

The role of intraspecific variability in driving community trait shifts along temperature and precipitation gradients in alpine and boreal semi-natural grasslands



Ragnhild Gya

Master of Science in Biology
Biodiversity, Evolution and Ecology



Department of Biology
University of Bergen
November 2017

Front cover photo: Rainbow over Gudmedalen (Sogn og Fjordane, Norway), by Ragnhild Gya

ACKNOWLEDGEMENTS

First, I want to thank my supervisor Vigdis Vandvik who has made this project possible and guided me through the whole process. Thanks for being so supportive, motivating and easy to talk to. I always left your office inspired and eager to continue my work.

A big special thanks to Francesca Jaroszynska for guidance, brainstorming, peer reviewing and mental support from the beginning of the project all the way to the end. And the rest of the FunCab team for all kinds of support in the field season and after. A big thanks to all the people who have helped in the field and with lab work over the long summer of 2016. A big special thanks to Eric Meineri who joined me for three weeks in the field, Mari Vold Bjordal for joining a good part of the field work, and for helping in the lab, and to all the other people who joined me in the field or in the lab. Thanks to Richard Telford for being my support wheels when it came to the statistics. Thanks to Hordaland fylkeskommune and the Norwegian Research Council for the funding of the project.

I couldn't have asked for a better research group (EECRG) to be a part of for this project. I have felt included from the very beginning, and I am grateful for being surrounded by so many brilliant people every day. Thanks for all the help in the writing group, for discussions in the reading group, and for being included in social happenings. And to the people in the reading room; thanks for being a part of this journey.

My high school teacher in biology, Alf Jacob Nilsen, needs a big thanks for introducing me to biology. Don't underestimate the power a teacher can have on your future!

I want to thank friends and family for keeping me grounded and keeping my focus on other things than biology every once in a while. I especially want to thank my fellow students on the teaching program for everything we have shared over the last five years – I wouldn't want to have shared it with anyone else! #lektorlove

Last but not least, I want to thank Lars Olav Hammer for being so patient and understanding when my passion for biology keeps me busy over the whole summer, or takes me away to Svalbard or China for weeks at a time. Your support has meant everything to me, and I couldn't have done this without that support. Thanks for keeping me grounded, and making me take breaks - and for all the fun we have in those breaks.

ABSTRACT

Climate projections show that western Norway will experience warmer and wetter conditions in the future. Investigations of trait changes with these climatic gradients can be used to understand the responses of species, communities and ecosystems to climate change. A main assumption within trait-based ecology has been that the variation in traits is larger between species than within species, and hence that mean-species-level trait values can be used in various applications of trait-based ecology. Recent studies find intraspecific trait variability to represent an unneglectable proportion of the total trait variability, and to play an important role in the ecosystems.

In this study, I investigated how the trait of alpine and boreal semi-natural grassland plants change with temperature (6.5-10.5 mean temperature in the four warmest months), and precipitation (650-2900 mm/year). All together 2780 leaves from 88 species were collected and used to calculate these functional traits; specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness, carbon to nitrogen ratio and vegetative height, which are all related to the leaf economic spectrum.

Community trait distributions change due to different abiotic and biotic stressors in the interaction between temperature and precipitation. These trends are driven by both intraspecific variability and species turnover effect, and some, but far from all species show patterns in the intraspecific variability that match the community-wide patterns. This study provides evidence that intraspecific trait variability in alpine and boreal semi-natural grasslands is relatively high compared to other habitats, and that it contributes to shape gradient-wide patterns.

The warmer and wetter alpine grasslands of the future are likely to lead to changes in species composition, traits, and ecosystem functioning of these habitats caused by increased abundance of species and genotypes with higher photosynthetic capacity. This change could be caused by shifts in trait distribution by species migrating into these habitats, or species already present, driven by the high proportion of intraspecific variability or by a shift in species abundance. For trait-based ecology these findings imply that the need for including intraspecific variability, by sampling local traits, should be considered for alpine grasslands.

TABLE OF CONTENT

Acknowledgements	i
Abstract	ii
Table of content	iii
Introduction	1
Methods	5
Site description	5
Vegetation analysis	6
Collection and measurement of leaf traits	7
Plant and leaf sampling and processing	7
Leaf trait measurements	8
Data management and statistical analysis	9
Results	12
Discussion	20
Shifts in traits with temperature and precipitation	20
Untangling intraspecific variability and species turnover effect	23
Intraspecific trait variability and within site variation	24
Single species and plant strategies	26
Implications for trait-based approaches to climate change impacts	27
Concluding remarks and future research	28
References	30
Appendix 1	37
Appendix 2	38
Appendix 3	41
Appendix 4	46
Appendix 5	50
Appendix 6	51

INTRODUCTION

Climate change is leading to many changes in terrestrial ecosystems, including changes in nutrient cycles (Hibbard et al., 2017), ecosystems functioning (Wu et al., 2011, Hibbard et al., 2017) and changes in biodiversity and range shifts (Pecl et al., 2017). In western Norway, climate projections show that we will be experiencing a warmer and wetter climate in the future (Walther et al., 2002, Kovats et al., 2014), which is expected to result in a change towards higher productivity in the ecosystems (Huxman et al., 2004, Wu et al., 2011). Understanding the effects of environmental factors on plant performance and ecosystem properties are important for predicting responses to climate change.

Analyses of traits can be used to investigate the responses of species and communities to external drivers such as climate change, as well as to understand how plants affect and mediate ecosystem processes and functioning (Violle et al., 2007, de Bello et al., 2010). Traits are morphological, physiological or phenological features measurable at the individual level (Violle et al., 2007), and are referred to as functional traits¹ when they indirectly impact an individual's fitness through growth, reproduction or survival (Violle et al., 2007) (see Appendix 1 for dictionary). The climate, with the abiotic and biotic challenges it entails, works on individuals, and not species per se, by eliminating individuals with traits that are not suitable for that specific habitat and community, and traits can therefore be used to study habitat filtering and community assembly (Violle et al., 2012). Ecosystem processes and their underlying plant functions like leaf construction costs, growth potential, protection, stress tolerance, productivity and photosynthetic rate, can be studied through traits (Wright et al., 2004, Perez-Harguindeguy et al., 2013, Diaz et al., 2016). For example, leaves with high specific leaf area (SLA) are associated with high photosynthetic rates but they are also short lived and vulnerable to herbivores (Wilson et al., 1999). Leaves with high leaf dry matter content (LDMC) are often tough and more tolerant to harsh environments and other disturbances (Perez-Harguindeguy et al., 2013). Leaf thickness can be linked to protective strategies against abiotic and biotic stressors, but thick leaves also have lower photosynthetic and growth rate than thinner, more productive leaves (Diaz et al., 2004, Onoda et al., 2011). The ratio of carbon to nitrogen is used as a proxy for understanding resource allocation in plants. High investments in photosynthetic capacity in the form of the protein Rubisco, give high relative nitrogen concentrations in the leaves, whereas allocation of resources to

¹ Throughout this thesis, functional trait will also be referred to as 'traits'.

protective structures results in high relative carbon concentrations in the leaves (Wright et al., 2004, Kattge et al., 2009). Vegetative height is an important trait related to growth, photosynthetic rate and the competitive ability of species (Westoby, 1998).

These general trait-environment and trait-process relationships allow us to make specific predictions about how plants and their traits will be affected by climate change. For example, warming of boreal and alpine areas will likely lead to the selection of species and individuals that invest relatively more in photosynthetic rates, and less in protection against harsh environments (i.e., higher SLA, lower LDMC, lower C/N ratio and thinner leaves) (Hulshof et al., 2013, Perez-Harguindeguy et al., 2013, Jiang and Ma, 2015). Though few studies have investigated trait responses to increased precipitation, several studies have investigated the impact of drought on traits and found that dry climates select for leaves that have protective strategies (i.e., low SLA, thicker leaves, high LDMC) (Cornwell and Ackerly, 2009, Sandel et al., 2010, Onoda et al., 2011, Jung et al., 2014). Vegetative height is correlated with productivity, and has been found to increase in productive habitats with relatively high temperatures and ‘enough’ precipitation (Huxman et al., 2004, Lhotsky et al., 2016).

One of the main assumptions of trait based ecology has been that the differences in trait values are larger between species than within species (McGill et al., 2006), which led to a consensus of using species-level trait means in trait-based analyses (Violle et al., 2007). Recently, a number of studies have empirically explored intraspecific trait variability (hereafter: intraspecific variability). These studies have found that intraspecific variability is often comparable in magnitude with interspecific variability (Albert et al., 2010a, Messier et al., 2010), or of an unneglectable proportion (Kichenin et al., 2013, Siefert et al., 2015), and the ecological importance of intraspecific variability is being examined (Albert et al., 2011, Violle et al., 2012, Siefert et al., 2015). These studies have implied that intraspecific variability should be taken into consideration when using traits as tools for understanding community dynamics and ecosystem functioning in certain habitats and for certain traits. The scale of which traits vary and the taxonomic level at which the trait variation is found varies considerable between traits. In general, chemical leaf traits and whole plant traits (like plant height) tend to be highly variable traits within species (Kattge et al., 2009, Albert et al., 2010a, Kichenin et al., 2013, Siefert et al., 2015), SLA and LDMC are intermediately variable within species (Albert et al., 2010a, Siefert et al., 2015), whereas leaf mechanical traits like leaf thickness and leaf area are relatively invariable within species (Siefert et al., 2015). In a global assessment, it has also been concluded that intraspecific variability is more pronounced

in certain habitats, and whether intraspecific variability should be included or not depends on the focus of the study (Albert et al., 2011). For instance, intraspecific variability is relatively greater in species-poor and colder habitats (Siefert et al., 2015). Intraspecific variability should therefore be included when studying climatic effects on traits in cold, species-poor habitats.

The observed response of traits along climatic gradients, could be driven by either intraspecific variability, species turnover (quantitative and qualitative) or both (Sultan, 2000, Leps et al., 2011). In many cases the intraspecific variability and the species turnover effect will select for similar dominant trait values (Leps et al., 2011, Jung et al., 2014, Volf et al., 2016), by selecting for certain trait values and species with said value. For example, in more productive environments the competition for light will lead to dominance of tall species (species turnover), and at the same time individuals who grow taller will be selected for (shift in trait mean driven by intraspecific variability). Some studies have found that the relative contribution of intraspecific variability to changes in community means were larger than for the species turnover effect (Jung et al., 2014), whereas others have found the opposite (Cornwell and Ackerly, 2009). In a short timescale, changes in climatic factors will first influence intraspecific variability, and will ultimately result in changes in species composition (Hudson et al., 2011, Jung et al., 2014, Volf et al., 2016), although see Sandel et al. (2010). Further studies to investigate the underlying drivers of community trait responses along climatic gradients are needed.

Studies on intraspecific variability in traits have been conducted within on site (Jung et al., 2014, Volf et al., 2016), along a climatic gradient in different habitats (Cornwell and Ackerly, 2009, Albert et al., 2010a, Hulshof et al., 2013) and globally across biomes (Violle et al., 2012, Siefert et al., 2015). To my knowledge, no studies have investigated one habitat with the same vegetation type across climatic gradients. Cold and species-poor habitats, have been found to show a relatively high proportion of intraspecific variability (Siefert et al., 2015), and it is therefore interesting to further investigate intraspecific variability in such habitats. Alpine and boreal semi-natural grasslands is a habitat covering these criteria. Although specie-poor in comparison to tropical habitats, semi-natural grassland have been found to have the record of species richness on the smaller spatial scale (Wilson et al., 2012). Being present in both boreal and alpine areas yields a broad climatic spectrum, here focusing on temperature and precipitation gradients. Temperature and precipitation gradients are particularly interesting climatic gradients because of their relevance to ongoing climate change. Traits vary in

synchrony and are dependent on other traits (Diaz et al., 2016), and different combinations of trait values could result in the same ecosystem functioning (Forrestel et al., 2017), and it has therefore been suggested to study an individual's trait syndrome (set of traits) rather than single traits (Albert et al., 2011).

In this study, I will investigate intraspecific variability of several leaf traits (SLA, LDMC, leaf thickness and C/N ratio) and vegetative height, on the community and species-specific level, across a large climatic gradient within the same habitat, semi-natural grasslands. The objectives of this study are to; (1) investigate how traits of the flora and the community change with temperature and precipitation within cold semi-natural grasslands; (2) assess the relative importance of intraspecific and interspecific trait variation in cold climate semi-natural grasslands, and understand the role of these components of variation in driving patterns with climate; and (3) assess patterns of within species variability with climate.

METHODS

SITE DESCRIPTION

To investigate how plant traits change with different abiotic stress factors, this study was conducted along temperature and precipitation gradients, in south western Norway (Figure 1, Table 1).

