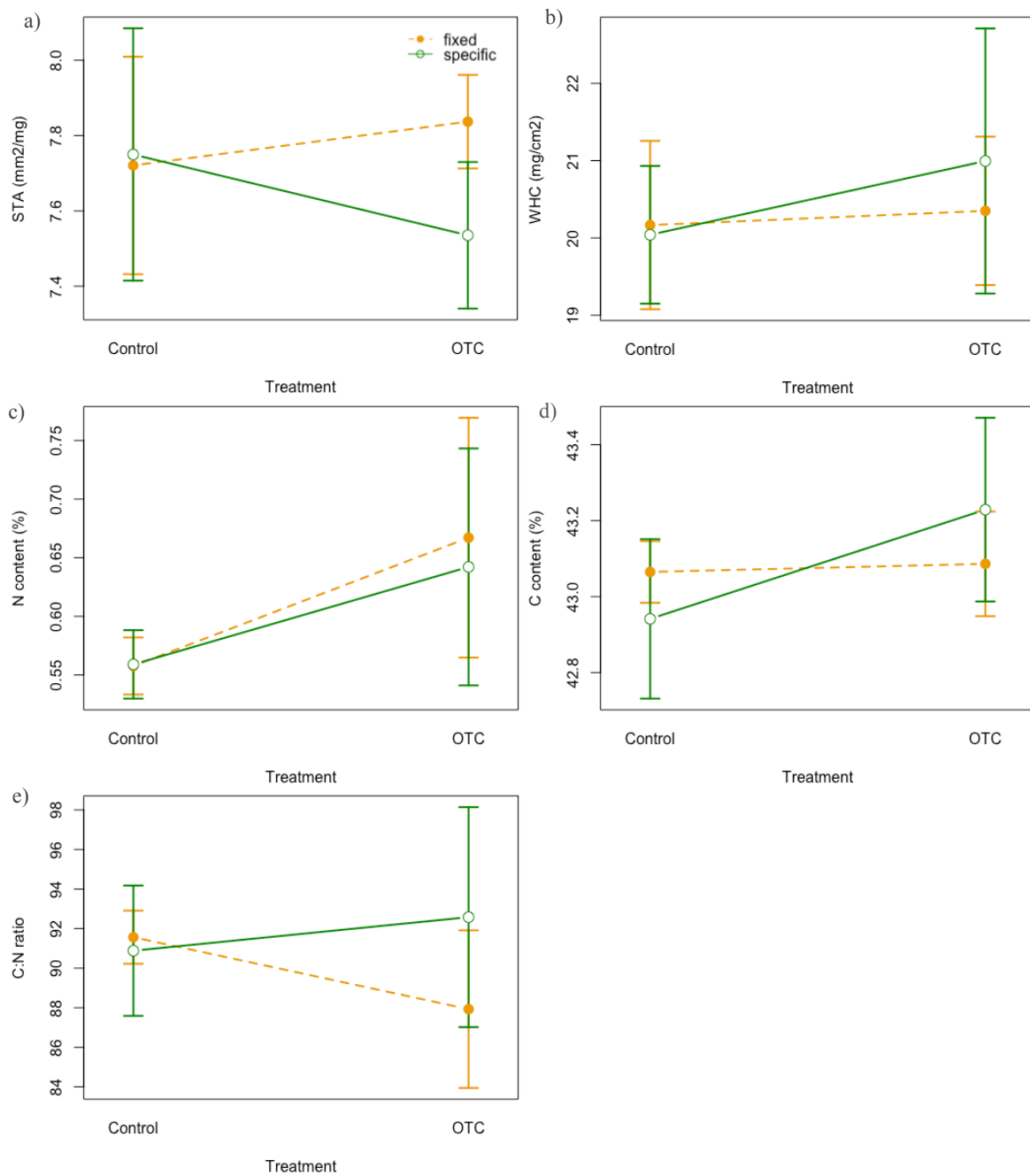


Figure 2. Community-weighted mean values of traits (a) STA (specific thallus area), (b) WHC (water holding capacity), (c) N (nitrogen content), (d) C (carbon content) and (e) C:N (carbon to nitrogen ratio) for lichens in the two treatments control and OTC (open top chamber). The community-weighted *specific mean* was calculated from the trait values recorded in each plot for each species in a community. The community-weighted *fixed mean* was calculated from the averaged trait values of each species in a community. Error bars indicate confidence intervals (95 %). Table 1 shows the results of the corresponding ANOVA tests.

3.2. INTRASPECIFIC VARIATION AT SPECIES LEVEL

For vascular plants, the t-tests showed a significant difference in SLA between treatments only for *Dryas octopetala*, which decreased 8.9 % from control plots to the OTCs (Table 2). None of the species showed significant differences between treatments in trait LDMC. Nitrogen content was significantly lower in the OTCs compared to the controls for the species *Bistorta vivipara* (13.1 %), *D. octopetala* (20.9 %) and *Salix reticulata* (21.9 %). The C:N ratio differed significantly between treatments with an increase of 13.6 % for *B. vivipara*, 27.0 % for *D. octopetala* and 27.6 % for *S. reticulata* in the OTCs. Carbon content decreased significantly in OTC plots for the species *B. vivipara* (2.3 %) and *D. octopetala* (1.4 %).

For lichens, the t-test showed significant responses to the treatment in STA for *Thamnolia vermicularis*, which increased with 27.6 % from controls to OTCs (Table 3). Water holding capacity in *T. vermicularis* decreased significantly from controls to OTCs, with 16.7 % lower trait values in OTCs. None of the other species responded significantly in these traits. Nitrogen content in *Cladonia gracilis* decreased significantly (8.3 %) from controls to OTC. *T. vermicularis* also showed a significant response in N content, with an increase of 17.7 % from control plots to OTCs. The C:N ratio differed significantly between species for both *C. gracilis* and *T. vermicularis*, where *C. gracilis* increased with 9.0 % and *T. vermicularis* decreased with 12.6 % from controls to OTCs. There were no significant differences between treatments in C content for any of the lichen species. Overall, the direction of the responses in trait values differed between lichen species.

Table 2. Mean trait values \pm standard error (SE) of SLA (specific leaf area), LDMC (leaf dry matter content), C (carbon content), N (nitrogen content) and C:N (carbon to nitrogen ratio) per species of vascular plants in the two treatments control and OTC (open top chamber). Highlighted p-values denote significant differences (< 0.05) between treatments. T value gives the difference in units of SE.

	n	Control	OTC	T	p
<i>Bistorta vivipara</i> ‡	20				
SLA		13.7 \pm 0.21	14.0 \pm 0.35	-0.44	0.669
LDMC		255 \pm 5.6	258 \pm 5.3	-0.32	0.759
N		3.49 \pm 0.11	3.04 \pm 0.14	3.1	0.013
C		47.4 \pm 0.29	46.3 \pm 0.29	W = 49	0.027 †
C:N		13.7 \pm 0.42	15.5 \pm 0.74	-2.7	0.023
<i>Dryas octopetala</i> ‡	20				
SLA		9.10 \pm 0.24	8.30 \pm 0.20	3.2	0.011
LDMC		498 \pm 17	481 \pm 13	1.1	0.301
N		1.86 \pm 0.038	1.47 \pm 0.081	W = 53	0.006 †
C		50.2 \pm 0.12	49.5 \pm 0.30	W = 52	0.01 †
C:N		27.1 \pm 0.55	34.4 \pm 1.6	W = 2	0.006 †
<i>Salix herbacea</i>	11				
SLA		14.6 \pm 0.40	14.2 \pm 0.56	0.53	0.614
LDMC		381 \pm 7.2	402 \pm 29	W = 14	0.931 †
N		2.38 \pm 0.13	2.23 \pm 0.15	0.72	0.489
C		47.2 \pm 0.90	48.3 \pm 0.87	-0.90	0.392
C:N		20.1 \pm 0.87	22.0 \pm 1.5	-1.1	0.304
<i>Salix reticulata</i>	16				
SLA		11.3 \pm 0.15	11.2 \pm 0.50	W = 41	0.351 †
LDMC		354 \pm 5.9	366 \pm 9.0	-1.1	0.23
N		2.66 \pm 0.074	2.08 \pm 0.089	5.1	< 0.001
C		46.8 \pm 0.28	46.3 \pm 0.26	W = 43	0.252 †
C:N		17.7 \pm 0.47	22.5 \pm 1.1	-4.1	0.003
<i>Silene acaulis</i>	18				
SLA		15.2 \pm 0.58	14.9 \pm 0.48	0.36	0.723
LDMC		225 \pm 7.1	229 \pm 7.44	-0.43	0.671
N		1.53 \pm 0.10	1.39 \pm 0.079	1.1	0.294
C		42.4 \pm 0.74	42.3 \pm 0.85	0.13	0.895
C:N		28.4 \pm 1.4	31.1 \pm 1.62	-1.2	0.242