These sites are part of the SeedClim grid and have been used for different experiments (Klanderud et al., 2015, Guittar et al., 2016, Olsen et al., 2016). The twelve sites in these temperature and precipitation gradients form a grid of three temperature levels (mean of the four warmest months: 6.5, 8.5 and 10.5 °C) and

four precipitation levels (mean mm per year: 650, 1300, 1950, 2900) (interpolated climate data provided by the Norwegian Meteorological Institute, www.met.no), which vary independently from each other (Table 1). The two sites furthest apart from each other are separated by 175 km in geographical distance. All the plant communities are within the plant sociological association *Potentillo-Festucetum ovinae* (Fremstad, 1997), or when using NiN-mapping; semi-natural grassland with a tendency towards alpine grasslands of snowbed and leaside type in the alpine (Halvorsen et al., 2015). The most prevalent and common species in these systems are the graminoids *Agrostis capillaris*, *Anthoxanthum odoratum*, *Deschampsia cespitosa* and *Nardus stricta*, and the forbs *Achillea millefolium*, *Bistorta vivipara*, and *Potentilla erecta*. Sites were selected so that except for precipitation and temperature the conditions were as constant as possible; slopes oriented south-westwards, similarly calcareous bedrock and similar grazing and land-use history (Table 1, see Klanderud et al. (2015) for

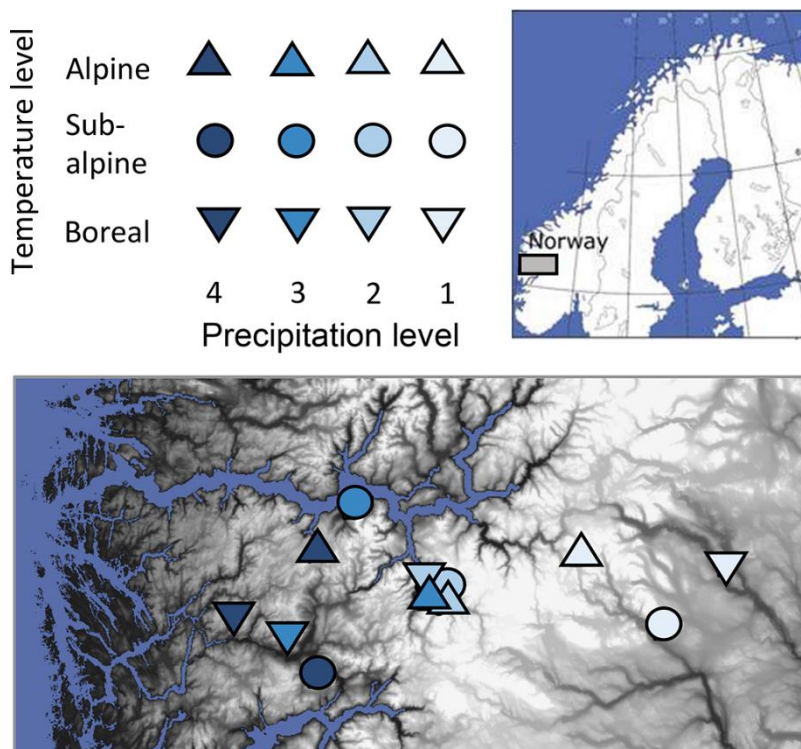


Figure 1: Twelve sites located in south western Norway in a temperature and precipitation gradient. Elevation is used to simulate temperature change, which is visualized with lighter colors for higher elevations. Temperature levels are calculated from mean temperature of the four warmest months and are 6.5, 8.5 and 10.5 °C. The natural precipitation gradient from the wet west coast of Norway to the drier inland east part of Norway gives the four precipitation levels of 650, 1300, 1950 and 2900 mean mm per year. Climate data provided by the Norwegian Meteorological Institute (www.met.no). Figure from Klanderud et al. (2015)

more information). To avoid disturbance from grazing animals the experimental sites are fenced during the summer season, and mowing is used to simulate grazing in these naturally grazed areas.

Table 1: GPS coordinates, altitude, precipitation, temperature, bedrock and vegetation type for twelve sites making up a temperature and precipitation gradient in south-western Norway.

Site	UTM zone 33 Coordinate x	UTM zone 33 Coordinate y	Altitude (m.a.s.)	Precipitation (average mm/year)	Temperature (average summer temperature °C)	Bedrock
Alpine						
Ulvehaugen	128833.00	6785010.00	1208	596	6.17	Rhyolite.
Låvisdalen	80587.50	6767820.00	1097	1321	6.45	Rhyodacite. Dacite
Gudmedalen	75285.30	6769540.00	1213	1925	5.87	Phyllite. Mica schist
Skjellingahaugen	35627.60	6785870.00	1088	2725	6.58	Phyllite. Mica schist Marble
Sub-Alpine						
Årust	157951.00	6759200.00	815	789	9.14	(Meta)sandstone. Shale
Høgsete	75917.50	6774330.00	700	1356	9.17	Phyllite. Mica schist
Rambera	49407.80	6801320.00	769	1848	8.77	Phyllite. Mica schist
Veskre	35390.20	6742090.00	797	3029	8.67	(Meta)sandstone. Shale
Boreal						
Fauske	180405.00	6781200.00	589	600	10.3	Phyllite. Mica schist
Vikesland	75604.70	6774850.00	474	1161	10.55	Phyllite. Mica schist
Arhelleren	27494.10	6756720.00	431	2044	10.60	Phyllite. Mica Schist
Øvstedal	7643.94	6762220.00	346	2923	10.78	Rhyolite. Rhyodacite. Dacite

VEGETATION ANALYSIS

The control plots for experiments conducted in these sites were used for vegetation analysis. In each site, there were two 25x25 cm control plots in four blocks, making a total of eight plots per site. All vascular plants were identified to species, and percent cover was visually estimated for each vascular plant species and collectively for the functional groups (forbs, graminoids and bryophytes). As vegetation can be layered the summed covers of species or functional groups could exceed 100%. The average vegetation height was measured four times in each plot (data not used). Lid and Lid (2005) was used for species identification, and taxonomy followed the species name list of the Norwegian Biodiversity Information Center which was also used to collect systematic information about each species (Artsdatabanken, 2015). *Deschampsia alpina* was included in *D. cespitosa* and *Anthoxanthum nipponicum* was

included in *A. odoratum* since these species are hard to distinguish in vegetative form (Rothera and Davy, 1986, Lid and Lid, 2005). These vegetation analyses were conducted in the peak of the growing season in 2016, between the 20th of June and the 8th of July, with assistance from Eric Meineri and Francesca Jaroszynska.

COLLECTION AND MEASUREMENT OF TRAITS

With the goal of collecting traits to represent the whole community, species selected for trait measurements at each site collectively made up 90% of the community, but for species rich sites the target was changed to cover a minimum of 80% of the community (as suggested by (Garnier et al., 2007, Pakeman and Quested, 2007). Inventory lists from the sites of previous years vegetation analysis were used, and the collection of species followed the list, starting with the most abundant species until the threshold was met. The number of species per site varied between 13 and 47 (see Appendix 2).

The traits measured in this study are all associated with plant productivity and are important in the leaf economic spectrum (Wright et al., 2004, Perez-Harguindeguy et al., 2013). Traits measured were: vegetative height, leaf area, leaf thickness, carbon and nitrogen content, fresh and dry mass of the leaf, which was then used to calculate specific leaf area (SLA, leaf area (cm²)/dry mass (g)), leaf dry matter content (LDMC, dry mass (g)/wet mass (g)) and the carbon to nitrogen ratio (C% in leaf / N% in leaf) (Perez-Harguindeguy et al., 2013). Specific leaf area (SLA) is one of the most common trait to measure (Kattge et al., 2011), as it plays an important part in predicting the leaf economic spectrum (Wright et al., 2004). This trait will therefore be investigated more thoroughly than the other traits in this paper.

Plant and leaf sampling and processing

The leaves used for trait measurements were collected in the area surrounding the fenced-in sites with a maximum 50-meter radius. For each target species and site ten different individuals were collected. Leaves were collected from a representative and sun exposed (i.e., not extensively shaded) individual, with as few as possible visible signs of damage from herbivores, fungi or UV-radiation (Perez-Harguindeguy et al., 2013). To avoid variation caused by phenological and developmental stage, flowering individuals were chosen if the species were flowering when the collection took place, otherwise mature vegetative individuals were sampled, avoiding juvenile and older individuals (Perez-Harguindeguy et al., 2013). When possible, the individuals were at least two meters apart to ensure that they were not from the same genets.

For each individual, the vegetative height was measured. For forbs that was the standing height, which is measured from the ground to the tallest vegetative organ, without stretching (Figure 2). For graminoids the stretched height was measured, which is stretching the longest leaf up, and measuring its height. This was done to get a better picture of the photosynthetic organ of the graminoids, as suggested by Cornelissen et al. (2003).

From each individual one leaf was picked by hand, including the petiole, but not the ligule. Each leaf was put in a moistened plastic bag to keep the leaves hydrated, and stored in a cooler until arrival at the lab. In a few cases, the space in the coolers was

limited and the newly picked leaves could not be cooled until arrival at the lab, which was usually within 24 hours. All the samples were stored in a refrigerator in the lab until they were further processed. Ideally these measurements should be taken within two days after collection (Perez-Harguindeguy et al., 2013), however, for practical reasons this was not always possible, and all leaves were processed within four days of sampling. The collection of leaves was conducted in the peak growing season, from the 11th of July to the 11th of August 2016, with assistance from several people.

Leaf trait measurements

The leaf thickness of each leaf was measured three times on separate parts of the leaf, avoiding the midrib using a digital micrometer (Micromar 40 EWR) with a resolution of 0.001 mm +/- 0.0002. For smaller leaves where three measurements were impossible, leaf thickness was measured one or two times. The average of the measurements per leaf was calculated, and used for further analysis. The wet mass of the leaf was measured by using two balances (Sartorius CP 224 S and Sartorius BP221S), both with a resolution of 0.0001 g +/- 0.0001 g. Excess water on the leaf surface was removed before weighing the leaves. Leaves



Figure 2: Measuring the standing height of an individual of *Veronica alpina* at the alpine site Låvisdalen, Norway. Picture by Ragnhild Gya

were then scanned with the scanner CanoScan LiDE 210, and the leaf area calculated using the program ImageJ (Abràmoff et al., 2004).

The leaves were then dried in an oven (Termaks TS 5410) at 65 °C for 72 hours before being stored in a dark-colored plastic box with silica gel. The dry weight was measured three to six weeks after the drying on the same scale as the first weighing was done to avoid any potential errors due to differences between the scales. After the dry weight was measured the leaves were returned to the box of silica gel until the carbon and nitrogen measurements were conducted.

Carbon and nitrogen content of leaves were measured for three leaves of each species at each site. These leaves were picked out randomly by choosing the first three leaves that were over the minimum weight threshold (5 mg). For the species where none of the leaves were above the minimum weight limit, several leaves were combined into one sample. The leaves were ground with a ball mill (Retsch MM400) in Eppendorf tubes with a metal ball for three minutes at 1680 revolutions per minute. Some leaves were tougher and needed another round in the ball mill. The analysis of carbon and nitrogen content in the leaves was conducted using combustion analysis with the machine Elementar vario MICRO cube. Gas chromatography was used to calculate the amount of carbon and nitrogen, and their ratio, in these samples.

DATA MANAGEMENT AND STATISTICAL ANALYSIS

Before statistical analysis could be conducted some adjustments were done to prepare the dataset for analysis. Any leaf with dry mass that was recorded to be under 0.0005 g was removed from the dataset as the resolution of the scale makes these small numbers inaccurate. Leaf areas under 0.1 (cm²/g) was also removed as it was believed that so small numbers would not give accurate values of SLA. All species that had less than four leaves per site were excluded from the analyses (see Appendix 2). *Alchemilla sp* and *Taraxacum sp* were removed from the dataset as these are groups of several species that could behave differently.

Hypericum maculatum collected at Ålrust were removed from the dataset since this species had been collected from inside the fenced area as opposed to the other species. Any plots that had communities were less than 70% of the community (close to the suggested threshold of 80% (Garnier et al., 2007, Pakeman and Quested, 2007)) was represented by trait data were removed. Vegetative height and C/N ratio were log transformed before analyses were conducted because of non-normal distribution, as suggested by Westoby (1998). Because of

the difference in methods the vegetative height of forbs and graminoids were separated in the analysis.

To investigate how important intraspecific variability and species turnover are when it comes to trait shifts along climatic gradients these analyses were built on the theory from Leps et al. (2011). This was done by comparing means calculated so that each species-site combination had one mean, making it a site-specific mean (hereafter: specific mean), to means calculated for the species across all sites where traits were collected from (hereafter: fixed mean). The nature of species turnover effect on trait shifts along climatic gradients was investigated by having both non-weighted (representing presence/absence) and community weighted means (CWM, including species abundance information).

The objectives of this study were answered by using mixed effect models in four different ways. The first set of models were constructed to assess how traits of the local species pools and communities changed along the abiotic stress gradient (objective 1), and to investigate the role of intraspecific and interspecific variability in driving these patterns (objective 2). In these models, the response variables were the raw trait data (hereafter: all observations), specific means, fixed means, specific CWM and fixed CWM of each trait (SLA, LDMC, C/N ratio, leaf thickness and vegetative height of forbs and graminoids). Temperature and precipitation and their interaction were used as fixed effects, and all models had site as a random effect. Estimates of significance of these models, were obtained from 95% confidence intervals, were a significant trend had a confidence interval that did not include 0.

To investigate the taxonomic level of the trait variance (objective 2), a variation partitioning analysis was used. A mixed effect model was made with order, family, genus and species, nested in each other, as random effects, and no fixed effect. The method from Messier et al. (2010) was used to calculate the variance partitioning within these levels. The variance of different traits on the spatial scale was investigated using another method of variation partitioning, and another set of mixed effect models. The temperature levels that the sites were nested in, were used as a fixed effect, and site was a random effect. To calculate the variance partitioning that was associated with the fixed effect of the models, a method from Nakagawa and Schielzeth (2013) was used. The variance of the fixed effect was calculated by finding the variance of the predicted values of the model with the levels set to zero. The variance of the random effect obtained by the method in Messier et al. (2010) and the variance of the fixed effect was added up to the total amount of variance and afterwards used to

calculate the proportional variance of each the fixed, the random effect and the remaining variance, respectively.

To assess if and how the intraspecific variability responds to the abiotic stress gradients (objective 3), the 15 species for which I had trait measurements for at the most sites were selected for further analysis (Appendix 2). For each species and each trait one mixed effect model was made with temperature, precipitation and their interaction as fixed effects, and site as a random effect. Of these 15 species, the four most common species and their trends with SLA were investigated even further (that was: *Agrostis capillaris* (12 sites), *Anthoxanthum odoratum* (10 sites), *Campanula rotundifolia* (9 sites) and *Deschampsia cespitosa* (8 sites)). For the models with these species the predicted values were calculated and investigated further visually. Estimates of significance of the species specific models, were obtained from 95% confidence intervals, were a significant trend had a confidence interval that did not include 0.