† Wilcoxon test

‡ Data is paired

Table 3. Mean trait values \pm standard error (SE) of STA (specific thallus area), WHC (water holding capacity), C (carbon content), N (nitrogen content) and C:N (carbon to nitrogen ratio) per species of lichens in the two treatments control and OTC (open top chamber). Highlighted p-values denote significant differences (< 0.05) between treatments. T value gives the difference in units of SE.

	n	Control	OTC	T	p
<i>Cetraria islandica</i> ‡	20				
STA		7.58 \pm 0.24	6.76 \pm 0.38	1.5	0.167
WHC		17.2 \pm 0.73	19.7 \pm 1.7	-1.6	0.152
N		0.455 \pm 0.010	0.414 \pm 0.013	2.1	0.07
C		42.5 \pm 0.32	42.4 \pm 0.26	0.41	0.689
C:N		93.8 \pm 1.9	103 \pm 3.1	-2.1	0.067
<i>Cladonia arbuscula</i>	19				
STA		7.27 \pm 0.29	7.68 \pm 0.19	-1.2	0.255
WHC		20.9 \pm 1.0	18.8 \pm 0.67	1.7	0.103
N		0.475 \pm 0.021	0.457 \pm 0.018	0.68	0.508
C		43.5 \pm 0.11	43.8 \pm 0.18	-1.0	0.318
C:N		93.3 \pm 4.6	96.7 \pm 3.3	-0.60	0.554
<i>Cladonia gracilis</i>	14				
STA		4.92 \pm 0.29	4.37 \pm 0.11	W = 33	0.318 †
WHC		26.7 \pm 1.5	27.7 \pm 2.8	-0.34	0.742
N		0.491 \pm 0.012	0.450 \pm 0.010	2.4	0.032
C		43.2 \pm 0.32	43.3 \pm 0.50	-0.085	0.934
C:N		88.3 \pm 2.2	96.3 \pm 2.3	-2.5	0.028
<i>Cladonia uncialis</i>	15				
STA		7.23 \pm 0.32	7.10 \pm 0.18	0.36	0.729
WHC		18.0 \pm 0.73	17.4 \pm 0.49	0.76	0.462
N		0.421 \pm 0.019	0.375 \pm 0.015	1.8	0.089
C		44.4 \pm 0.69	44.3 \pm 0.30	W = 21	0.463 †
C:N		107.0 \pm 4.9	119 \pm 5.1	-1.7	0.112
<i>Flavocetraria cucullata</i>	16				
STA		9.01 \pm 0.41	9.33 \pm 0.46	W = 27	0.645 †
WHC		14.6 \pm 0.61	13.1 \pm 0.57	1.8	0.093
N		0.459 \pm 0.027	0.469 \pm 0.026	-0.26	0.799
C		43.1 \pm 0.53	44.6 \pm 0.90	W = 21	0.279 †
C:N		96.4 \pm 6.5	97.2 \pm 6.1	-0.089	0.93
<i>Flavocetraria nivalis</i>	19				
STA		10.4 \pm 0.22	9.77 \pm 0.22	1.9	0.08
WHC		12.3 \pm 0.51	12.5 \pm 0.65	-0.29	0.776
N		0.428 \pm 0.021	0.412 \pm 0.018	0.54	0.594
C		42.1 \pm 0.28	41.6 \pm 0.48	0.80	0.438
C:N		101 \pm 6.1	103 \pm 5.1	W = 40	0.72 †
<i>Stereocaulon sp.</i>	15				
STA		3.73 \pm 0.15	3.71 \pm 0.28	0.035	0.973
WHC		49.9 \pm 2.7	48.3 \pm 3.3	0.39	0.708
N		0.94 \pm 0.061	0.920 \pm 0.086	0.19	0.855
C		44.0 \pm 0.67	44.8 \pm 0.91	-0.66	0.522
C:N		48.9 \pm 4.1	51.0 \pm 5.2	-0.32	0.756
<i>Thamnolia vermicularis</i>	18				
STA		5.28 \pm 0.13	6.74 \pm 0.17	-6.8	< 0.001
WHC		27.8 \pm 0.96	23.1 \pm 0.62	4.1	0.001
N		0.538 \pm 0.014	0.634 \pm 0.023	-3.5	0.004
C		42.7 \pm 0.40	43.8 \pm 0.57	-1.6	0.13
C:N		79.7 \pm 2.5	69.7 \pm 2.5	2.9	0.011

† Wilcoxon test

‡ Data is paired

4. Discussion

My first hypothesis that increased warming would cause the functional trait values to shift to levels associated with higher resource acquisition, was not supported by my findings. In contrast with the hypothesis, vascular plant trait values for SLA and N content was lower in OTCs than in controls, and C:N ratio increased in the OTCs. Surprisingly, LDMC and C content in vascular plants and all traits measured for lichens did not respond to warming at the whole community level. Two of the lichen species did, however, respond. Although only for vascular plants, the prediction that changes in functional trait values would be detected at both community level and species level was supported. Contrasting to my second hypothesis, I found that the observed variation in community-weighted traits in vascular plants was solely due to intraspecific variation. These results are not in line with the findings in several recent studies of the relative importance of species turnover vs. intraspecific variation, where vascular plant traits were mostly driven by species turnover (Albert et al. 2010; Lepš et al. 2011; Kichenin et al. 2013; Kazakou et al. 2014; Siefert et al. 2015). Although I found no significant effects at the whole community level for lichens, the significant effects within species indicate that there is intraspecific variation but that this effect is species dependent.

4.1. SHIFTS IN FUNCTIONAL TRAITS WITH INCREASED TEMPERATURE

Plant SLA and lichen STA were expected to increase with increased temperature, as has been found in several studies of vascular plant trait responses to changes in temperature (Scheepens et al. 2010; Sundqvist et al. 2013; Read et al. 2014; Guittar et al. 2016). Specific leaf area is reflecting the trade-offs in the functional strategy of the plant, and with increased temperature, more nutrients become available and can be put to use in the production of plant biomass. Low-SLA leaves are slow-growing and have a higher leaf density due to deposition of more cell wall material and further less water relative to dry mass. Specific leaf area should thus increase with temperature because the leaves are growing faster and the leaf area is increasing relative to the dry mass of the leaf (Poorter & Garnier 1999). My results, with decreasing SLA for vascular plants in the OTCs, are therefore unexpected. However, interestingly, a recent study along an elevational gradient in the same general area, found increasing SLA with elevation, i.e. SLA decreased with temperature, in the studied vascular plant communities (van Zuijlen et al. 2018). Although this supports my findings, it should be mentioned that this study site was located on acidic bedrock, as opposed to the calcareous bedrock at Sanddalsnuten, and thus has a different plant community. The study site at Sanddalsnuten is situated at a relatively dry heath, and

moisture can thus act as a limiting factor in this environment. It is possible that the temperature increase in the open top chambers is amplifying drought stress rather than facilitating growth for the vascular plants, which could have led to the decrease in SLA. Studies have established that open top chambers largely affect moisture conditions (Marion et al. 1997; Aronson & McNulty 2009). On the other hand, Engler et al. (2011) argue that plant communities in Scandinavian alpine areas seem to be more resistant to increases in temperature compared to other alpine areas due to higher levels of precipitation, and this is highly relevant at Finse.

The responses in the chemical traits N content and C:N ratio for vascular plants showed tendencies of higher resource conservation in the warmed plots compared to the controls. These results are surprising as they are in contrast with the findings of most other studies, where N content has been shown to increase and C:N ratio to decrease with temperature, reflecting a shift towards levels associated with higher resource acquisition (Sundqvist et al. 2013). However, in a meta-analysis study, Read et al. (2014) found that N content was as likely to decrease with elevation as to increase, and further established a correlation between N content and SLA with increasing temperature at high elevation. Although in the opposite direction, this supports my findings, with both decreasing SLA and N content with increased temperature. Further, my results are supported by several studies that have found N content in vascular plants to decrease with increasing temperature (Tolvanen & Henry 2001; Nybakken et al. 2011; van Zuijlen et al. 2018). As for community-level, this reflects my observations at the species level, where the direction of change of N content and C:N ratio for *B. vivipara*, *D. octopetala* and *S. reticulata* indicates higher resource conservation. Rustad et al. (2001) found the effects of warming on N mineralization rates to be less pronounced in tundra systems compared to forests, which can be an explanation of why several studies conducted in alpine systems show no increase in N content with increased temperature. The C:N ratio was significantly higher in the OTCs compared to the control plots, suggesting that the decrease in N content in the OTCs is due to dilution, as was found in Nybakken et al. (2011). However, if dilution alone was the reason for the observed trend, I would expect SLA in the OTCs to be higher.