The StrateFy protocol from Pierce et al. (2017), validated by Li and Shipley (2017), was used to calculate CSR strategies for all the species using the average leaf area, wet mass and dry mass of each species. All analysis were conducted using R version 3.4.0 (R Foundation for Statistical Computing, Vienna, Austria) and R studio (version 1.0.143) with the packages ape (version 4.1) (Paradis et al., 2004), nlme (Pinheiro et al., 2009) and lme4 (Bates et al., 2014).

RESULTS

Both temperature and precipitation and their interactions affected the trait distribution of communities in alpine grasslands, but to different extent. The size of these trends was affected by intraspecific variability and species turnover, the later in the form of both species exchange and change in species dominance.

When investigating trends along the temperature gradient for the different traits, all the trait data gathered in this study, were used in the first analysis, which includes intraspecific variability on a non-weighted community. Among all the traits, when using all trait observations (dictionary in Appendix 1), it was only specific leaf area (SLA) and vegetative height in forbs and graminoids that had a significant increasing trend with increasing temperature (Figure 3, Table 2). SLA increased by $14.5 \text{ cm}^2/\text{g}$ (SE: ± 4.79) per unit increased temperature. The vegetative height of forbs and graminoids increased by 1.7 mm (SE: ± 1.2) and 1.8 mm (SE: ± 1.2) per unit increased temperature, respectively. When using all the trait observations, the interaction between temperature and precipitation for SLA was significant, making the increasing trend with temperature stronger in wetter environments. Along the precipitation gradient SLA, LDMC, leaf thickness and C/N ratio increased, and vegetative height decreased with increased precipitation, although these trends were not significant.

For investigating the effect of excluding intraspecific variability and including information about species abundance, the fixed community-weighted mean (fixed CWM) was used (Appendix 1 for dictionary). The fixed CWM of SLA and vegetative height of forbs and graminoids significantly increased with increasing temperature (Figure 3, Table 2). On the other hand, LDMC, leaf thickness and C/N ratio decreased with increasing temperature, although these trends were not significant. The fixed CWM of SLA changed $11.90 \text{ cm}^2/\text{g}$ (SE: ± 5.60) and the fixed CWM of vegetative height increased 1.3 mm (SE: ± 1.1) per unit increased temperature for both forbs and graminoids. Along the precipitation gradient the fixed CWM of LDMC increased by 0.014 mm (SE: ± 0.0067) per unit increased precipitation. None of the other traits showed significant trends along the precipitation gradient. The direction of the non-significant trends with the fixed CWMs show the same directions as the trends in the model with all the trait observations, except for SLA which changes from a positive to a negative relationship with increasing precipitation (Table 2).

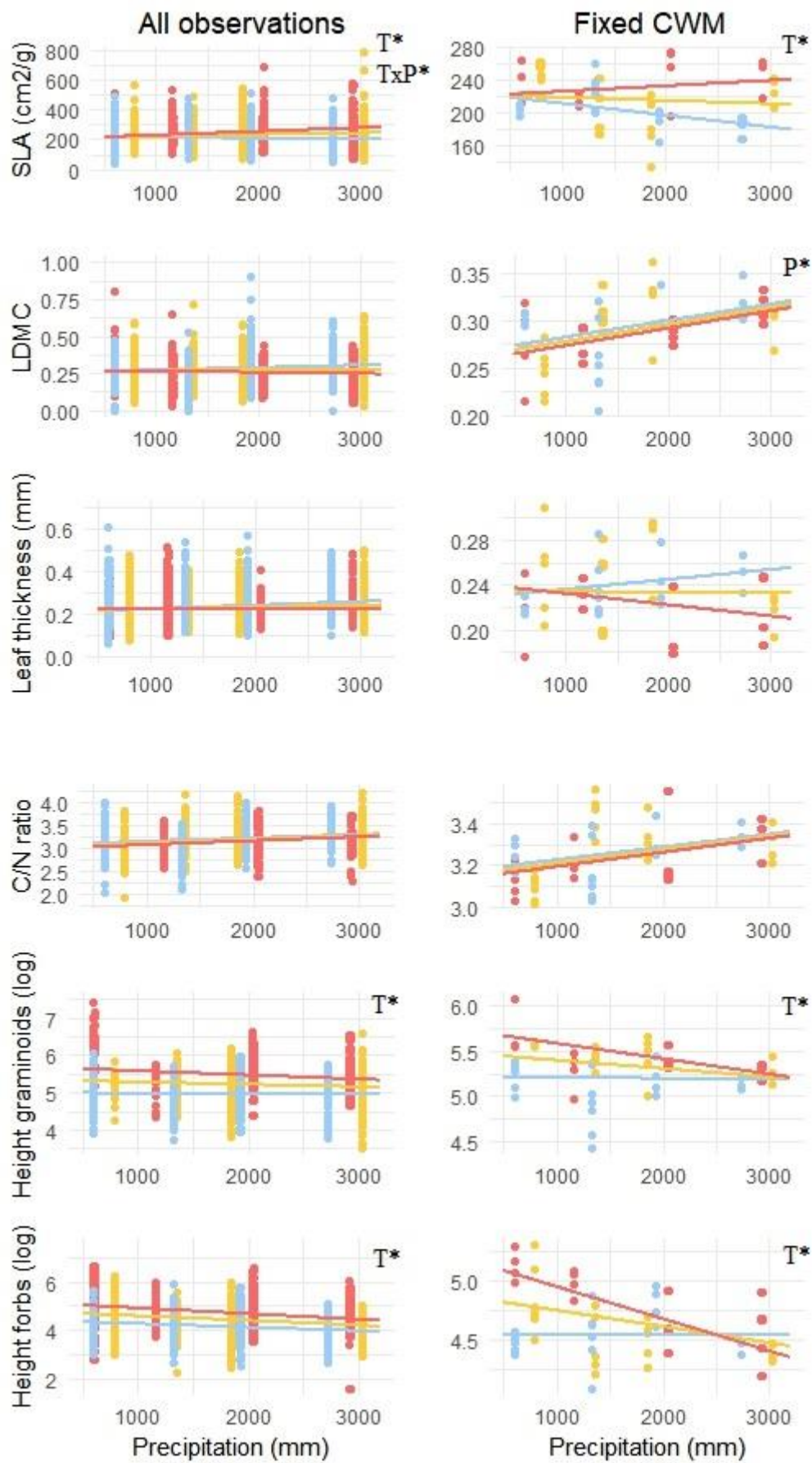


Figure 3: Figure legend on the next page.

Figure 3 (previous page): Six traits (Specific leaf area (SLA – cm²/g), leaf dry matter content (LDMC), leaf thickness (mm), C/N ratio and vegetative height of forbs and graminoids) and how they change with precipitation and temperature (red = 10.5 °C, yellow = 8.5 °C and blue = 6.5 °C in mean temperature of the four warmest months). ‘All observations’ show all trait measurements of all leaves, the fixed community weighted mean (CWM) show the community weighted mean trait value calculated by using the average of all trait measurements per species from all sites, weighted by species cover. Predictions were made from a mixed effect model with temperature, precipitation and their interaction as the fixed effect and site a random effect. Significant trends (*) are trends with 95% confidence intervals that didn’t include 0. Traits were collected from alpine and boreal semi-natural grasslands in south-western Norway over the summer of 2016.

To further investigate the role of intraspecific and interspecific trait variability, and the two component of species turnover effect (species presence/absence and species abundance), the trends along the climatic gradients with the different trait means were compared (see Appendix 1 for a dictionary explaining the different means).

All models of SLA and vegetative height of forbs and graminoids showed a significant increase with temperature (Table 2). For these traits, the specific CWM gave the strongest trend along the temperature gradient. All traits showed the same direction of trends along the temperature gradient, no matter which way of calculating trait values was used. LDMC decreased, leaf thickness and C/N ratio increased with temperature although these trends were non-significant.

With increasing precipitation SLA, LDMC, leaf thickness and C/N ratio showed increasing trends, while vegetative height of forbs and graminoids decreased, although all these trends were non-significant (Table 2). The fixed CWM of SLA and the fixed mean of leaf thickness showed a decreasing trend with precipitation, in contrast to other calculations of SLA and leaf thickness. The fixed mean of vegetative height in forbs had a significant decrease with increasing precipitation.

SLA and C/N ratio has a positive interaction between temperature and precipitation, although only significant for SLA when using all trait observations and specific mean (Table 2). The interaction between temperature and precipitation was of a negative nature for vegetative height, although not significant. LDMC and leaf thickness show different interactions between temperature and precipitation depending on which trait mean is used for the model.

Table 2: Slope for the change in leaf traits per unit scaled temperature (°C) and scaled precipitation (mm), calculated for trait values using all trait observations, means per species per site (specific mean), means per species across sites (fixed mean), community weighted means using the specific mean (specific CWM), and community weighted means using the fixed mean (fixed CWM). Significance (in bold) was derived from 95% confidence intervals that doesn't include 0. Leaves for trait observations were sampled during the summer of 2016 in alpine and boreal semi-natural grasslands in south western Norway.

	SLA	LDMC (*10 ⁻³)	Leaf thickness (*10 ⁻³)	C/N ratio (log) (*10 ⁻²)	Height graminoids (log) (*10 ⁻²)	Height forbs (log) (*10 ⁻²)
Temperature						
All trait observations	14.45	-9.54	-4.580	-2.930	22.80	25.61
Specific mean	13.93	-9.41	-4.545	-2.962	22.10	24.78
Fixed mean	8.68	-5.92	-3.679	-2.643	10.28	12.74
Specific CWM	18.34	-6.95	-7.415	-2.907	26.19	26.34
Fixed CWM	11.90	-3.65	-6.600	-1.252	13.86	14.91
Precipitation						
All trait observations	7.67	4.39	8.18	6.54	-4.55	-14.88
Specific mean	9.12	4.33	8.23	7.03	-3.68	-15.01
Fixed mean	2.33	7.76	-1.03	4.93	-3.78	-10.87
Specific CWM	0.85	8.89	10.60	8.16	-1.12	-1.15
Fixed CWM	-4.07	14.39	0.35	5.20	-3.40	-3.98
Interaction between temperature and precipitation						
All trait observations	9.68	-8.84	-5.70	0.46	-3.43	-2.95
Specific mean	9.581	-8.91	-5.70	0.16	-3.92	-1.48
Fixed mean	2.613	4.97	0.94	1.58	-7.52	-4.00
Specific CWM	11.20	-15.96	-12.88	0.39	-4.21	-3.02
Fixed CWM	7.535	0.30	6.68	0.24	-7.03	-5.97

Specific leaf area showed a large range of trait values, ranging from 21 to 787 cm²/g, with a mean of 225 cm²/g (Figure 4). Going from all trait observations to the site-specific means (specific mean), to the species means across sites (fixed mean), the variance shrank but the mean stayed the same. For the community weighted mean the variance shrank even more, and the mean changed to 218 cm²/g (specific CWM), and 215 cm²/g (fixed CWM). The same trend of shrinking trait distributions when going from all trait observations to the fixed CWM, was found in the other traits as well (Appendix 3). For all traits, I found that there was a more or less obvious jump in the mean trait value from the non-weighted means to the community weighted means (Appendix 3, Figure 4). For LDMC, leaf thickness, and C/N ratio the mean trait value increased when incorporating information about species abundance by using the

community weighted data (Appendix 3). Whereas the mean trait value of vegetative height in both graminoids and forbs decreased when using the community weighted data.

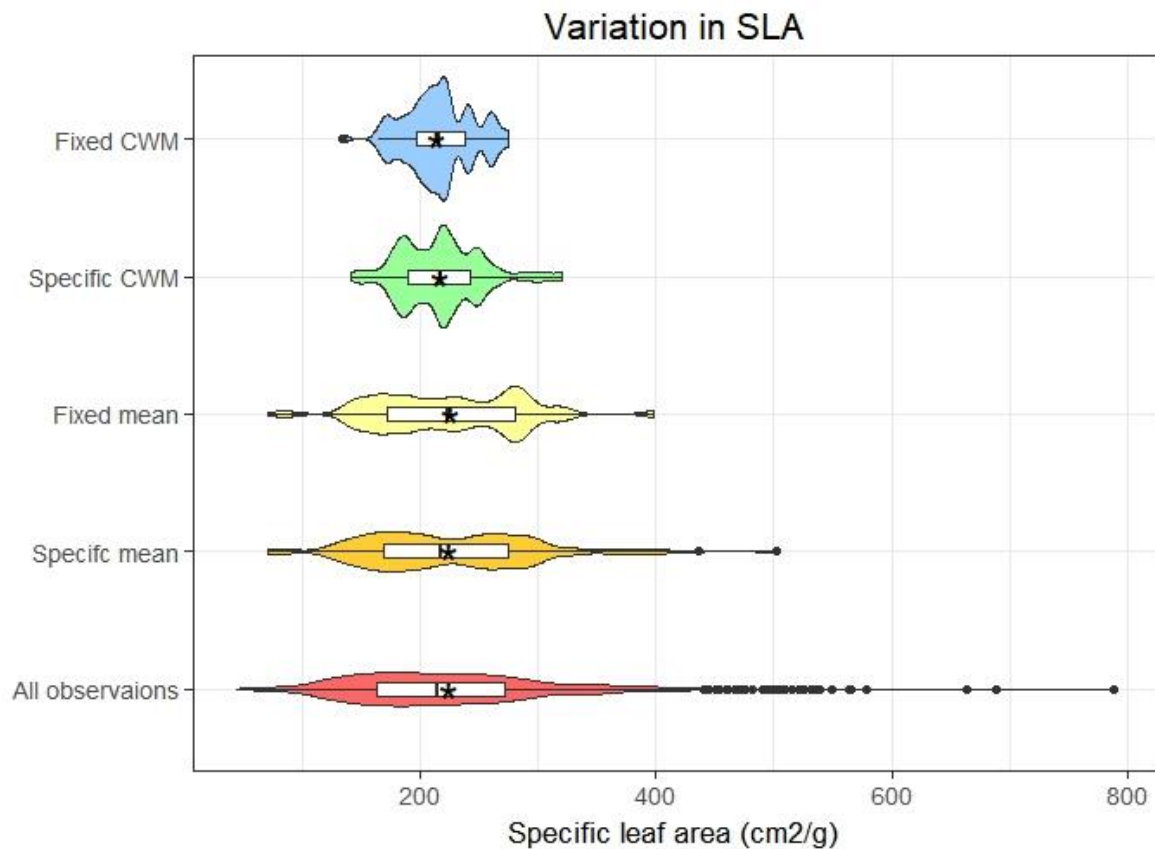


Figure 4: The distribution of specific leaf area (SLA, cm^2/g) with the median, mean (*) and quantiles. This is shown for trait values using all trait measurements (all observations), means per species per site (specific mean), means per species across sites (fixed mean), community weighted means using the specific mean (specific CWM), and community weighted means using the fixed mean (fixed CWM). Leaves were collected from alpine and boreal semi-natural grasslands in the south-western part of Norway in the summer of 2016.