Less is known about the responses of lichen traits to changes in temperature, which generally may have resulted in an underrepresentation of the contribution from lichens to the ecosystem function, especially at high elevations (St Martin & Mallik 2017). The lack of significant responses in any traits for lichens at the whole community level is interesting and in contrast with the findings in the elevational gradient study of van Zuijlen et al. (2018). They found the community-weighted STA and N content in lichens to increase and WHC to decrease with elevation, i.e. with decreasing temperature. As opposed to vascular plants, lichens have no

active water and nutrient uptake and are dependent solely on rainwater or dew for both water and nutrient supply. Lichens can easily dry out and stop their growth if moisture conditions changes and therefore do not experience drought stress (Nash 2008). This may explain why there were no significant differences between treatments in the lichen community-weighted traits at Sanddalsnuten, as opposed to the vascular plant community-weighted traits. However, the lichen morphology is closely linked to water availability, and it would be likely for the lichen thalli to increase in thickness, i.e. decreasing their STA, to retain water in drier environments (Gauslaa 2014). At the species level, two of the studied species showed significant responses to the increased temperature. Interestingly, *T. vermicularis* responded more to increased temperature than all other lichen species, and with responses in all traits except C content, of which the morphological traits STA and WHC responded the most. Specific thallus area and WHC was negatively correlated, as was found by van Zuijlen et al. (2018) and by Gauslaa and Coxson (2011) when addressing species-level trait variation between xeric and mesic habitats. The increase in STA suggests a decrease in thallus dry matter leading to a decrease in WHC in the OTCs. In general, the traits of *T. vermicularis* shifted towards levels associated with higher resource acquisition, as opposed to the trends shown for all other species in this study. This is supported by Nybakken et al. (2011) who also found *T. vermicularis* to be the only lichen species that had increased N content and decreased C:N ratio in the OTCs. Increased N content may be explained by *T. vermicularis* achieving improved N uptake when temperature increases, which according to Asplund and Wardle (2014) can cause the observed increase in STA. *Cladonia gracilis* responded by showing the same trend as the vascular plant species, by decreasing N content and increasing C:N ratio in the OTCs, suggesting that the altered environmental conditions in the OTCs are forcing it to be conservative with its resources.

Knowledge of spatial patterns of functional traits has been used as background for determining which traits should be included in the analyzes. However, Guittar et al. (2016) suggest that even though there is a clear spatial association between plant functional traits and climate variables, spatial trait gradient patterns are not necessarily good predictors of the community responses to climate change. Which traits that are ecologically relevant to include, can depend on the vegetation types and locations (i.e. elevation and longitude) that are studied, and also by the methods in use. Several studies have highlighted that there are considerable regional differences in the plant responses to changes in temperature (Elmendorf et al. 2011; Engler et al. 2011; Gottfried et al. 2012). Further, Sundqvist et al. (2011) found that the response of foliar traits to elevation varied greatly between vegetation types and that this emphasizes the

importance of vegetation types in determining ecological responses to changes in temperature. The study site at Sanddalsnuten is a heathland dominated by *D. octopetala*, and studies from this exact site have shown that *D. octopetala* has a significant impact on its neighboring plant species through both competition and facilitation (Klanderud 2005; Klanderud & Totland 2005a; Åshild Hasvik unpubl.). Considering these findings, it is possible that the effect *D. octopetala* has on other species in this system can somewhat mask the effects of increased temperature, e.g. by giving shelter or by occupying resources.

4.2. THE RELATIVE IMPORTANCE OF SPECIES TURNOVER AND INTRASPECIFIC VARIATION

For vascular plants, intraspecific variation was the single significant contributor to the changes observed for all three community-weighted traits that responded to the increased temperature in the OTCs (SLA, N content and C:N ratio). Considering the majority of earlier studies, it is surprising that I found no significant importance of species turnover, especially for vascular plants. In fact, the negative covariation between species turnover and intraspecific variation observed for traits SLA and N content, suggests that species turnover and intraspecific variation are compensating each other rather than reinforcing each other's effects, likely by selecting for different dominant trait values (Lepš et al. 2011). Siefert et al. (2015) found that the relative extent of intraspecific trait variation increased with decreasing species richness, which can help explain the observed importance of intraspecific trait variation in alpine vascular plant communities. This is substantiated by Albert et al. (2010), who argue that we may expect less differences between species and hence increasing the relative importance of intraspecific variation when studying differences within homogeneous environments, as the study site at Sanddalsnuten. This can also be the reason why single site *in situ* experiments may fail to show clear trends of arrival and establishment of new species with environmental change (Gottfried et al. 2012). As explained by Elmendorf et al. (2011), there might also be differences in responses to environmental changes between ecosystems and regions, and it is possible that these differences can be expressed in the relative contribution of respectively species turnover and intraspecific variation. However, these results show the importance of taking intraspecific variation into account when assessing community-level responses in traits SLA, N content and C:N ratio to increased temperature, as is substantiated by several other studies (Albert et al. 2010; Lepš et al. 2011; Siefert et al. 2015).

It is argued that the relative extent of species turnover and intraspecific variation can vary extensively depending on the subset of species and the traits that are included in the study

(Wilson et al. 1999; Albert et al. 2010; Lepš et al. 2011; Kichenin et al. 2013). Specifically, studies have found that the relative extent of intraspecific variation was greater for chemical traits than for morphological traits (Kazakou et al. 2014; Siefert et al. 2015). My results show that intraspecific variation is the only contributor to the total trait variation found for all three community-weighted traits with significant responses to warming. However, variation in the chemical traits N content and C:N ratio is explained to a greater extent than variation in SLA by the OTC treatment. At intraspecific level, chemical traits are known to show strong plastic responses to environmental change compared to morphological traits, which are usually more stable (Kazakou et al. 2014; Siefert et al. 2015). The high intraspecific variation in N content and C:N ratio found in vascular plants may thus be explained by plants storing nutrients and carbon depending on the nutrient availability in the environment (Chapin et al. 1990). However, consistent with my results, studies have found intraspecific variation to be an important contributor to changes also in SLA (Kichenin et al. 2013; Siefert et al. 2015). Like N content, SLA is depicting the leaf economics of the plant, and traits linked to this function has been shown to vary at the intraspecific level due to strong plasticity in response to environmental variables (Rozendaal et al. 2006; Poorter et al. 2009; Kichenin et al. 2013).

For lichens, community-weighted traits were expected to respond to increased warming and mainly by intraspecific variation, considering earlier findings. Although not expressed by the community-weighted traits, I found intraspecific variation in species *T. vermicularis* and *C. gracilis*. Asplund and Wardle (2014) found that intraspecific variation was important to such a degree that accounting for it was necessary to reveal the total community-level responses in several chemical and morphological traits to changes in nutrient availability. The importance of intraspecific variation in explaining changes in functional traits in lichen species was also expressed by Gauslaa and Coxson (2011). My results may reflect that water availability is limiting the growth of the lichens in the OTCs. They may, however, also indicate that the lichens are not particularly responsive to the warming treatment. This is reflected by the low total community trait variation explained by the OTC treatment for lichens, ranging from 0.4 to 4.3 % for all traits, meaning that most of the variation in community-weighted traits between treatments remains unexplained. Also, considering the overall low abundance of lichen species in the plots, it is possible that the coverage estimates in the method used are not at a sufficient level of detail to capture potential variation between treatments.

5. Conclusions

Interestingly, I found significant responses to increased warming in the vascular plant communities shifting towards trait levels associated with higher resource conservation. For lichens, although no warming-induced variation in community-weighted traits was found, I found responses in several traits at the species level. These responses were contrasting, with *C. gracilis* shifting towards levels associated with higher resource conservation and *T. vermicularis* shifting towards levels associated with higher resource acquisition. The observed responses could be due to the dominating effect of *D. octopetala* on the vascular plant and lichen communities at Finse. Further, plant communities may respond differently to increases in temperature depending on the studied subsets of species, vegetation types and systems. It is likely that the OTC treatment may have altered the moisture conditions in the warmed plots, forcing especially the vascular plants to be conservative with their resources rather than facilitating increased nutrient availability and growth. It is likely that the vascular plants are more vulnerable than the lichens to possible secondary effects of the open top chamber method, i.e. enhanced drought stress.

My findings show that intraspecific variation can be of considerable importance in determining the community-level responses of vascular plants to increasing temperature. Neglecting the contribution of intraspecific variation to the total trait variation might therefore cause an underestimation of the effects of increasing temperatures on plant communities. Considering the high observed intraspecific variation in chemical traits explained by the OTC treatment, this will especially have implications for studies of nutrient availability and decomposition. The intraspecific variation in lichen functional traits found at the species level implies that intraspecific variation must be taken into account also when assessing variation in functional traits in lichen communities. The fact that all observed variation in the measured functional traits is explained solely by intraspecific variation, shows that the alpine plant and lichen communities are adaptable and thus can be relatively resistant to the increased warming. These strong plastic responses imply that these communities are less vulnerable to replacement by novel species, as would be an issue if species turnover was shown to be a more important driver of variation.

6. References

- Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S. & Lavorel, S. (2010). A multi-trait approach reveals the structure and the relative importance of intra-vs. interspecific variability in plant traits. *Functional Ecology*, 24 (6): 1192-1201.
- Alexander, J.M., Diez, J.M. & Levine, J.M. (2015). Novel competitors shape species' responses to climate change. *Nature*, 525 (7570): 515-518.
- Aronson, E.L. & McNulty, S.G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, 149 (11): 1791-1799.
- Asplund, J. & Wardle, D.A. (2014). Within-species variability is the main driver of community-level responses of traits of epiphytes across a long-term chronosequence. *Functional Ecology*, 28 (6): 1513-1522.
- Asplund, J. & Wardle, D.A. (2017). How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews*, 92 (3): 1720-1738.
- Bradshaw, W.E. & Holzapfel, C.M. (2006). Evolutionary response to rapid climate change. *Science*, 312 (5779): 1477-1478.
- Callaghan, T.V. & Jonasson, S. (1995). Implications for changes in arctic plant biodiversity from environmental manipulation experiments. In Chapin, F. S. & Körner, C. (eds) *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences*, pp. 151-166. Berlin, Germany: Heidelberg, Springer-Verlag.
- Chapin, F.S., Schulze, E.D. & Mooney, H.A. (1990). The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics*, 21 (1): 423-447.
- Chapin, F.S. (2003). Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany*, 91 (4): 455-463.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E. *et al.* (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51 (4): 335-380.
- Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. & During, H.J. (2007). Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, 99 (5): 987-1001.
- Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M. *et al.* (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, 3 (9): 2958-2975.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan, T.V. *et al.* (2011). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, 15 (2): 164-175.
- Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B. *et al.* (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17 (7): 2330-2341.
- Finse Alpine Research Center. (2010). *Location*: UiO. Available at: <http://www.finse.uio.no/about/location/>.
- Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K. *et al.* (2009). Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology*, 90 (3): 598-611.
- Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M. *et al.* (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85 (9): 2630-2637.

- Gauslaa, Y. & Coxson, D. (2011). Interspecific and intraspecific variations in water storage in epiphytic old forest foliose lichens. *Botany*, 89 (11): 787-798.
- Gauslaa, Y. (2014). Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *Lichenologist*, 46 (1): 1-16.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J.L.B. *et al.* (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2 (2): 111-115.
- Grabherr, G. (1994). Climate effects on mountain plants. *Nature*, 369: 448.
- Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86 (6): 902-910.
- Grytnes, J.A., Kapfer, J., Jurasinski, G., Birks, H.H., Henriksen, H., Klanderud, K. *et al.* (2014). Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecology and Biogeography*, 23 (8): 876-884.
- Guittar, J., Goldberg, D., Klanderud, K., Telford, R.J. & Vandvik, V. (2016). Can trait patterns along gradients predict plant community responses to climate change? *Ecology*, 97 (10): 2791-2801.
- Hudson, J.M.G., Henry, G.H.R. & Cornwell, W.K. (2011). Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Global Change Biology*, 17 (2): 1013-1021.
- Kazakou, E., Violle, C., Roumet, C., Navas, M.L., Vile, D., Kattge, J. *et al.* (2014). Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science*, 25 (1): 235-247.
- Keddy, P.A. (1992a). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, 3 (2): 157-164.
- Keddy, P.A. (1992b). A pragmatic approach to functional ecology. *Functional Ecology*, 6 (6): 621-626.
- Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W. & Freschet, G.T. (2013). Contrasting effects of plant inter-and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, 27 (5): 1254-1261.
- Klanderud, K. & Birks, H.J.B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene*, 13 (1): 1-6.
- Klanderud, K. (2005). Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, 93 (1): 127-137.
- Klanderud, K. & Totland, Ø. (2005a). The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, 93 (3): 493-501.
- Klanderud, K. & Totland, Ø. (2005b). Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology*, 86 (8): 2047-2054.
- Körner, C. (2003). *Alpine plant life: functional plant ecology of high mountain ecosystems*. Berlin: Springer.
- Lenoir, J. & Svenning, J.C. (2013). Latitudinal and elevational range shifts under contemporary climate change. In Levin, S. A. (ed.) *Encyclopedia of biodiversity*, pp. 599-611. Waltham, MA: Academic Press.
- Lepš, J., de Bello, F., Šmilauer, P. & Doležal, J. (2011). Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography*, 34 (5): 856-863.
- MacArthur, R.H. (1972). *Geographical ecology: patterns in the distribution of species*: Princeton University Press.
- Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H. *et al.* (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, 3 (S1): 20-32.

- Matveyeva, N. & Chernov, Y. (2000). Biodiversity of terrestrial ecosystems. In Nuttall, M. C. & Callaghan, T. V. (eds) *The Arctic: Environment, People, Policy*, pp. 233-273. Reading, UK: Harwood Academic Publishers.
- Mayor, J.R., Sanders, N.J., Classen, A.T., Bardgett, R.D., Clément, J.C., Fajardo, A. *et al.* (2017). Elevation alters ecosystem properties across temperate treelines globally. *Nature*, 542 (7639): 91-95.
- McCarty, J.P. (2001). Ecological consequences of recent climate change. *Conservation Biology*, 15 (2): 320-331.
- Molau, U. & Mølgaard, P. (1996). *ITEX manual*: Danish Polar Center.
- Nash, T.H. (2008). Nutrients, elemental accumulation, and mineral cycling. In Nash, T. H. (ed.) *Lichen Biology*, pp. 234-251. Cambridge University Press.
- NGU. *Berggrunn*: Norges geologiske undersøkelse. Available at: <http://geo.ngu.no/kart/berggrunn/>.
- Normand, S., Treier, U.A., Randin, C.F., Vittoz, P., Guisan, A. & Svenning, J.C. (2009). Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography*, 18 (4): 437-449.
- Nybakken, L., Sandvik, S.M. & Klanderud, K. (2011). Experimental warming had little effect on carbon-based secondary compounds, carbon and nitrogen in selected alpine plants and lichens. *Environmental and Experimental Botany*, 72 (3): 368-376.
- Olsen, S.L. & Klanderud, K. (2014). Exclusion of herbivores slows down recovery after experimental warming and nutrient addition in an alpine plant community. *Journal of Ecology*, 102 (5): 1129-1137.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421 (6918): 37-42.
- Poorter, H. & Garnier, E. (1999). Ecological significance of inherent variation in relative growth rate and its components. In Pugnaire, F. I. & Valladares, F. (eds) *Handbook of functional plant ecology*, pp. 81-120. New York: Marcel Dekker.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, 182 (3): 565-588.
- R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: <http://www.R-project.org/>.
- Read, Q.D., Moorhead, L.C., Swenson, N.G., Bailey, J.K. & Sanders, N.J. (2014). Convergent effects of elevation on functional leaf traits within and among species. *Functional Ecology*, 28 (1): 37-45.
- Rozendaal, D.M.A., Hurtado, V.H. & Poorter, L. (2006). Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology*, 20 (2): 207-216.
- Rustad, L.E., Campbell, J., Marion, G.M., Norby, R., Mitchell, M., Hartley, A. *et al.* (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126 (4): 543-562.
- Scheepens, J.F., Frei, E.S. & Stöcklin, J. (2010). Genotypic and environmental variation in specific leaf area in a widespread Alpine plant after transplantation to different altitudes. *Oecologia*, 164 (1): 141-150.
- Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9 (7): 671-675.

- Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A. *et al.* (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18 (12): 1406-1419.
- St Martin, P. & Mallik, A.U. (2017). The status of non-vascular plants in trait-based ecosystem function studies. *Perspectives in Plant Ecology, Evolution and Systematics*, 27: 1-8.
- Sundqvist, M.K., Giesler, R. & Wardle, D.A. (2011). Within-and across-species responses of plant traits and litter decomposition to elevation across contrasting vegetation types in subarctic tundra. *PloS one*, 6 (10): e27056.
- Sundqvist, M.K., Sanders, N.J. & Wardle, D.A. (2013). Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. *Annual Review of Ecology, Evolution, and Systematics*, 44: 261-280.
- Taudiere, A. & Violle, C. (2016). cati: an R package using functional traits to detect and quantify multi-level community assembly processes. *Ecography*, 39 (7): 699-708.
- Tolvanen, A. & Henry, G.H.R. (2001). Responses of carbon and nitrogen concentrations in high arctic plants to experimental warming. *Canadian Journal of Botany*, 79 (6): 711-718.
- Valladares, F., Gianoli, E. & Gómez, J.M. (2007). Ecological limits to plant phenotypic plasticity. *New Phytologist*, 176 (4): 749-763.
- van Zuijlen, K., Roos, R.E., Birkemoe, T., Klanderud, K., Lang, S.I., Bokhorst, S. *et al.* (2018). *Functional traits of lichens, bryophytes and vascular plants across elevation: species turnover vs intraspecific variation*: Poster at the Nordic Oikos Conference, Trondheim (21.02.2018).
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116 (5): 882-892.
- Walther, G.R. (2003). Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics*, 6 (3): 169-185.
- Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS biology*, 6 (12): e325.
- Wilson, P.J., Thompson, K.E.N. & Hodgson, J.G. (1999). Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, 143 (1): 155-162.
- Yr. (2018). *Weather statistics for Finse, Ulvik (Hordaland)*. Available at: <https://www.yr.no/sted/Norge/Hordaland/Ulvik/Finse/statistikk.html>.

APPENDIX 1. Relative cover (%) and trait values for SLA (specific leaf area), LDMC (leaf dry matter content), N (nitrogen content), C (carbon content) and C:N (carbon to nitrogen ratio) of all collected vascular plant species in all plots. Sorted by plots in pairs.

Plot	Treatment	Species	Rel. cover (%)	SLA	LDMC	N	C	C:N
K10A	Control	<i>Dryas octopetala</i>	87.71	10.11	515.5	2.039	50.14	24.59
K10A	Control	<i>Saussurea alpina</i>	3.56	12.2	239.5	2.866	45.29	15.8
K10A	Control	<i>Salix reticulata</i>	3.56	11.83	363.9	2.904	46.72	16.09
K10A	Control	<i>Bistorta vivipara</i>	2.58	13.58	273.2	3.744	46.98	12.55
K10A	Control	<i>Salix herbacea</i>	1.72	13.65	382.3	2.762	48.08	17.41
K10A	Control	<i>Silene acaulis</i>	0.86	15.95	219.4	2.134	44.48	20.84
K10C	Control	<i>Dryas octopetala</i>	94.53	8.51	491.7	1.837	49.78	27.1
K10C	Control	<i>Salix reticulata</i>	2.46	10.99	354.2	2.536	46.2	18.22
K10C	Control	<i>Bistorta vivipara</i>	1.79	13.32	249.2	3.068	47.46	15.47
K10C	Control	<i>Salix herbacea</i>	1.23	13.7	377.3	2.568	49.11	19.12
K10D	Control	<i>Dryas octopetala</i>	94.34	10.62	422.9	2.043	50.54	24.74
K10D	Control	<i>Carex rupestris</i>	2.27	14.02	407.9	2.134	46.25	21.67
K10D	Control	<i>Bistorta vivipara</i>	1.7	12.81	276.4	3.666	47.08	12.84
K10D	Control	<i>Salix reticulata</i>	1.13	11.26	362.3	2.368	46.38	19.59
K10D	Control	<i>Silene acaulis</i>	0.57	13.04	241.2	1.285	40.5	31.52
K1A	Control	<i>Dryas octopetala</i>	56.25	8.64	498.9	1.927	50.05	25.98
K1A	Control	<i>Silene acaulis</i>	31.25	16.85	201.1	1.83	43.67	23.87
K1A	Control	<i>Salix herbacea</i>	3.91	15.44	377.7	1.795	42.85	23.88
K1A	Control	<i>Carex atrata</i>	3.13	19.05	368.6	2.446	45.57	18.63
K1A	Control	<i>Potentilla crantzii</i>	2.34	13.06	345.3	2.655	45.08	16.98
K1A	Control	<i>Bistorta vivipara</i>	1.56	14.95	247	3.987	47.48	11.91
K1A	Control	<i>Salix reticulata</i>	1.56	11.88	334.9	2.943	49.02	16.65
K1C	Control	<i>Silene acaulis</i>	26.96	18.26	218.7	1.574	44.44	28.23
K1C	Control	<i>Dryas octopetala</i>	26.09	8.72	611	1.789	50.97	28.48
K1C	Control	<i>Cassiope hypnoides</i>	13.91	17.29	526.1	1.243	52.55	42.28
K1C	Control	<i>Juncus trifidus</i>	6.96	15.02	336.2	3.023	46.01	15.22
K1C	Control	<i>Saussurea alpina</i>	6.96	11.71	224.8	2.732	44.01	16.11
K1C	Control	<i>Bistorta vivipara</i>	5.22	13.84	267.8	3.538	46.78	13.22
K1C	Control	<i>Carex vaginata</i>	3.48	18.22	280.8	3.146	45.73	14.54
K1C	Control	<i>Luzula spicata</i>	3.48	13.09	299.5	1.834	44.46	24.24
K1C	Control	<i>Viscaria alpina</i>	3.48	11.14	239.6	1.672	45.24	27.06
K1C	Control	<i>Salix herbacea</i>	1.74	16.01	354.7	2.389	47.85	20.03
K1C	Control	<i>Salix reticulata</i>	1.74	11.54	317.9	2.845	46.59	16.38
K3C	Control	<i>Dryas octopetala</i>	89.38	8.49	516.7	1.777	49.7	27.96
K3C	Control	<i>Silene acaulis</i>	7.5	13.78	208.8	1.206	42.76	35.44
K3C	Control	<i>Bistorta vivipara</i>	1.88	14.06	224.6	2.897	46.82	16.16
K3C	Control	<i>Salix herbacea</i>	1.25	14.71	409.5	2.406	47.96	19.93
K3D	Control	<i>Dryas octopetala</i>	95.73	9.15	444.2	1.893	50.3	26.57
K3D	Control	<i>Bistorta vivipara</i>	1.83	14.49	243.2	3.63	47.5	13.09
K3D	Control	<i>Silene acaulis</i>	1.83	15.34	269.7	1.466	40.92	27.91
K3D	Control	<i>Salix reticulata</i>	0.61	10.81	365.7	2.737	46.91	17.14
K5D	Control	<i>Dryas octopetala</i>	83.33	8.42	543.4	1.663	50.04	30.09
K5D	Control	<i>Silene acaulis</i>	10.83	13	235.4	1.202	37.88	31.51
K5D	Control	<i>Salix reticulata</i>	3.33	10.79	376.9	2.668	46.49	17.42
K5D	Control	<i>Bistorta vivipara</i>	2.5	13.02	279.3	3.757	49.89	13.28
K6A	Control	<i>Dryas octopetala</i>	93.18	9.46	470.7	1.77	50.36	28.44
K6A	Control	<i>Silene acaulis</i>	3.41	15.54	208.1	1.563	43.81	28.03
K6A	Control	<i>Salix reticulata</i>	1.7	11	351.8	2.657	46.36	17.45
K6A	Control	<i>Bistorta vivipara</i>	1.14	13.28	255.1	3.229	47.28	14.64
K6A	Control	<i>Salix herbacea</i>	0.57	13.93	384.3	2.35	47.29	20.12
K8D	Control	<i>Dryas octopetala</i>	84.33	8.9	464.1	1.885	50.2	26.63
K8D	Control	<i>Empetrum nigrum</i>	2.99	7.58	476.6	1.153	51.06	44.28
K8D	Control	<i>Silene acaulis</i>	2.24	15.19	218	1.52	43.35	28.52
K8D	Control	<i>Bistorta vivipara</i>	1.49	13.97	242.7	3.425	46.82	13.67
K8D	Control	<i>Carex rupestris</i>	1.49	14.83	371.7	2.018	46.78	23.18
K8D	Control	<i>Festuca sp.</i>	1.49	9.94	481.2	1.288	45.53	35.35
K8D	Control	<i>Luzula spicata</i>	1.49	15.65	266.6	1.672	45.33	27.11