When investigating the shifts in traits across the temperature and precipitation gradients for species as opposed to the community, thirteen out of the fifteen species with the most trait data gathered across sites, showed the same increasing trend in SLA with increased temperature, as was seen for the community (Figure 5). Out of those thirteen, four showed a significant increase in SLA with increasing temperature; *Avenella flexuosa*, *Agrostis capillaris*, *Anthoxanthum odoratum* and *Bistorta vivipara*. Different species showed different trends, both in direction and certainty (size of confidence intervals), with temperature and precipitation. For precipitation, there was greater divergence between species, where ten species had a negative trend of SLA with precipitation, and the remaining five had positive trends, none of these trends were significant (Figure 5). For most species, the interaction between temperature and precipitation was positive, although none were significant (Figure 5).

The same analysis was conducted for the other traits and can be found in Appendix 4. For C/N ratio only one species; *Trifolium repens*, increased significantly with precipitation, and this correlated negatively with temperature (Figure VI in Appendix 4). The overall trend of increasing height with increased temperature was seen in eleven species, and significant for three (Figure VII in Appendix 4). Whereas the trends with precipitation and the interaction between temperature and precipitation was negative for approximately half of the species and positive for the other half. Leaf thickness decreased with temperature for nine of fifteen species, in which three of them were significant (Figure VIII in Appendix 4). With increased precipitation, leaf thickness increased in twelve of fifteen species, showing significant trends for four species.

Approximately half of the interactions between temperature and precipitation were negative for leaf thickness. Thirteen out of fifteen species had a decreasing trend for LDMC along the temperature gradient, but only one species, *Anthoxanthum odoratum*, trends were significant (Figure IX in Appendix 4). With increasing precipitation, LDMC increased in half of the species and decreased in the other half (not significant). The effect of the interaction between temperature and precipitation on LDMC was mostly negative (for twelve species), and significant for one of these species.

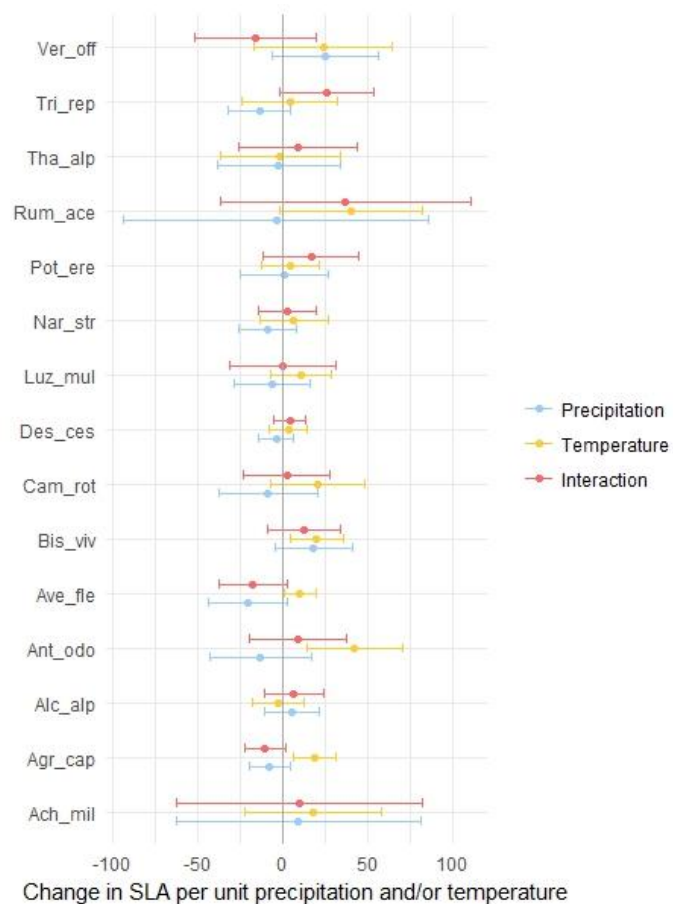


Figure 5: Changes in SLA per unit precipitation and/or temperature (scaled values) for each of the 15 most common species that were collected in alpine and boreal semi-natural grassland in south-western Norway over the summer of 2016. The points show the estimate of the change in SLA per unit precipitation and/or temperature, the whiskers show the 95% confidence interval. The predictions were made from a mixed effect model where temperature, precipitation and their interaction were fixed effects and site was a random effect. Ach_mil = *Achillea millefolium*, Agr_cap = *Agrostis capillaris*, Alc_alp = *Alchemilla alpine*, Ant_odo = *Anthoxanthum odoratum*, Ave_fle = *Avenella flexuosa*, Bis_viv = *Bistorta vivipara*, Cam_rot = *Campanula rotundifolia*, Des_ces = *Deschampsia cespitosa*, Luz_mul = *Luzula multiflora*, Nar_str = *Nardus stricta*, Pot_ere = *Potentilla erecta*, Rum_ace = *Rumex acetosa*, Tha_alp = *Thalictrum alpinum*, Tri_rep = *Trifolium repens*, Ver_off = *Veronica officinalis*.

The four species with the greatest sampling coverage showed different trends in SLA along the climate gradients. For *Agrostis capillaris*, *Anthoxanthum odoratum* and *Campanula rotundifolia* the individuals in higher temperature had higher values of SLA (Figure 6 a, b and c), although this trend is not significant for *C. rotundifolia* (confidence interval in Figure 5). When precipitation increased the difference with temperature became less prominent for *A. capillaris* (Figure 6 a), whereas the opposite was true for *A. odoratum* (Figure 6 b), although these trends in interactions were not significant (Figure 5). For *C. rotundifolia* there was no interaction between temperature and precipitation (Figure 6 c). *Deschampsia cespitosa* had a small decrease in SLA with increasing precipitation, and no obvious trend with temperature (Figure 6 d), but none of these trends were significant (see confidence intervals on Figure 5).

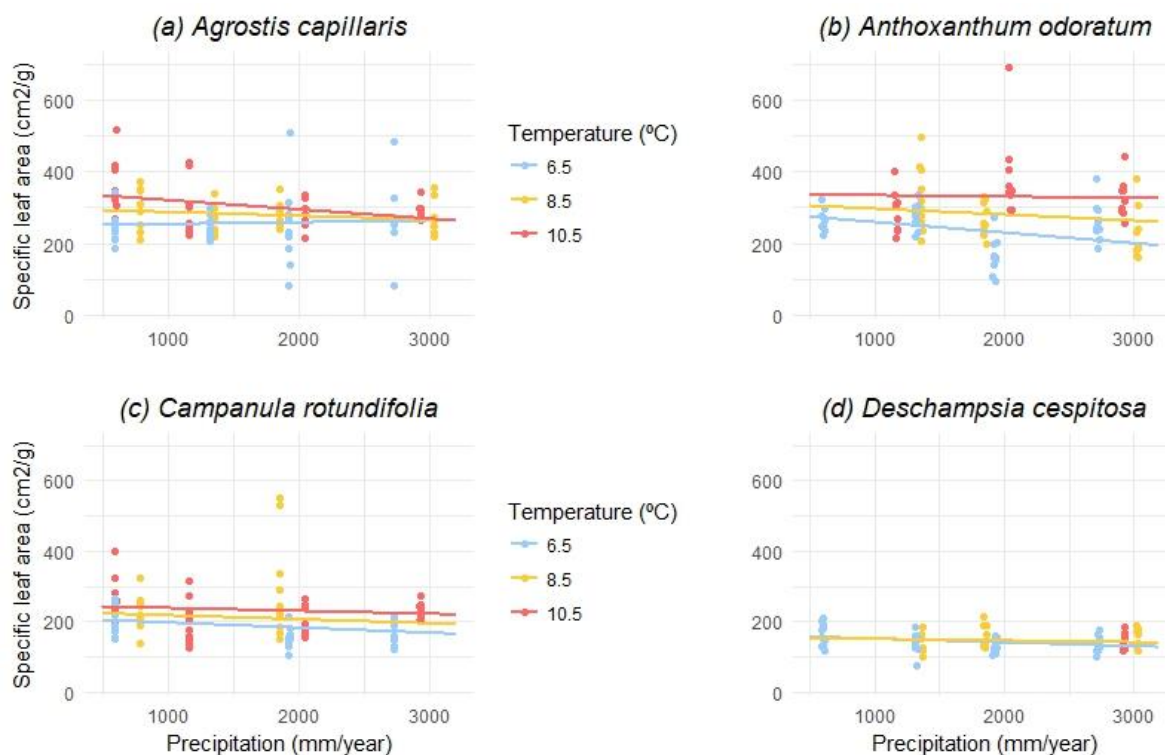


Figure 6: Changes in specific leaf area (SLA) with precipitation and temperature for four species; (a) *Agrostis capillaris*, (b) *Anthoxanthum odoratum*, (c) *Campanula rotundifolia* and (d) *Deschampsia cespitosa*. The predictions were made from a mixed effect model where temperature, precipitation and their interaction were fixed effects and site was a random effect. SLA calculations were made on leaves collected from alpine and boreal semi-natural grasslands in south-western Norway over the summer of 2016.

Intraspecific variability for all traits in this study were between 30-45% of the total variance in the trait, except for vegetative height in graminoids where it was only 11% (Figure 7). Specific leaf area was the trait that had the highest proportion of intraspecific variability, with 45%, followed by C/N ratio with 41% (Figure 7). For all traits except vegetative height in graminoids, most of the variance was found within species, followed by the variation between species (Figure 7). The variance found in the higher taxonomic levels, family and order, were

generally low and always less than 36% (for LDMC) (Figure 7). This was even more extreme for the vegetative height of forbs and graminoids, where none of the variance was found in the higher taxonomic levels (Figure 7). Different traits show different variance allocation patterns (Figure 7).

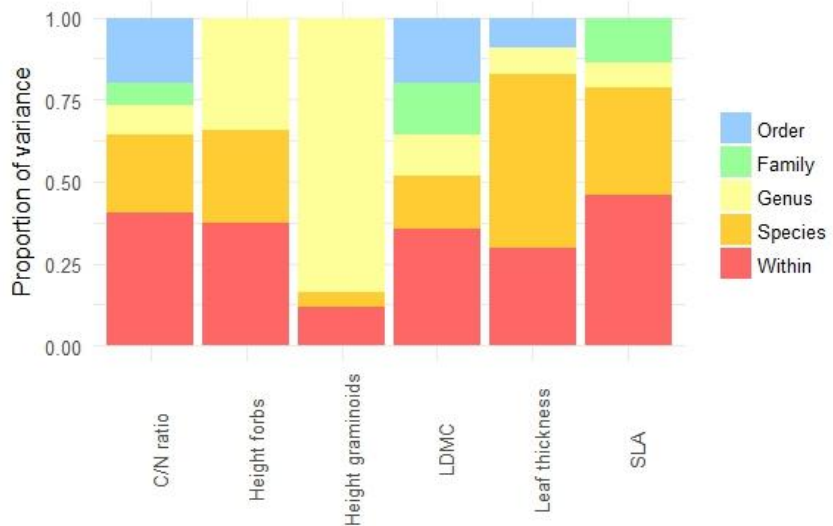


Figure 7: Variance partitioning of traits between levels of within species, between species, between genus, between families and between orders. The variance was calculated to make the total amount of variance 1, to get the proportional variance. Traits were collected from alpine and boreal semi-natural grasslands in south-western Norway over the summer of 2016

The variation in traits on

a spatial scale was mostly found within each site, and almost none of the variance was found between temperature levels (Figure 8). Only vegetative height of forbs and graminoids had more than 15% of the variance explained by site, and more than 14% by temperature. Precipitation only explained 0.1% to 3.1% of the variance in the traits (for LDMC and C/N ratio respectively) (Appendix 5).

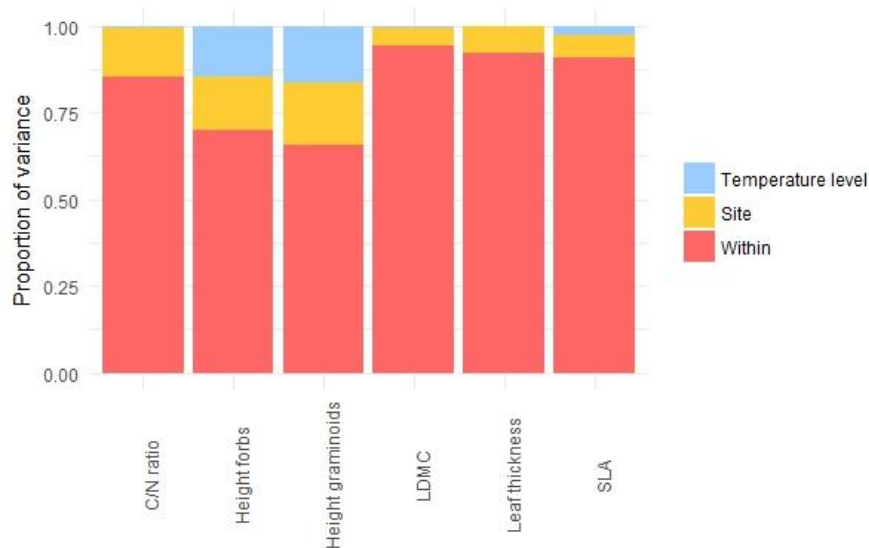


Figure 8: Variance partitioning of traits between levels of within site, between site and between the temperature level that the sites were nested in. These variance partitionings are approximate, using the total variance in the trait measurements to calculate the partitioning. Traits were collected from alpine and boreal semi-natural grasslands in south-western Norway over the summer of 2016.

DISCUSSION

SHIFTS IN TRAITS WITH TEMPERATURE AND PRECIPITATION

There is evidence that the interaction between temperature and precipitation affects the distribution of traits in grasslands (Figure 3, Table 2; Fontana et al. (2017)). Some traits change significantly with temperature, but along the precipitation gradient all traits show weaker and non-significant trends (Figure 3, Table 2). The traits that do show significant shifts along the temperature gradient, are also the traits with higher variability.

When it gets warmer plants grow taller, leaves become thinner and increase their photosynthetic capacity (Wright et al., 2004, Perez-Harguindeguy et al., 2013), demonstrated by the increased vegetative height and SLA with increasing temperature (Figure 3). A similar trend of taller plants and larger leaves was found in five arctic species after 16 years of experimental warming (Hudson et al., 2011). Results from both studies indicate that as climate change leads to a warming of these habitats plants don't have to spend as much energy on protective strategies as in harsher environmental conditions, and increased temperature may thus allow plants to allocate energy to increased productivity.

Although not significant, decreasing LDMC, leaf thickness and C/N ratio with increasing temperature (Figure 3, Table 2) match expectations from previous findings and ecological theory (Choler, 2005, Kattge et al., 2009, Kichenin et al., 2013, Perez-Harguindeguy et al., 2013, Jiang and Ma, 2015). Previous studies have linked these changes to increase in elevation, changes in wind-exposure and harsher habitats and not directly to the effect of decreasing temperature. This indicates that the non-significant trends of LDMC, leaf thickness and C/N ratio with temperature found in this study could be affected by other factors associated with changes in temperature.

I found that trait with a significant trend with temperature are traits with high intraspecific variability. SLA is a trait with more intraspecific variability than for example LDMC (Wilson et al., 1999, Kichenin et al., 2013). The same is true for vegetative height, as it has been found to be a highly variable trait, both within and between communities, in a global meta-analysis of variation in traits (Siefert et al., 2015). Leaf chemical traits have been found to be minimally sensitive to warming (Hudson et al., 2011), which could explain why we find that the chemical trait C/N ratio does not respond to the climatic gradient, even if it has been found to have high intraspecific variability both in my study and others (Kattge et al., 2009,

Albert et al., 2010a, Kichenin et al., 2013). This implies that intraspecific variability might be positively linked to the strength of trait changes along climatic gradients.

The non-significant trends for LDMC, leaf thickness and C/N ratio could be true trends that this study don't find significant because of one, or several of three reasons; (1) it is not temperature itself, driving the trend, and other factors could sum up to counteract the expected effects; or (2) these traits have lower variability than SLA and vegetative height so the changes driven by temperature are smaller and therefore harder to detect; or (3) the sampling design of this study gives a low sample size ($n = 12$ sites), which gives low statistical power to discover potential trends along the temperature gradient, even if present.

The precipitation gradient itself didn't drive large changes in trait distribution in these habitats, although LDMC and height of forbs showed a significant trend (increasing LDMC and decreasing height) in some cases (Table 2). The abiotic filter that the increased precipitation creates is causing an exchange of species resulting in a community with smaller stature species. On the other hand, the increasing trend in LDMC is driven by the change in species abundance; species with higher LDMC are more abundant in wetter habitats. For both traits, the trends are only significant when excluding intraspecific variability. Other studies have found stronger trends along precipitation gradients in traits; for example as a response to drought, studies have found decreased SLA (Wright et al., 2001, Cornwell et al., 2007, Cornwell and Ackerly, 2009), increased nitrogen content in leaves (Wright et al., 2001, Cornwell and Ackerly, 2009) and increased LDMC and leaf carbon content (Jung et al., 2014). However, Wright et al. (2001) found that these trends were different between nutrient rich and nutrient poor sites, where the trend of decreasing SLA in dry habitats was not present in nutrient poor sites. Our sites being relatively nutrient poor and low productive, could be the reason why we don't see strong trends along the precipitation gradient.

Studies that have found a decreased SLA with decreased precipitation have investigated extremely dry habitats (387 mm/year) (Cornwell et al., 2007) or extremely wet habitats (5400 mm/year) (Wright et al., 2001). On the other hand, the precipitation gradient in this study, has a large range of precipitation (650-2900 mm/year), but does not encompass the extremes of the global precipitation gradient (Moles et al., 2014, Diaz et al., 2016). This reveals one reason why the individuals don't seem to experience enough stress to select on traits which lead to obvious trends along the gradient. No trends were found with precipitation for architectural traits in the same habitat and gradient as this study (Guittar et al., 2016), supporting the theory that this precipitation range isn't causing a stress gradient for these

species. Since the gradient in our study lies in the middle of two extremes, a bell-shaped curve could be expected, which already has been suggested for LDMC and plant height (Albert et al., 2010b). If this is the case for traits in this study and their response to the precipitation gradient, this could explain the weak non-significant trends of the traits to this climatic effect. Thus, the precipitation gradient in this study does not seem to result in creating a large enough stress filtering effect on the vegetation to drive a shift in the community trait distribution, which indicates a bell-shaped response curve of these traits along the gradient.

Links between traits and precipitation might be of a more complex nature. Studies find that experimentally increasing the amount of precipitation leads to species with smaller seeds, shorter leaf life spans and higher nitrogen in the leaves, on the other hand the opposite trend is true for in-situ measurements (Sandel et al., 2010). This suggests that in-situ experiments may have more abiotic factors that vary alongside precipitation which are not detected in studies such as mine. Precipitation level and the actual access to water for plants are weakly correlated and depend on other factors like seasonal distribution of rainfall, soil type, soil temperature and groundwater (Moles et al., 2014). This implies a more nuanced picture where other abiotic factors and their effect alongside precipitation on community traits, needs to be considered.

The interactions found in the climatic gradients indicate that it is the combined effects of temperature and precipitation that decides the functions of the community. One interpretation of this is that, the longer growing season in drier habitats, due to early snowmelt, gives the individuals in the drier sites more time to grow taller during the growing season (Jonas et al., 2008, Rammig et al., 2010), creating more competition for light. In addition, the warm sites in this study have been found to have higher competition than the cold sites (Olsen et al., 2016). The combined effect of more competition in warm and wet sites creates a community where plants need to grow taller to optimize photosynthetic capacity (Figure 9). I find that species in warm and wet sites don't grow as tall as the species in the dry sites (Figure 9). One way to interpret this is that the light limiting effect caused by the increased cloud cover, drives plants to invest in strategies to optimize photosynthetic capacity, and resources are allocated to leaves rather than plant height (Figure 9). When plants are experiencing both the stress of low temperatures and limiting light due to thick cloud cover in high precipitation habitats, they produce lower stature plants with thick leaves and low photosynthetic capacity (Figure 9). This confirms that important ecological processes that affect growth, allocation of resources

and survival, and thus traits, are not driven by one abiotic factor alone, but the collective abiotic and biotic factors in these habitats (Fontana et al., 2017).

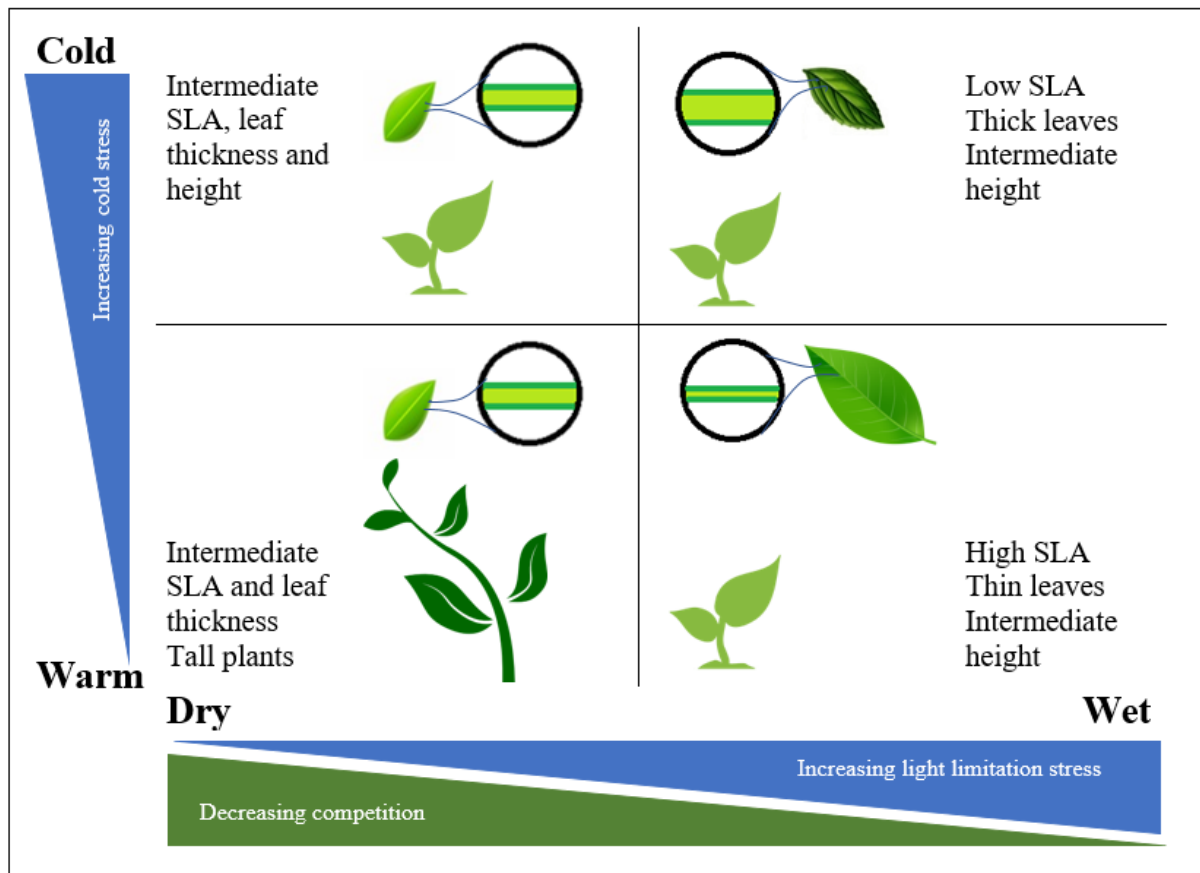


Figure 9: An interpretation of the interactive effects of temperature and precipitation on traits across temperature and precipitation gradients in south-western Norway.

UNTANGLING INTRASPECIFIC VARIABILITY AND SPECIES TURNOVER EFFECT

I found that both intraspecific variability and species turnover effect (both shifts in abundance and presence/absence of species) are important for driving the shifts in traits along the climatic gradients. The trends of increasing SLA and vegetative height with increasing temperature are showing the strongest trends (steeper slope) when both parts of the species turnover effect are included. Other studies have found species exchange to be more important than shifts in species abundance for driving trait shifts along an elevation gradient in alpine vegetation (Kichenin et al., 2013). Since elevation gradients includes shifts other than just in temperature, these abiotic factors could be the reason for the different conclusion of mine and Kichenin et al. (2013) study. This emphasize the need for further investigation to untangle the role of species richness and abundance and their role in driving trait shifts along different abiotic gradient.

The increasing trends with increasing temperature found in SLA and vegetative height are strongest (steeper slopes) when including the intraspecific variability (Table 2). This implies that the trends are driven both by species turnover and intraspecific variability. Previous studies showed differing results on trait community responses to climatic gradients, where intraspecific variability has a small (Volf et al., 2016) and large (Jung et al., 2014) effect, compared to species turnover. In these studies (Jung et al., 2014, Volf et al., 2016) intraspecific variability in traits investigated, is found to be of a relatively small extent. On the other hand, in my study, SLA and vegetative height are traits with high intraspecific variability. Although the relative importance of intraspecific variability and species turnover for driving the trends along the climatic gradients in this study have not been investigated, the high amount of intraspecific variability, and the stronger trend when including it in the analysis, could indicate that intraspecific variability is important in driving these trends.

INTRASPECIFIC TRAIT VARIABILITY AND WITHIN SITE VARIATION

Intraspecific variability represents a large proportion of the total variability in traits in these alpine grasslands relative to the global average (Siefert et al., 2015). The proportion of within site variation is also very high in this study compared to other studies (Wright et al., 2004, Moles et al., 2014). The method used is the standardized protocol of Perez-Harguindeguy et al. (2013), which is designed to limit the amount of intraspecific variability. Consequently, if a random sampling design had been used one could expect to find even higher levels of intraspecific variability than what is found in this study.

Alpine environments harbor more intraspecific variability than the global average (27% (Jung et al., 2014) and 30% (Albert et al., 2010a) compared to 25% (Siefert et al., 2015)), which aligns with the 8.5% greater allocation to intraspecific variability found in my study compared to the global average (Siefert et al., 2015). The large climatic gradient across the alpine and boreal semi-natural grasslands in my study encompass more intraspecific variability than the mosaic of different alpine habitats in the study of Albert et al. (2010a). All these results imply that the intraspecific variability in traits in alpine and boreal semi-natural grasslands is higher, and thus plays a larger role for the community, compared to other ecosystems. This supports the claim that the relative amount of intraspecific variability increases with decreasing temperature and is generally high in species-poor systems (Hulshof et al., 2013, Siefert et al., 2015).