K8D	Control	Saussurea alpina	1.49	10.73	218.3	2.753	45.58	16.55
K8D	Control	Salix reticulata	1.49	11.72	360.9	2.321	46.79	20.16
K8D	Control	Thalictrum alpinum	1.49	13.32	325.4	2.708	44.76	16.53
O5B	OTC	Dryas octopetala	69.23	8.6	458.4	1.414	49.75	35.18
O5B	OTC	Silene acaulis	25.64	14.72	213.8	1.458	45.37	31.12
O5B	OTC	Bistorta vivipara	3.21	13.11	276.5	3.269	47.2	14.44
O5B	OTC	Salix reticulata	1.28	10.24	367.8	2.066	45.92	22.23
O5B	OTC	Salix herbacea	0.64	14.14	362	2.788	47.83	17.16
O6A	OTC	Dryas octopetala	68.75	8.47	473.9	1.644	49.78	30.28
O6A	OTC	Silene acaulis	20.63	16.61	191.7	1.649	44.55	27.01
O6A	OTC	Salix reticulata	3.75	10.21	365.5	2.253	46.72	20.73
O6A	OTC	Bistorta vivipara	3.13	13.6	245.5	3.255	46.42	14.26
O6A	OTC	Carex rupestris	3.13	14	453.8	2.217	46.83	21.13
O6A	OTC	Salix herbacea	0.63	12.09	514.5	1.945	51.45	26.45
O2D	OTC	Empetrum nigrum	52.63	6.53	506.8	0.751	52.19	69.47
O2D	OTC	Dryas octopetala	21.93	8.58	461.5	1.293	49.76	38.48
O2D	OTC	Bartsia alpina	4.39	20.9	276.4	2.466	45.93	18.63
O2D	OTC	Saussurea alpina	4.39	14.16	204.2	1.879	43.06	22.92
O2D	OTC	Bistorta vivipara	3.51	15.3	246.5	3.057	46.36	15.17
O2D	OTC	Juncus trifidus	3.51	13.76	396.7	2.236	46.69	20.88
O2D	OTC	Poa alpina	2.63	11.67	399.9	1.048	43.8	41.78
O2D	OTC	Silene acaulis	2.63	14.36	246.6	1.286	42	32.65
O2D	OTC	Antennaria dioica	1.75	17.4	296.7	1.201	46.54	38.76
O2D	OTC	Salix reticulata	1.75	12.27	385.3	1.898	47.4	24.98
O2D	OTC	Salix herbacea	0.88	14.7	381.4	1.962	46.16	23.53
O7A	OTC	Dryas octopetala	76.42	6.89	570.7	1.286	49.62	38.58
O7A	OTC	Bistorta vivipara	2.83	12.16	292	2.966	46.36	15.63
O7A	OTC	Carex vaginata	2.83	15.28	349.9	2.3	45.59	19.82
O7A	OTC	Festuca sp.	2.83	10.25	450.6	1.213	44.67	36.84
O7A	OTC	Salix reticulata	2.83	10.87	368.7	2.126	46.62	21.93
O7A	OTC	Astragalus alpinus	1.89	12.83	293.1	3.419	44.54	13.03
O7A	OTC	Oxytropis lapponica	1.89	14.08	274	3.025	45.33	14.98
O7A	OTC	Carex rupestris	1.89	13.18	470.3	1.746	45.68	26.16
O7A	OTC	Potentilla crantzii	1.89	11.92	393	2.072	45.19	21.81
O7A	OTC	Saussurea alpina	1.89	10.37	266.9	2.019	43.32	21.46
O7A	OTC	Thalictrum alpinum	1.89	12.63	373.7	2.105	43.97	20.89
O7A	OTC	Silene acaulis	0.94	13.48	267.4	1.09	43.4	39.8
O4B	OTC	Dryas octopetala	74.83	8.51	524.9	1.308	50.53	38.64
O4B	OTC	Carex vaginata	8.84	15.76	341.5	2.946	45.32	15.39
O4B	OTC	Silene acaulis	4.76	15.72	221.2	1.648	45.17	27.4
O4B	OTC	Bistorta vivipara	4.08	12.33	264.7	3.789	47.33	12.49
O4B	OTC	Salix reticulata	3.4	10.82	343.4	2.207	46.21	20.93
O4B	OTC	Saussurea alpina	2.72	13.48	224.2	2.342	44.24	18.89
O4B	OTC	Salix herbacea	1.36	15.29	392.1	2.192	48.46	22.11
O10C	OTC	Dryas octopetala	86.63	7.85	500.8	1.383	49.88	36.07
O10C	OTC	Festuca sp.	8.42	9.7	431	1.189	44.6	37.51
O10C	OTC	Bistorta vivipara	2.48	14.91	253.8	2.233	46.47	20.81
O10C	OTC	Silene acaulis	2.48	17.52	218.8	1.684	42.07	24.97
O8B	OTC	Dryas octopetala	78.18	7.76	469.9	2.136	47.04	22.02
O8B	OTC	Silene acaulis	7.27	13.74	246.6	1.093	39.38	36.03
O8B	OTC	Bistorta vivipara	4.55	14.04	241.5	2.527	43.95	17.4
O8B	OTC	Carex rupestris	3.64	15.57	360.7	1.088	48.4	44.47
O8B	OTC	Juncus trifidus	3.64	15.74	349.2	2.342	47.59	20.32
O8B	OTC	Salix herbacea	1.82	14.84	359	2.275	47.68	20.96
O8B	OTC	Salix reticulata	0.91	13.75	330.3	2.349	45.17	19.23
O7B	OTC	Dryas octopetala	89.74	8.36	471.1	1.404	49.97	35.59
O7B	OTC	Silene acaulis	3.21	15.07	220	1.414	38.68	27.36
O7B	OTC	Oxytropis lapponica	1.92	16.79	298.3	3.743	45.24	12.09
O7B	OTC	Carex rupestris	1.92	15.46	363.5	2.409	46.03	19.11
O7B	OTC	Salix reticulata	1.92	10.29	400.9	1.66	46.16	27.81
O7B	OTC	Bistorta vivipara	1.28	14.7	259.4	3.349	46.33	13.83
O3A	OTC	Dryas octopetala	88.89	8.9	436.8	1.476	49.03	33.22

O3A	OTC	Carex rupestris	8.15	13.39	393.4	2.186	45.94	21.01
O3A	OTC	Bistorta vivipara	2.96	14.69	237.8	3.193	46.18	14.46
O2A	OTC	Dryas octopetala	81.01	9.04	437.2	1.392	49.47	35.54
O2A	OTC	Vaccinium uliginosum	13.41	16.62	353.4	2.788	49.57	17.78
O2A	OTC	Silene acaulis	5.03	13.3	234.5	1.203	39.85	33.11
O2A	OTC	Bistorta vivipara	0.56	14.69	264.1	2.743	46.62	17

APPENDIX 2. Relative cover (%) and trait values for STA (specific thallus area), WHC (water holding capacity), N (nitrogen content), C (carbon content) and C:N (carbon to nitrogen ratio) of all collected lichen species in all plots. Sorted by plots in pairs.