The high intraspecific variability is causing a wide trait distribution across these alpine grasslands, although the trait values for the most dominant species are of a much narrower range (Figure 4, Appendix 3). Since intraspecific variability can be thought of as species niche width (Violle et al., 2012), trait distribution can tell you something about abiotic and biotic filtering (Violle et al., 2011, Violle et al., 2012, Enquist et al., 2015, Garnier et al., 2016). A wider trait distribution indicates biotic filtering through limiting similarity between species as a response to competition (Violle et al., 2011), and is found in more productive habitats (Hulshof et al., 2013), whereas abiotic filters shrink trait distribution and is found in for example high latitudes (Hulshof et al., 2013). This implies that in my study, there is an abiotic filtering effect that yields the effect of a small trait space occupied by the common species, although not strong enough to filter out all individuals with higher or lower trait values (Figure 4, Appendix 3). With climate warming in alpine areas, less abiotic stress is expected which could lead to a widening of trait space available.

The proportion of intraspecific variability have been found to be different in different traits, follow the pattern of highest proportion in leaf chemical and whole plant traits, intermediate in SLA and LDMC and lowest in leaf mechanical traits (Siefert et al., 2015). The results of my study broadly support these trends with two exceptions. First, the intraspecific variability of SLA showing a high, as opposed to intermediate, proportion. Second, the height of graminoids show a low proportion of intraspecific variability, even though height in forbs shows the expected high amount (Figure 7). This means that either there is a difference in variability in height of forbs and graminoids, or the methodology used to measure height could explain some of this. When stretching the leaves of graminoids to measure height, as described in the method section, I effectively measure leaf length. Leaf length has been found to be highly heritable, and when measured with the same method, and at the same growing stage, a lot of the variation present is excluded (Barre et al., 2015), and could explain why measuring vegetative height in this way for graminoids leads to less variation. Although leaf length reflects allocation of resources to leaf production rather than whole plant stature, leaf length is highly correlated with plant height for graminoids (Barre et al., 2015), and thus could represent the true variation in vegetative height for graminoids. To my knowledge no other studies have separated forbs and graminoids when measuring height, thus a further investigation of the difference in resource allocation of functional groups is needed.

Globally, and in many different traits, the proportion of within-site variability is high and usually contributing to around half of the total variability (Wright et al., 2004, Moles et al.,

2014), while in this study that proportion of within-site variation is higher (Figure 8). A lot of this is explained by the fact that this study only looks at forbs and graminoids in the same habitat, whereas the work by Wright et al. (2004) and Moles et al. (2014) include multiple biomes and several functional groups, increasing the total variance. The high within-site variation in my study could also be caused by high local heterogeneity in abiotic factors like soil nutrients and soil moisture (Jung et al., 2014). Other studies have found that the most important proportion of intraspecific variability occurred at a fine spatial scale rather than between locations along strong abiotic gradients (Albert et al., 2010b, Jung et al., 2014). Similarly, the variability linked to the temperature and precipitation in my study is generally low (Figure 8). The traits that have relatively more variation linked to temperature and precipitation are also the traits that have significant trends along the temperature gradient; SLA and vegetative height (Figure 8, Figure 3). These results, where most of the variation is within one site, and then between sites and eventually between temperature and precipitation levels has also been found in other studies (e.g. Jung et al. (2014)). Comparing sites of the same vegetation type, and when this habitat is linked to high abiotic heterogeneity, yields high within-site trait variability.

SINGLE SPECIES AND PLANT STRATEGIES

Species are not necessarily showing the same trends as the community with the climatic gradient. Thirteen out of the fifteen most common species show the same increasing trend in SLA with increased temperature, although only four of those species have a significant trend (Figure 5). This is even lower for traits where the community has weaker trends along the climatic gradient (Appendix 4). Other studies have found the same, with as little as 20% of the studied species showing the same significant trends as the overall community to a drought experiment (Jung et al., 2014). This can come from two different causes. First, traits vary in synchrony and are dependent on other traits by trade-offs between functions (Diaz et al., 2016). Abiotic factors selecting for certain functions might not have the same effect in different species or different habitats for the same trait (Forrestel et al., 2017). Second, traits represent a species niche (Violle et al., 2012), and trait values of species are expected to follow a bell-shaped response curve along environmental gradients (Violle et al., 2007). Thus, trait response to climatic gradients can vary depending on if you move the species closer or away from their ecological optimum. These findings support the claim that when investigating shifts in community traits with different environmental changes, a large proportion of the

community (80% suggested by Pakeman and Quested (2007)) should be represented in the trait data.

Species that are found across the range of the climatic gradient in this study show different strategies and trends in SLA, some showing the same trend as the community, others don't. A species that does show the same trend as the community in SLA with temperature is *Anthoxanthum odoratum*. *A. odoratum* is a species with high phenotypic plasticity in reproduction and growth (Platenkamp, 1990), and is related to a stress-tolerant and ruderal strategy (Appendix 6). *Deschampsia cespitosa* is a species which is related to a stress tolerant strategy (Appendix 6), with low growth rate, long-lived organs and low morphological plasticity (Collet et al., 1996). This species doesn't have a change in SLA along the climatic gradient, and shows a mean half the size, and variation ten times smaller in SLA compared to *A. odoratum*. These species represent two very different plant strategies and growth forms but are both able to successfully grow under the wide range of climatic conditions in these habitats. Keep in mind that the closely related alpine species, *Deschampsia alpina* and *Anthoxanthum nipponicum* could be included in samples, and would then imply more variation than expected from a single species. With this in mind, the results still indicate that there are many ways a species could successfully be adapted to different climatic conditions, and it is the collective change of the whole trait syndrome that adds up to a species fitness (Forrestel et al., 2017).

IMPLICATIONS FOR TRAIT-BASED APPROACHES TO CLIMATE CHANGE IMPACTS

The Norwegian climate is changing, and the future will bring warmer and wetter conditions (Walther et al., 2002, Kovats et al., 2014), and my research suggests this will lead to alpine communities that grow taller plants with thinner leaves of higher photosynthetic capacity. These community trait shifts are driven by both intraspecific variability in traits and species turnover, the latter both through species exchange and changes in species abundance. In addition, the wide distribution of traits present in the flora (Figure 4, Appendix 3), indicates that the variation needed for the community to adjust to future climates could already be present. This implies that there might not be a huge need for species migration, but rather a shift in trait space either within species by plasticity, or by a shift in relative abundance of species, as also suggested by Kichenin et al. (2013). Seeing that some species are more variable in their traits than others (Figure 6), these species are candidates for species that may be more important in driving these trait and functional shifts. The high functional diversity represented by the large range in trait values in these systems, the high intraspecific variability

and the wide variety of strategies in species of these habitats, could according to the insurance hypothesis (Yachi and Loreau, 1999) indicate that alpine and boreal semi-natural grasslands are associated with high resilience. Although, with warming of these alpine systems we could expect a widening of trait space occupied by the community, which could either be caused by changes in intraspecific variability or by new species coming in from other habitats. In conclusion, the warmer and wetter alpine grasslands of the future, could lead to a change in ecosystem functioning of these habitats caused by increased abundance of species and phenotypes with higher photosynthetic capacity either by changing relative abundance or trait expressions in species already present, or by new species migrating into these habitats.

This study provides further evidence for the importance of intraspecific variability in alpine grasslands (Siefert et al., 2015). To obtain accurate interpretations of local community functions, these findings support the claim by Cordlandwehr et al. (2013) that trait measurements should be sampled locally, or retrieved from databases only when these traits are sampled from similar habitats under comparable climatic conditions. Intraspecific variability has been thought to be most important in driving trends during short term changes and in habitats with high local heterogeneity, as opposed to along broad environmental gradients (Albert et al., 2011, Jung et al., 2014). On the other hand, this study finds that studies in alpine grasslands should also include intraspecific variability when investigating broad climatic gradients on the regional scale. For trait-based ecology these findings imply that the need for including intraspecific variability, by sampling local traits, should be considered for alpine grasslands and regional studies in cold and species-poor habitats.

CONCLUDING REMARKS AND FUTURE RESEARCH

In this study, I found that community trait distributions change due to different abiotic and biotic stressors in response to the interactive effects of temperature and precipitation. Plants grow taller in warm and dry habitats, produce leaves with high photosynthetic capacity in warm and wet habitats, and produce better protected leaves in cold and wet habitats. These trends are driven by both intraspecific variability and species turnover effect, and some, but far from all species show patterns in the intraspecific variability that match the community-wide patterns. This study provides evidence that intraspecific variability in alpine and boreal semi-natural grasslands is relatively high compared to other habitats. This has implications for how trait-based research, studying these systems, should be conducted.

Analyses of how intraspecific variability change across the climatic gradient were not conducted within this thesis. Trait driver theory indicates that the mean, variance and skewness of traits all give different information about the processes underlying the ecosystems functioning, and in particular that these moments of the variance carry important information about the strength of different biotic and abiotic stressors (Enquist et al., 2015). In these habitats, we know that the nature of the biotic interaction changes from competitive to facilitative as the temperature decreases (Olsen et al., 2016). It would be of interest to learn more about the effects abiotic and biotic filters have on the communities in alpine grasslands, which the change in trait variance across climatic gradients could be used for. While the data collected allows such analyses, they have not been conducted as part of the thesis.

Another interesting further research direction could be to use the information from this study on traits related to the leaf economic spectrum (Wright et al., 2004), and investigate the links between the dynamics of traits, individual plants, communities and ecosystem functioning (Diaz et al., 2007, Suding et al., 2008). Leaf chemical and morphological traits have been linked to carbon and nutrient cycles through effects on evapotranspiration, carbon sequestration and decomposition (de Bello et al., 2010). Accordingly, an interesting aspect could be to investigate how these leaf traits are linked to primary production and carbon storage of these grasslands.

REFERENCES

- ABRÀMOFF, M. D., MAGALHÃES, P. J. & RAM, S. J. 2004. Image processing with ImageJ. *Biophotonics international*, 11, 36-42.
- ALBERT, C. H., GRASSEIN, F., SCHURR, F. M., VIEILLEDENT, G. & VIOLLE, C. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology Evolution and Systematics*, 13, 217-225.
- ALBERT, C. H., THUILLER, W., YOCCOZ, N. G., DOUZET, R., AUBERT, S. & LAVOREL, S. 2010a. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology*, 24, 1192-1201.
- ALBERT, C. H., THUILLER, W., YOCCOZ, N. G., SOUDANT, A., BOUCHER, F., SACCONI, P. & LAVOREL, S. 2010b. Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, 98, 604-613.
- ARTSDATABANKEN 2015. Artsnavnebasen. Norsk taksonomisk database. <http://www.artsportalen.artsdatabanken.no/>, accessed 08/2017.
- BARRE, P., TURNER, L. B. & ESCOBAR-GUTIERREZ, A. J. 2015. Leaf Length Variation in Perennial Forage Grasses. *Agriculture-Basel*, 5, 682-696.
- BATES, D., MÄCHLER, M., BOLKER, B. & WALKER, S. 2014. Fitting linear mixed-effects models using lme4. *arXiv:1406.5823*.
- CHOLER, P. 2005. Consistent shifts in Alpine plant traits along a mesotopographical gradient. *Arctic Antarctic and Alpine Research*, 37, 444-453.
- COLLET, C., FROCHOT, H. & GUEHL, J. M. 1996. Growth dynamics and water uptake of two forest grasses differing in their growth strategy and potentially competing with forest seedlings. *Canadian Journal of Botany-Revue Canadienne De Botanique*, 74, 1555-1561.
- CORDLANDWEHR, V., MEREDITH, R. L., OZINGA, W. A., BEKKER, R. M., VAN GROENENDAEL, J. M. & BAKKER, J. P. 2013. Do plant traits retrieved from a database accurately predict on-site measurements? *Journal of Ecology*, 101, 662-670.
- CORNELISSEN, J. H. C., LAVOREL, S., GARNIER, E., DIAZ, S., BUCHMANN, N., GURVICH, D. E., REICH, P. B., TER STEEGE, H., MORGAN, H. D., VAN DER HEIJDEN, M. G. A., PAUSAS, J. G. & POORTER, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335-380.
- CORNWELL, W. K. & ACKERLY, D. D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79, 109-126.
- CORNWELL, W. K., BHASKAR, R., SACK, L., CORDELL, S. & LUNCH, C. K. 2007. Adjustment of structure and function of Hawaiian *Metrosideros* polymorpha at high vs. low precipitation. *Functional Ecology*, 21, 1063-1071.
- DE BELLO, F., LAVOREL, S., DIAZ, S., HARRINGTON, R., CORNELISSEN, J. H. C., BARDGETT, R. D., BERG, M. P., CIPRIOTTI, P., FELD, C. K., HERING, D., DA SILVA, P. M., POTTS, S. G., SANDIN, L., SOUSA, J. P., STORKEY, J., WARDLE, D. A. & HARRISON, P. A. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, 19, 2873-2893.
- DIAZ, S., HODGSON, J. G., THOMPSON, K., CABIDO, M., CORNELISSEN, J. H. C., JALILI, A., MONTSERRAT-MARTI, G., GRIME, J. P., ZARRINKAMAR, F., ASRI, Y., BAND, S. R., BASCONCELO, S., CASTRO-DIEZ, P., FUNES, G.,

- HAMZEHEE, B., KHOSHNEVI, M., PEREZ-HARGUINDEGUY, N., PEREZ-RONTOME, M. C., SHIRVANY, F. A., VENDRAMINI, F., YAZDANI, S., ABBAS-AZIMI, R., BOGAARD, A., BOUSTANI, S., CHARLES, M., DEHGHAN, M., DE TORRES-ESPUNY, L., FALCZUK, V., GUERRERO-CAMPO, J., HYND, A., JONES, G., KOWSARY, E., KAZEMI-SAEED, F., MAESTRO-MARTINEZ, M., ROMO-DIEZ, A., SHAW, S., SIAVASH, B., VILLAR-SALVADOR, P. & ZAK, M. R. 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, 15, 295-304.
- DIAZ, S., KATTGE, J., CORNELISSEN, J. H. C., WRIGHT, I. J., LAVOREL, S., DRAY, S., REU, B., KLEYER, M., WIRTH, C., PRENTICE, I. C., GARNIER, E., BONISCH, G., WESTOBY, M., POORTER, H., REICH, P. B., MOLES, A. T., DICKIE, J., GILLISON, A. N., ZANNE, A. E., CHAVE, J., WRIGHT, S. J., SHEREMET'EV, S. N., JACTEL, H., BARALOTO, C., CERABOLINI, B., PIERCE, S., SHIPLEY, B., KIRKUP, D., CASANOVES, F., JOSWIG, J. S., GUNTHER, A., FALCZUK, V., RUGER, N., MAHECHA, M. D. & GORNE, L. D. 2016. The global spectrum of plant form and function. *Nature*, 529, 167-173.
- DIAZ, S., LAVOREL, S., DE BELLO, F., QUETIER, F., GRIGULIS, K. & ROBSON, M. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 20684-20689.
- ENQUIST, B. J., NORBERG, J., BONSER, S. P., VIOLLE, C., WEBB, C. T., HENDERSON, A., SLOAT, L. L. & SAVAGE, V. M. 2015. Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research*, 52, 249-318.
- FONTANA, V., KOHLER, M., NIEDRIST, G., BAHN, M., TAPPEINER, U. & FRENCK, G. 2017. Decomposing the land-use specific response of plant functional traits along environmental gradients. *Science of the Total Environment*, 599, 750-759.
- FORRESTEL, E. J., DONOGHUE, M. J., EDWARDS, E. J., JETZ, W., DU TOIT, J. C. O. & SMITH, M. D. 2017. Different clades and traits yield similar grassland functional responses. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 705-710.
- FREMSTAD, E. 1997. *Vegetasjonstyper i Norge*, Trondheim, Norsk institutt for naturforskning.
- GARNIER, E., LAVOREL, S., ANSQUER, P., CASTRO, H., CRUZ, P., DOLEZAL, J., ERIKSSON, O., FORTUNEL, C., FREITAS, H., GOLODETS, C., GRIGULIS, K., JOUANY, C., KAZAKOU, E., KIGEL, J., KLEYER, M., LEHSTEN, V., LEPS, J., MEIER, T., PAKEMAN, R., PAPADIMITRIOU, M., PAPANASTASIS, V. P., QUESTED, H., QUETIER, F., ROBSON, M., ROUMET, C., RUSCH, G., SKARPE, C., STERNBERG, M., THEAU, J. P., THEBAULT, A., VILE, D. & ZAROVALI, M. P. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99, 967-985.
- GARNIER, E., NAVAS, M.-L. & GRIGULIS, K. 2016. *Plant functional diversity: Organism traits, community structure, and ecosystem properties*, Oxford University Press.
- 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, 2791-2801.
- HALVORSEN, R., BRYN, A., ERIKSTAD, L. & LINDGAARD, A. 2015. Natur i Norge-NiN. Versjon 2.0. 0. Artsdatabanken, Trondheim, <http://www.artsdatabanken.no/nin>, accessed 09/2017.

- HIBBARD, K., HOFFMAN, F., HUNTZINGER, D. N. & WEST, T. 2017. Changes in land cover and terrestrial biogeochemistry. 405-442. *In: WUEBBLES, D. J., FAHEY, D. W., HIBBARD, K. A., DOKKEN, D. J., STEWART, B. C. & MAYCOCK, T. K. (eds.) Climate Science Special Report: A Sustained Assessment Activity of the U.S. Global Change Research Program.* Washington, DC, USA: U.S. Global Change Research Program.
- 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, 1013-1021.
- HULSHOF, C. M., VIOLLE, C., SPASOJEVIC, M. J., MCGILL, B., DAMSCHEN, E., HARRISON, S. & ENQUIST, B. J. 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Science*, 24, 921-931.
- HUXMAN, T. E., SMITH, M. D., FAY, P. A., KNAPP, A. K., SHAW, M. R., LOIK, M. E., SMITH, S. D., TISSUE, D. T., ZAK, J. C., WELTZIN, J. F., POCKMAN, W. T., SALA, O. E., HADDAD, B. M., HARTE, J., KOCH, G. W., SCHWINNING, S., SMALL, E. E. & WILLIAMS, D. G. 2004. Convergence across biomes to a common rain-use efficiency. *Nature*, 429, 651-654.
- JIANG, Z. H. & MA, K. M. 2015. Environmental filtering drives herb community composition and functional trait changes across an elevational gradient. *Plant Ecology and Evolution*, 148, 301-310.
- JONAS, T., RIXEN, C., STURM, M. & STOECKLI, V. 2008. How alpine plant growth is linked to snow cover and climate variability. *Journal of Geophysical Research-Biogeosciences*, 113, G03013.
- JUNG, V., ALBERT, C. H., VIOLLE, C., KUNSTLER, G., LOUCOUGARAY, G. & SPIEGELBERGER, T. 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology*, 102, 45-53.
- KATTGE, J., DIAZ, S., LAVOREL, S., PRENTICE, C., LEADLEY, P., BONISCH, G., GARNIER, E., WESTOBY, M., REICH, P. B., WRIGHT, I. J., CORNELISSEN, J. H. C., VIOLLE, C., HARRISON, S. P., VAN BODEGOM, P. M., REICHSTEIN, M., ENQUIST, B. J., SOUDZILOVSKAIA, N. A., ACKERLY, D. D., ANAND, M., ATKIN, O., BAHN, M., BAKER, T. R., BALDOCCHI, D., BEKKER, R., BLANCO, C. C., BLONDER, B., BOND, W. J., BRADSTOCK, R., BUNKER, D. E., CASANOVES, F., CAVENDER-BARES, J., CHAMBERS, J. Q., CHAPIN, F. S., CHAVE, J., COOMES, D., CORNWELL, W. K., CRAINE, J. M., DOBRIN, B. H., DUARTE, L., DURKA, W., ELSER, J., ESSER, G., ESTIARTE, M., FAGAN, W. F., FANG, J., FERNANDEZ-MENDEZ, F., FIDELIS, A., FINEGAN, B., FLORES, O., FORD, H., FRANK, D., FRESCHET, G. T., FYLLAS, N. M., GALLAGHER, R. V., GREEN, W. A., GUTIERREZ, A. G., HICKLER, T., HIGGINS, S. I., HODGSON, J. G., JALILI, A., JANSEN, S., JOLY, C. A., KERKHOFF, A. J., KIRKUP, D., KITAJIMA, K., KLEYER, M., KLOTZ, S., KNOPS, J. M. H., KRAMER, K., KUHN, I., KUROKAWA, H., LAUGHLIN, D., LEE, T. D., LEISHMAN, M., LENS, F., LENZ, T., LEWIS, S. L., LLOYD, J., LLUSIA, J., LOUAULT, F., MA, S., MAHECHA, M. D., MANNING, P., MASSAD, T., MEDLYN, B. E., MESSIER, J., MOLES, A. T., MULLER, S. C., NADROWSKI, K., NAEEM, S., NIINEMETS, U., NOLLERT, S., NUSKE, A., OGAYA, R., OLEKSYN, J., ONIPCHENKO, V. G., ONODA, Y., ORDONEZ, J., OVERBECK, G., OZINGA, W. A., et al. 2011. TRY - a global database of plant traits. *Global Change Biology*, 17, 2905-2935.

- KATTGE, J., KNORR, W., RADDATZ, T. & WIRTH, C. 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, 15, 976-991.
- 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, 1254-1261.
- KLANDERUD, K., VANDVIK, V. & GOLDBERG, D. 2015. The Importance of Biotic vs. Abiotic Drivers of Local Plant Community Composition Along Regional Bioclimatic Gradients. *PLoS ONE*, 10, e0130205.
- KOVATS, R. S., VALENTINI, R., BOUWER, L. M., GEORGOPOULOU, E., JACOB, D., MARTIN, E., ROUNSEVELL, M. & SOUSSANA, J.-F. 2014. Europe. 1267-1326. *In: BARROS, V. R., FIELD, C. B., DOKKEN, D. J. M., M.D. , MACH, K. J., BILIR, T. E., CHATTERJEE, M., EBI, K. L., ESTRADA, Y. O., GENOVA, R. C., GIRMA, B., KISSEL, E. S., LEVY, A. N., MACCRACKEN, S., MASTRANDREA, P. R. & WHITE, L. L. (eds.) Climate Change 2014: Impacts, Adaptation and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.
- LEPS, J., DE BELLO, F., SMILAUER, P. & DOLEZAL, J. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography*, 34, 856-863.
- LHOTSKY, B., KOVACS, B., ONODI, G., CSECSERITS, A., REDEI, T., LENGYEL, A., KERTESZ, M. & BOTTA-DUKAT, Z. 2016. Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *Journal of Ecology*, 104, 507-517.
- LI, Y. Z. & SHIPLEY, B. 2017. An experimental test of CSR theory using a globally calibrated ordination method. *Plos One*, 12, e0175404.
- LID, J. & LID, D. T. 2005. *Norsk Flora*, Oslo, Det Norske Samlaget. 7th edition by Reidar Elven.
- MCGILL, B. J., ENQUIST, B. J., WEIHER, E. & WESTOBY, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178-185.
- MESSIER, J., MCGILL, B. J. & LECHOWICZ, M. J. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology letters*, 13, 838-848.
- MOLES, A. T., PERKINS, S. E., LAFFAN, S. W., FLORES-MORENO, H., AWASTHY, M., TINDALL, M. L., SACK, L., PITMAN, A., KATTGE, J., AARSSSEN, L. W., ANAND, M., BAHN, M., BLONDER, B., CAVENDER-BARES, J., CORNELISSEN, J. H. C., CORNWELL, W. K., DIAZ, S., DICKIE, J. B., FRESCHET, G. T., GRIFFITHS, J. G., GUTIERREZ, A. G., HEMMINGS, F. A., HICKLER, T., HITCHCOCK, T. D., KEIGHERY, M., KLEYER, M., KUROKAWA, H., LEISHMAN, M. R., LIU, K. W., NIINEMETS, U., ONIPCHENKO, V., ONODA, Y., PENUELAS, J., PILLAR, V. D., REICH, P. B., SHIODERA, S., SIEFERT, A., SOSINSKI, E. E., SOUDZILOVSKAIA, N. A., SWAINE, E. K., SWENSON, N. G., VAN BODEGOM, P. M., WARMAN, L., WEIHER, E., WRIGHT, I. J., ZHANG, H. X., ZOBEL, M. & BONSER, S. P. 2014. Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science*, 25, 1167-1180.
- NAKAGAWA, S. & SCHIELZETH, H. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133-142.

- OLSEN, S. L., TOPPER, J. P., SKARPAAS, O., VANDVIK, V. & KLANDERUD, K. 2016. From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Global Change Biology*, 22, 1915-1926.
- ONODA, Y., WESTOBY, M., ADLER, P. B., CHOONG, A. M. F., CLISSOLD, F. J., CORNELISSEN, J. H. C., DIAZ, S., DOMINY, N. J., ELGART, A., ENRICO, L., FINE, P. V. A., HOWARD, J. J., JALILI, A., KITAJIMA, K., KUROKAWA, H., MCARTHUR, C., LUCAS, P. W., MARKESTEIJN, L., PEREZ-HARGUINDEGUY, N., POORTER, L., RICHARDS, L., SANTIAGO, L. S., SOSINSKI, E. E., VAN BAELE, S. A., WARTON, D. I., WRIGHT, I. J., WRIGHT, S. J. & YAMASHITA, N. 2011. Global patterns of leaf mechanical properties. *Ecology Letters*, 14, 301-312.
- PAKEMAN, R. J. & QUESTED, H. M. 2007. Sampling plant functional traits: What proportion of the species need to be measured? *Applied Vegetation Science*, 10, 91-96.
- PARADIS, E., CLAUDE, J. & STRIMMER, K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289-290.
- PECL, G. T., ARAUJO, M. B., BELL, J. D., BLANCHARD, J., BONEBRAKE, T. C., CHEN, I. C., CLARK, T. D., COLWELL, R. K., DANIELSEN, F., EVENGARD, B., FALCONI, L., FERRIER, S., FRUSHER, S., GARCIA, R. A., GRIFFIS, R. B., HOBDAI, A. J., JANION-SCHEEPERS, C., JARZYNA, M. A., JENNINGS, S., LENOIR, J., LINNETVED, H. I., MARTIN, V. Y., MCCORMACK, P. C., MCDONALD, J., MITCHELL, N. J., MUSTONEN, T., PANDOLFI, J. M., PETTORELLI, N., POPOVA, E., ROBINSON, S. A., SCHEFFERS, B. R., SHAW, J. D., SORTE, C. J. B., STRUGNELLE, J. M., SUNDAY, J. M., TUANMU, M. N., VERGES, A., VILLANUEVA, C., WERNBERG, T., WAPSTRA, E. & WILLIAMS, S. E. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355, eaai9214.
- PEREZ-HARGUINDEGUY, N., DIAZ, S., GARNIER, E., LAVOREL, S., POORTER, H., JAUREGUIBERRY, P., BRET-HARTE, M. S., CORNWELL, W. K., CRAINE, J. M., GURVICH, D. E., URCELAY, C., VENEKLAAS, E. J., REICH, P. B., POORTER, L., WRIGHT, I. J., RAY, P., ENRICO, L., PAUSAS, J. G., DE VOS, A. C., BUCHMANN, N., FUNES, G., QUETIER, F., HODGSON, J. G., THOMPSON, K., MORGAN, H. D., TER STEEGE, H., VAN DER HEIJDEN, M. G. A., SACK, L., BLONDER, B., POSCHLOD, P., VAIERETTI, M. V., CONTI, G., STAYER, A. C., AQUINO, S. & CORNELISSEN, J. H. C. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167-234.
- PIERCE, S., NEGREIROS, D., CERABOLINI, B. E. L., KATTGE, J., DIAZ, S., KLEYER, M., SHIPLEY, B., WRIGHT, S. J., SOUZZILOVSKAIA, N. A., ONIPCHENKO, V. G., VAN BODEGOM, P. M., FRENETTE-DUSSAULT, C., WEIHER, E., PINHO, B. X., CORNELISSEN, J. H. C., GRIME, J. P., THOMPSON, K., HUNT, R., WILSON, P. J., BUFFA, G., NYAKUNGA, O. C., REICH, P. B., CACCIANIGA, M., MANGILI, F., CERIANI, R. M., LUZZARO, A., BRUSA, G., SIEFERT, A., BARBOSA, N. P. U., CHAPIN, F. S., CORNWELL, W. K., FANG, J. Y., FERNANDES, G. W., GARNIER, E., LE STRADIC, S., PENUELAS, J., MELO, F. P. L., SLAVIERO, A., TABARELLI, M. & TAMPUCCI, D. 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology*, 31, 444-457.
- PINHEIRO, J., BATES, D., DEBROY, S., SARKAR, D. & TEAM, R. C. 2009. nlme: Linear and nonlinear mixed effects models.