Plot	Treatment	Species	Rel. cover (%)	STA	WHC	N	C	C:N
K10A	Control	Flavocetraria nivalis	21.62	9.945	14.84	0.4054	42.01	103.6
K10A	Control	Cetraria islandica	16.22	8.676	19.57	0.473	41.59	87.94
K10A	Control	Flavocetraria cucullata	10.81	8.378	15.59	0.4991	41.95	84.05
K10A	Control	Bryocaulon divergens	8.11	7.074	13.5	0.4891	39.33	80.43
K10A	Control	Cladonia arbuscula	5.41	7.567	22.91	0.4635	43.21	93.24
K10A	Control	Thamnolia vermicularis	5.41	5.223	28.88	0.5596	42.22	75.45
K10A	Control	Stereocaulon sp.	5.41	4.4	39.72	0.6513	48.27	74.11
K10A	Control	Peltigera aphthosa	5.41	10.211	25.77	2.1817	45.94	21.06
K10A	Control	Cladonia uncialis	5.41	8.794	14.79	0.3772	43.51	115.3
K10A	Control	Alectoria ochroleuca	5.41	9.31	10.54	0.4001	43.26	108.1
K10A	Control	Sphaerophorus globosus	5.41	6.721	17.91	0.3627	42.62	117.5
K10A	Control	Alectoria nigricans	5.41	12.987	8.21	0.5427	43.14	79.49
K10C	Control	Flavocetraria cucullata	41.76	8.846	13.49	0.3624	45	124.2
K10C	Control	Cetraria islandica	24.18	8.078	15.68	0.4257	41.81	98.21
K10C	Control	Flavocetraria nivalis	17.58	9.748	11.29	0.2998	42.52	141.8
K10C	Control	Cladonia arbuscula	5.49	8.779	15.75	0.3526	43.8	124.2
K10C	Control	Stereocaulon sp.	4.4	3.076	65.14	1.0716	44.28	41.32
K10C	Control	Thamnolia vermicularis	3.3	4.625	27.26	0.4765	43.75	91.83
K10C	Control	Cladonia uncialis	2.2	7.524	19.7	0.391	49.16	125.7
K10C	Control	Peltigera malacea	1.1	13.134	21.05	3.0106	45.39	15.08
K10D	Control	Flavocetraria nivalis	59.26	10.796	12.84	0.4336	43.44	100.2
K10D	Control	Cetraria islandica	7.41	8.839	19.53	0.4811	43.79	91.02
K10D	Control	Peltigera malacea	7.41	6.976	57.61	2.5673	45.31	17.65
K10D	Control	Bryocaulon divergens	4.44	9.023	12.65	0.4953	43.4	87.62
K10D	Control	Cladonia arbuscula	2.96	8.223	21.24	0.4104	43.81	106.8
K10D	Control	Cladonia uncialis	2.96	5.967	20.33	0.3926	44.42	113.1
K10D	Control	Alectoria ochroleuca	2.96	8.645	9.47	0.4196	45.24	107.8
K10D	Control	Sphaerophorus globosus	2.96	5.745	25.42	0.3216	42.96	133.6
K10D	Control	Cladonia rangiferina	2.22	7.495	22.24	0.5115	43.94	85.9
K10D	Control	Cladonia gracilis	1.48	5.086	25.58	0.507	44.06	86.91
K10D	Control	Thamnolia vermicularis	1.48	5.215	24.26	0.4973	44.13	88.74
K10D	Control	Cladonia sp.	1.48	3.32	41.27	0.5316	44.9	84.48
K10D	Control	Flavocetraria cucullata	1.48	11.742	17.82	0.5205	44.84	86.15
K10D	Control	Vulpicida juniperinus	1.48	9.065	12.21	0.4349	39.71	91.31
K1A	Control	Cladonia arbuscula	30.77	7.385	17.09	0.4158	43.21	103.9
K1A	Control	Cetraria islandica	24.62	7.193	14.9	0.4733	42.9	90.64
K1A	Control	Stereocaulon sp.	9.23	3.373	54.89	0.9969	43.75	43.89
K1A	Control	Flavocetraria nivalis	9.23	9.595	12.26	0.4643	42.03	90.54
K1A	Control	Cladonia gracilis	6.15	4.425	32.56	0.4287	41.91	97.75
K1A	Control	Thamnolia vermicularis	6.15	5.046	25.58	0.5209	41.22	79.12
K1A	Control	Cladonia uncialis	6.15	6.998	16.41	0.377	43.21	114.6
K1A	Control	Peltigera aphthosa	4.62	7.715	32.55	2.3089	45.24	19.59
K1A	Control	Peltigera malacea	3.08	10.516	26.06	2.6976	45.75	16.96
K1C	Control	Cetraria islandica	33.33	7.187	13.8	0.4507	43.47	96.46
K1C	Control	Cladonia arbuscula	16.67	6.827	19.57	0.5099	43.69	85.69
K1C	Control	Stereocaulon sp.	16.67	3.766	40.75	1.0653	41.87	39.31
K1C	Control	Cladonia gracilis	11.11	4.236	27.27	0.4708	44.17	93.82
K1C	Control	Thamnolia vermicularis	11.11	5.868	28.72	0.6251	42.99	68.77
K1C	Control	Cladonia sp.	11.11	3.515	41.17	0.428	43.87	102.5
K3C	Control	Flavocetraria nivalis	36.73	9.832	11.81	0.3791	43.02	113.5
K3C	Control	Cetraria islandica	16.33	6.979	17.36	0.4559	44.18	96.9
K3C	Control	Cladonia uncialis	8.16	6.374	17.82	0.3857	43.34	112.4
K3C	Control	Flavocetraria cucullata	6.12	9.084	12.54	0.44	44.11	100.2
K3C	Control	Cladonia gracilis	4.08	4.163	25.45	0.5118	43.85	85.68
K3C	Control	Cladonia arbuscula	4.08	6.156	20.48	0.5206	43.34	83.24
K3C	Control	Thamnolia vermicularis	4.08	5.355	25.31	0.5327	42.85	80.43
K3C	Control	Stereocaulon sp.	4.08	3.506	57.4	0.7573	45.79	60.47

K3C	Control	Alectoria ochroleuca	4.08	9.21	10.07	0.4039	47.5	117.6
K3C	Control	Bryocaulon divergens	4.08	8.566	12.87	0.5292	40.96	77.41
K3C	Control	Sphaerophorus globosus	4.08	4.593	23.84	0.369	42.54	115.3
K3C	Control	Alectoria nigricans	4.08	14.549	7.11	0.593	46.39	78.23
K3D	Control	Cetraria islandica	52.78	6.688	19.06	0.3963	42.14	106.3
K3D	Control	Cladonia arbuscula	19.44	6.548	24.51	0.491	43.06	87.7
K3D	Control	Flavocetraria nivalis	8.33	10.32	13.6	0.5319	41.2	77.47
K3D	Control	Stereocaulon sp.	5.56	3.693	47.38	0.8818	43.14	48.92
K3D	Control	Peltigera aphthosa	5.56	7.198	36.54	2.0817	44.88	21.56
K3D	Control	Flavocetraria cucullata	4.17	7.916	14.27	0.565	41.12	72.79
K3D	Control	Cladonia uncialis	4.17	8.019	16.84	0.5276	43.85	83.12
K5D	Control	Flavocetraria nivalis	31.03	10.835	13.4	0.4419	42.14	95.37
K5D	Control	Cetraria islandica	13.79	6.97	20.46	0.4573	42.62	93.2
K5D	Control	Peltigera aphthosa	13.79	6.885	36.16	2.2844	44.73	19.58
K5D	Control	Flavocetraria cucullata	10.34	8.708	15.88	0.5185	41.48	80.01
K5D	Control	Cladonia gracilis	3.45	5.382	26.54	0.5325	42.6	79.99
K5D	Control	Cladonia arbuscula	3.45	6.426	25.9	0.5133	43.49	84.73
K5D	Control	Thamnolia vermicularis	3.45	5.791	31.76	0.5302	43.78	82.57
K5D	Control	Cladonia sp.	3.45	3.306	45.56	0.532	44.92	84.43
K5D	Control	Stereocaulon sp.	3.45	4.412	46.52	1.0096	43.73	43.32
K5D	Control	Cladonia uncialis	3.45	6.776	20.73	0.4613	43.56	94.42
K5D	Control	Alectoria ochroleuca	3.45	8.191	12.28	0.5295	43.32	81.82
K5D	Control	Bryocaulon divergens	3.45	8.326	16.68	0.4909	40.71	82.93
K5D	Control	Sphaerophorus globosus	3.45	5.058	23.2	0.3225	42.29	131.1
K6A	Control	Cetraria islandica	50	7.847	16.14	0.4868	41.68	85.63
K6A	Control	Flavocetraria nivalis	12.5	10.421	10.15	0.431	40.89	94.88
K6A	Control	Cladonia arbuscula	8.33	6.493	23.36	0.5015	44.24	88.22
K6A	Control	Thamnolia vermicularis	8.33	5.419	32.36	0.54	42.55	78.8
K6A	Control	Stereocaulon sp.	8.33	3.952	47.13	0.7928	43.65	55.06
K6A	Control	Flavocetraria cucullata	8.33	9.001	13.21	0.3927	42.95	109.4
K6A	Control	Cladonia gracilis	4.17	4.848	29.3	0.4854	42.75	88.07
K8D	Control	Cetraria islandica	31.25	7.341	15.83	0.4504	41.24	91.58
K8D	Control	Flavocetraria nivalis	18.75	11.67	10.5	0.4668	41.24	88.36
K8D	Control	Thamnolia vermicularis	12.5	4.965	25.92	0.5661	40.52	71.58
K8D	Control	Cladonia gracilis	6.25	6.306	19.99	0.5024	43.28	86.16
K8D	Control	Cladonia arbuscula	6.25	8.273	18.27	0.5805	43.46	74.87
K8D	Control	Stereocaulon sp.	6.25	3.356	50.15	1.2354	41.8	33.84
K8D	Control	Flavocetraria cucullata	6.25	8.423	13.89	0.3809	43.47	114.1
K8D	Control	Cladonia uncialis	6.25	7.386	17.68	0.4537	44.29	97.61
K8D	Control	Alectoria ochroleuca	3.13	9.078	10.81	0.4088	44.63	109.2
K8D	Control	Vulpicida juniperinus	3.13	10.347	10.29	0.5164	40.51	78.45
O5B	OTC	Peltigera malacea	40.82	9.02	40.52	2.6812	45.41	16.94
O5B	OTC	Cetraria islandica	32.65	4.677	31.65	0.3954	42.02	106.3
O5B	OTC	Cladonia arbuscula	8.16	8.723	20.44	0.4371	43.84	100.3
O5B	OTC	Flavocetraria nivalis	6.12	9.069	15.14	0.4402	41.08	93.32
O5B	OTC	Cladonia gracilis	4.08	4.452	29.93	0.4627	41.13	88.9
O5B	OTC	Thamnolia vermicularis	4.08	6.302	23.54	0.6939	42.45	61.17
O5B	OTC	Stereocaulon sp.	4.08	3.586	50.2	0.895	42.64	47.64
O6A	OTC	Cetraria islandica	40	6.074	20.29	0.4238	42.82	101.1
O6A	OTC	Flavocetraria nivalis	29.09	8.81	13.58	0.4504	42.99	95.45
O6A	OTC	Thamnolia vermicularis	10.91	6.615	23.49	0.5624	44.2	78.6
O6A	OTC	Flavocetraria cucullata	7.27	7.708	14.48	0.4273	43.19	101.1
O6A	OTC	Cladonia uncialis	7.27	7.224	18.12	0.4208	45.35	107.8
O6A	OTC	Cladonia arbuscula	3.64	7.95	18.6	0.5263	44.83	85.18
O6A	OTC	Stereocaulon sp.	1.82	4.994	37.05	0.7591	47.63	62.74
O2D	OTC	Cladonia arbuscula	20	7.298	17.66	0.4134	43.14	104.3
O2D	OTC	Cetraria islandica	20	7.309	17.91	0.3995	41.1	102.9
O2D	OTC	Flavocetraria nivalis	16	10.113	11.23	0.356	41.33	116.1
O2D	OTC	Flavocetraria cucullata	12	8.493	13.8	0.4596	42.84	93.21
O2D	OTC	Cladonia gracilis	8	3.789	28.04	0.3978	42.96	108
O2D	OTC	Peltigera aphthosa	8	11.354	20.92	2.5275	44.85	17.75
O2D	OTC	Cladonia uncialis	6	6.575	16.98	0.3748	43.02	114.8

O2D	OTC	Thamnolia vermicularis	4	7.236	22.35	0.611	44	72.02
O2D	OTC	Cladonia rangiferina	4	8.327	18.05	0.4722	42.79	90.6
O2D	OTC	Vulpicida juniperinus	2	10.852	11.3	0.4758	42.47	89.27
O7A	OTC	Flavocetraria nivalis	50.67	9.613	11.24	0.3071	42.25	137.6
O7A	OTC	Cladonia arbuscula	12	8.098	16.76	0.4357	44.15	101.3
O7A	OTC	Cetraria islandica	10.67	8.379	13.12	0.3921	43.83	111.8
O7A	OTC	Cladonia uncialis	6.67	7.599	16.6	0.3044	44.04	144.7
O7A	OTC	Cladonia gracilis	4	4.315	24.33	0.4543	44.63	98.23
O7A	OTC	Thamnolia vermicularis	4	6.198	21.64	0.5647	45.26	80.16
O7A	OTC	Cladonia sp.	4	3.226	39.31	0.5834	45.02	77.17
O7A	OTC	Flavocetraria cucullata	2.67	9.857	13.55	0.4514	46.01	101.9
O7A	OTC	Vulpicida juniperinus	2.67	10.668	8.97	0.3782	41.89	110.8
O7A	OTC	Sphaerophorus globosus	2.67	4.751	22.48	0.2894	46.22	159.7
O4B	OTC	Cetraria islandica	32.26	7.052	18.56	0.4753	42.76	89.97
O4B	OTC	Peltigera aphthosa	25.81	5.17	43.67	1.7803	44.66	25.09
O4B	OTC	Cladonia arbuscula	12.9	7.637	17.08	0.5427	43.37	79.92
O4B	OTC	Flavocetraria nivalis	9.68	10.263	10.85	0.5019	41.62	82.91
O4B	OTC	Cladonia gracilis	6.45	4.733	17.29	0.4722	44.85	94.98
O4B	OTC	Thamnolia vermicularis	6.45	7.383	21.27	0.775	46.11	59.49
O4B	OTC	Cladonia sp.	3.23	4.327	28.58	0.5662	44.52	78.63
O4B	OTC	Flavocetraria cucullata	3.23	10.141	11.14	0.6022	45.3	75.22
O10C	OTC	Cetraria islandica	20	6.773	17.05	0.3709	42.95	115.8
O10C	OTC	Peltigera aphthosa	20	7.268	32.7	2.2079	45.14	20.45
O10C	OTC	Flavocetraria cucullata	13.33	8.092	13.77	0.3939	43.85	111.3
O10C	OTC	Flavocetraria nivalis	13.33	10.933	9.32	0.4659	43.35	93.04
O10C	OTC	Cladonia gracilis	6.67	4.516	24.14	0.483	44.04	91.19
O10C	OTC	Thamnolia vermicularis	6.67	6.714	20.72	0.5925	44.38	74.91
O10C	OTC	Peltigera malacea	6.67	9.947	25.47	2.7266	45.32	16.62
O10C	OTC	Stereocaulon sp.	3.33	2.872	58	0.96	45.97	47.89
O10C	OTC	Cladonia uncialis	3.33	7.21	15.14	0.3704	44.91	121.2
O10C	OTC	Alectoria ochroleuca	3.33	13.52	8.55	0.279	56.11	201.1
O10C	OTC	Bryocaulon divergens	3.33	5.951	17.73	0.5284	43.21	81.78
O8B	OTC	Flavocetraria nivalis	43.18	9.856	11.53	0.375	43.71	116.6
O8B	OTC	Cetraria islandica	18.18	7.929	15.1	0.4747	42.63	89.81
O8B	OTC	Cladonia arbuscula	15.91	6.801	17.69	0.4351	44.1	101.4
O8B	OTC	Cladonia uncialis	6.82	6.463	18.48	0.3849	43.79	113.8
O8B	OTC	Thamnolia vermicularis	5.68	5.952	24.99	0.6579	44.78	68.06
O8B	OTC	Cladonia sp.	2.27	3.031	47.02	0.4726	44.63	94.44
O8B	OTC	Stereocaulon sp.	2.27	3.688	43.08	0.6745	46.24	68.57
O8B	OTC	Flavocetraria cucullata	2.27	9.646	10.79	0.4817	43.25	89.78
O8B	OTC	Bryocaulon divergens	2.27	7.763	14.56	0.4017	41.36	103
O8B	OTC	Peltigera aphthosa	1.14	6.99	32.81	2.1373	45.55	21.31
O7B	OTC	Cetraria islandica	33.33	6.894	20.84	0.3895	41.52	106.6
O7B	OTC	Flavocetraria nivalis	22.22	8.812	15.02	0.4374	40.52	92.63
O7B	OTC	Cladonia gracilis	5.56	4.441	41.33	0.4327	42.3	97.77
O7B	OTC	Cladonia arbuscula	5.56	7.955	17.13	0.5043	43.79	86.84
O7B	OTC	Thamnolia vermicularis	5.56	7.152	26.48	0.5957	40.74	68.4
O7B	OTC	Cladonia sp.	5.56	4.441	30.8	0.5839	44.64	76.45
O7B	OTC	Stereocaulon sp.	5.56	3.528	56.25	1.2905	41.93	32.49
O7B	OTC	Flavocetraria cucullata	5.56	8.952	15.22	0.5475	42.28	77.21
O7B	OTC	Cladonia uncialis	5.56	7.747	18.91	0.4207	44.04	104.7
O7B	OTC	Bryocaulon divergens	2.78	6.845	14.17	0.5003	37.11	74.18
O7B	OTC	Vulpicida juniperinus	2.78	9.343	12.28	0.4207	39.54	94
O3A	OTC	Cladonia arbuscula	31.58	7.21	21.85	0.3982	43.33	108.8
O3A	OTC	Cetraria islandica	31.58	4.95	25.1	0.37	42.59	115.1
O3A	OTC	Flavocetraria nivalis	15.79	10.239	12.49	0.4143	40.55	97.87
O3A	OTC	Stereocaulon sp.	10.53	3.618	44.94	0.9427	44.27	46.96
O3A	OTC	Cladonia uncialis	5.26	6.866	17.34	0.3512	44.77	127.5
O3A	OTC	Vulpicida juniperinus	5.26	9.901	9.99	0.3949	47.4	120.1
O2A	OTC	Cetraria islandica	46.67	7.529	17.87	0.4541	41.6	91.61
O2A	OTC	Cladonia arbuscula	20	7.428	21.57	0.4238	43.25	102
O2A	OTC	Flavocetraria cucullata	13.33	11.718	11.83	0.3929	50.09	127.5

O2A	OTC	Cladonia gracilis	6.67	4.375	29.11	0.4521	43.06	95.23
O2A	OTC	Thamnolia vermicularis	6.67	7.081	23.86	0.6555	42.1	64.23
O2A	OTC	Flavocetraria nivalis	6.67	9.985	14.97	0.3798	38.68	101.9



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