- PLATENKAMP, G. A. J. 1990. Phenotypic Plasticity and Genetic Differentiation in the Demography of the Grass *Anthoxanthum-Odoratum*. *Journal of Ecology*, 78, 772-788.
- RAMMIG, A., JONAS, T., ZIMMERMANN, N. E. & RIXEN, C. 2010. Changes in alpine plant growth under future climate conditions. *Biogeosciences*, 7, 2013-2024.
- ROTHERA, S. L. & DAVY, A. J. 1986. Polyploidy and Habitat Differentiation in *Deschampsia-Cespitosa*. *New Phytologist*, 102, 449-467.
- SANDEL, B., GOLDSTEIN, L. J., KRAFT, N. J., OKIE, J. G., SHULDMAN, M. I., ACKERLY, D. D., CLELAND, E. E. & SUDING, K. N. 2010. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist*, 188, 565-575.
- SIEFERT, A., VIOLLE, C., CHALMANDRIER, L., ALBERT, C. H., TAUDIERE, A., FAJARDO, A., AARSSSEN, L. W., BARALOTO, C., CARLUCCI, M. B., CIANCIARUSO, M. V., DANTAS, V. D., DE BELLO, F., DUARTE, L. D. S., FONSECA, C. R., FRESCHET, G. T., GAUCHERAND, S., GROSS, N., HIKOSAKA, K., JACKSON, B., JUNG, V., KAMIYAMA, C., KATABUCHI, M., KEMBEL, S. W., KICHENIN, E., KRAFT, N. J. B., LAGERSTROM, A., LE BAGOUSSE-PINGUET, Y., LI, Y. Z., MASON, N., MESSIER, J., NAKASHIZUKA, T., MCC OVERTON, J., PELTZER, D. A., PEREZ-RAMOS, I. M., PILLAR, V. D., PRENTICE, H. C., RICHARDSON, S., SASAKI, T., SCHAMP, B. S., SCHOB, C., SHIPLEY, B., SUNDQVIST, M., SYKES, M. T., VANDEWALLE, M. & WARDLE, D. A. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18, 1406-1419.
- SUDING, K. N., LAVOREL, S., CHAPIN, F. S., CORNELISSEN, J. H. C., DIAZ, S., GARNIER, E., GOLDBERG, D., HOOPER, D. U., JACKSON, S. T. & NAVAS, M. L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, 14, 1125-1140.
- SULTAN, S. E. 2000. Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, 5, 537-542.
- VIOLLE, C., ENQUIST, B. J., MCGILL, B. J., JIANG, L., ALBERT, C. H., HULSHOF, C., JUNG, V. & MESSIER, J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in ecology & evolution*, 27, 244-252.
- VIOLLE, C., NAVAS, M. L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. 2007. Let the concept of trait be functional! *Oikos*, 116, 882-892.
- VIOLLE, C., NEMERGUT, D. R., PU, Z. C. & JIANG, L. 2011. Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, 14, 782-787.
- VOLF, M., REDMOND, C., ALBERT, A. J., LE BAGOUSSE-PINGUET, Y., BIELLA, P., GOTZENBERGER, L., HRAZSKY, Z., JANECEK, S., KLIMESOVA, J., LEPS, J., SEBELIKOVA, L., VLASATA, T. & DE BELLO, F. 2016. Effects of long- and short-term management on the functional structure of meadows through species turnover and intraspecific trait variability. *Oecologia*, 180, 941-950.
- WALTHER, G. R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J. M., HOEGH-GULDBERG, O. & BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature*, 416, 389-395.
- WESTOBY, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199, 213-227.
- WILSON, J. B., PEET, R. K., DENGLER, J. & PARTEL, M. 2012. Plant species richness: the world records. *Journal of Vegetation Science*, 23, 796-802.

- WILSON, P. J., THOMPSON, K. & HODGSON, J. G. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, 143, 155-162.
- WRIGHT, I. J., REICH, P. B. & WESTOBY, M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, 15, 423-434.
- WRIGHT, I. J., REICH, P. B., WESTOBY, M., ACKERLY, D. D., BARUCH, Z., BONGERS, F., CAVENDER-BARES, J., CHAPIN, T., CORNELISSEN, J. H. C., DIEMER, M., FLEXAS, J., GARNIER, E., GROOM, P. K., GULIAS, J., HIKOSAKA, K., LAMONT, B. B., LEE, T., LEE, W., LUSK, C., MIDGLEY, J. J., NAVAS, M. L., NIINEMETS, U., OLEKSYN, J., OSADA, N., POORTER, H., POOT, P., PRIOR, L., PYANKOV, V. I., ROUMET, C., THOMAS, S. C., TJOELKER, M. G., VENEKLAAS, E. J. & VILLAR, R. 2004. The worldwide leaf economics spectrum. *Nature*, 428, 821-827.
- WU, Z. T., DIJKSTRA, P., KOCH, G. W., PENUELAS, J. & HUNGATE, B. A. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, 17, 927-942.
- YACHI, S. & LOREAU, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 1463-1468.

APPENDIX 1

Table 1: A dictionary for expressions used in the thesis “The role of intraspecific variability in driving community trait shifts along temperature and precipitation gradients in alpine and boreal semi-natural grasslands”.

Expression	Explanation
Trait	Any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization (Violle et al 2007).
Functional trait	Any trait which impacts fitness indirectly via its effects on growth, reproduction and survival (Violle et al 2007).
All trait observations	Raw data, includes measurement of all leaves from all species.
Specific mean	Trait mean that incorporates information about interspecific and intraspecific variability and presence/absence of species (Leps et al., 2011).
Fixed mean	Trait mean that incorporates information about interspecific variability and presence/absence of species (Leps et al., 2011).
Specific community weighted mean (CWM)	Trait mean that incorporates information about interspecific and intraspecific trait variability, presence/absence as well as abundance of species (Leps et al., 2011).
Fixed community weighted mean (CWM)	Trait mean that incorporates information about interspecific trait variability and presence/absence and abundance of species (Leps et al., 2011).
Abbreviations	Explanations
CWM	Community weighted mean. When the mean is weighted by the relative abundance of the species in a species site.
SLA	Specific leaf area (leaf area (cm ²)/ dry mass (g)). Is linked to photosynthetic capacity (Wright et al., 2004)
LDMC	Leaf dry matter content (dry mass (g)/ wet mass (g)). Is linked to protective strategies (Perez-Harguindeguy et al., 2013).

APPENDIX 2

Table II: All the species and number of leaves (individuals) at each site, in the leaf trait collection over the summer of 2016 in alpine and boreal semi-natural grasslands in south-western Norway over the summer of 2016. The whole table is over three pages. Site abbreviations: Ulv = Ulvehaugen, Lav = Låvisdalen, Gud = Gudemedalen, Skj = Skjellingahaugen, Alr = Ålrust, Hog = Høgsete, Ram = Rambera, Ves = Veskre, Fau = Fauske, Vik = Vikesland, Arh = Arhelleren, Ovs = Ovstedal

Species	Ulv	Lav	Gud	Skj	Alr	Hog	Ram	Ves	Fau	Vik	Arh	Ovs
<i>Achillea millefolium</i>			10		10	10	10		10	10		
<i>Agrostis capilaris</i>	10	10	10	10	10	10	10	10	10	10	10	10
<i>Alchemilla alpina</i>	10	10	9	10		10	10	10				
<i>Alchemilla sp</i>	10	10	2	10				10	10			
<i>Antennaria dioica</i>	10	10	10	10								
<i>Anthoxanthum odoratum</i>	10	10	10	10		10	10	10		10	10	10
<i>Astragalus alpinus</i>	10	10	10									
<i>Avenella flexuosa</i>	10	10	10	11		10	10				10	
<i>Bistorta vivipara</i>	10	10	10	10	10		10				10	
<i>Campanula rotundifolia</i>	10		10	10	10		10		10	10	10	10
<i>Carex bigelowii</i>	10	10	10				9					
<i>Carex capillaris</i>			10	10			10	10				
<i>Carex flava</i>			10					9				
<i>Carex leporina</i>						10						10
<i>Carex nigra</i>								5				10
<i>Carex norvegica</i>		8										
<i>Carex pallescens</i>						10		11			10	
<i>Carex panicea</i>								10				
<i>Carex pilulifera</i>							10	10				
<i>Carex vaginata</i>			10					1				
<i>Dactylis glomerata</i>									10			
<i>Deschampsia cespitosa</i>	10	10	10	10		10	10	10				10
<i>Dianthus deltooides</i>					10				10			
<i>Empetrum nigrum</i>		10	10									
<i>Epilobium anagallidifolium</i>				10			10					

Species	Ulv	Lav	Gud	Skj	Alr	Hog	Ram	Ves	Fau	Vik	Arh	Ovs
<i>Euphrasia sp</i>			10	10	10			10				
<i>Festuca ovina</i>	9		10			10				10		
<i>Festuca rubra</i>	1		3		10	10		10	10	10		
<i>Galium verum</i>									10	9		
<i>Gentianella campestris</i>					10							
<i>Geranium sylvaticum</i>			10						10		10	
<i>Hieracuim pilosella</i>			2		10		10	10	10			10
<i>Hieracium vulgatum</i>											10	
<i>Hypericum maculatum</i>					10	10				10	10	10
<i>Knautia arvensis</i>					10				10	10		
<i>Leotodon autumnalis</i>			7	10	10		10	10				
<i>Leucanthemum vulgare</i>					10				10			
<i>Lotus corniculatus</i>			10		10				10			
<i>Luzula multiflora</i>		11	10	10		10	10	10			10	
<i>Luzula pilosella</i>											5	
<i>Melampyrum pratense</i>											10	
<i>Nardus stricta</i>		10	10	10			9	10				10
<i>Noccaea caeruleascens</i>									10			
<i>Omalotheca supina</i>	10	10					8					
<i>Oxalis acetosella</i>							10					
<i>Oxyria digyna</i>		9										
<i>Parnassia palustris</i>			9	10								
<i>Phleum alpinum</i>	10											
<i>Pimpinella saxatilis</i>									10			
<i>Pinguicula vulgaris</i>							11					
<i>Plantago media</i>									10			
<i>Poa alpina</i>	10	10		9	10							
<i>Poa pratensis</i>						10						
<i>Potentilla crantzii</i>	10	10	3	9								
<i>Potentilla erecta</i>			9			10	10	11		10	10	10

Species	Ulv	Lav	Gud	Skj	Alr	Hog	Ram	Ves	Fau	Vik	Arh	Ovs
<i>Prunella vulgaris</i>					10		10	10				
<i>Pyrola minor</i>			10									
<i>Ranunculus acris</i>	10		8	1	10	10				10		
<i>Rhinanthus minor</i>					10							
<i>Rubus idaeus</i>										10		
<i>Rumex acetosa</i>		10					10		10	10	10	10
<i>Rumex acetosella</i>					10					10		10
<i>Salix herbacea</i>	11	10		10			10					
<i>Saussurea alpina</i>			10	10								
<i>Saxifraga aizoides</i>				2								
<i>Sibbaldia procumbens</i>	10	10		10			10	10				
<i>Silene acaulis</i>		10	10	10								
<i>Silene vulgaris</i>					10							
<i>Solidago virgaurea</i>			10									
<i>Stellaria graminea</i>										10		
<i>Succisa pratensis</i>												5
<i>Taraxacum sp</i>		10	11		10		10		10			
<i>Thalictrum alpinum</i>	10	10	11	10			10	10				
<i>Tofieldia pusilla</i>								10				
<i>Trifolium pratense</i>					10	10			10		10	
<i>Trifolium repens</i>					10	10		10	10	11	10	
<i>Vaccinium myrtillus</i>	9		10				10	1				
<i>Vaccinium uliginosum</i>			10					9				
<i>Vaccinium vitis-idaea</i>	10											
<i>Veronica alpina</i>	10	10	10	10			10	1				
<i>Veronica chamaedrys</i>						10				10	10	
<i>Veronica officinalis</i>					10	10	10	10	10	10	10	10
<i>Vicia craca</i>									10			
<i>Viola biflora</i>	10	10					11					
<i>Viola palustris</i>				10		10	9	10			10	10
<i>Viola riviniana</i>					10	10		10		10		

APPENDIX 3

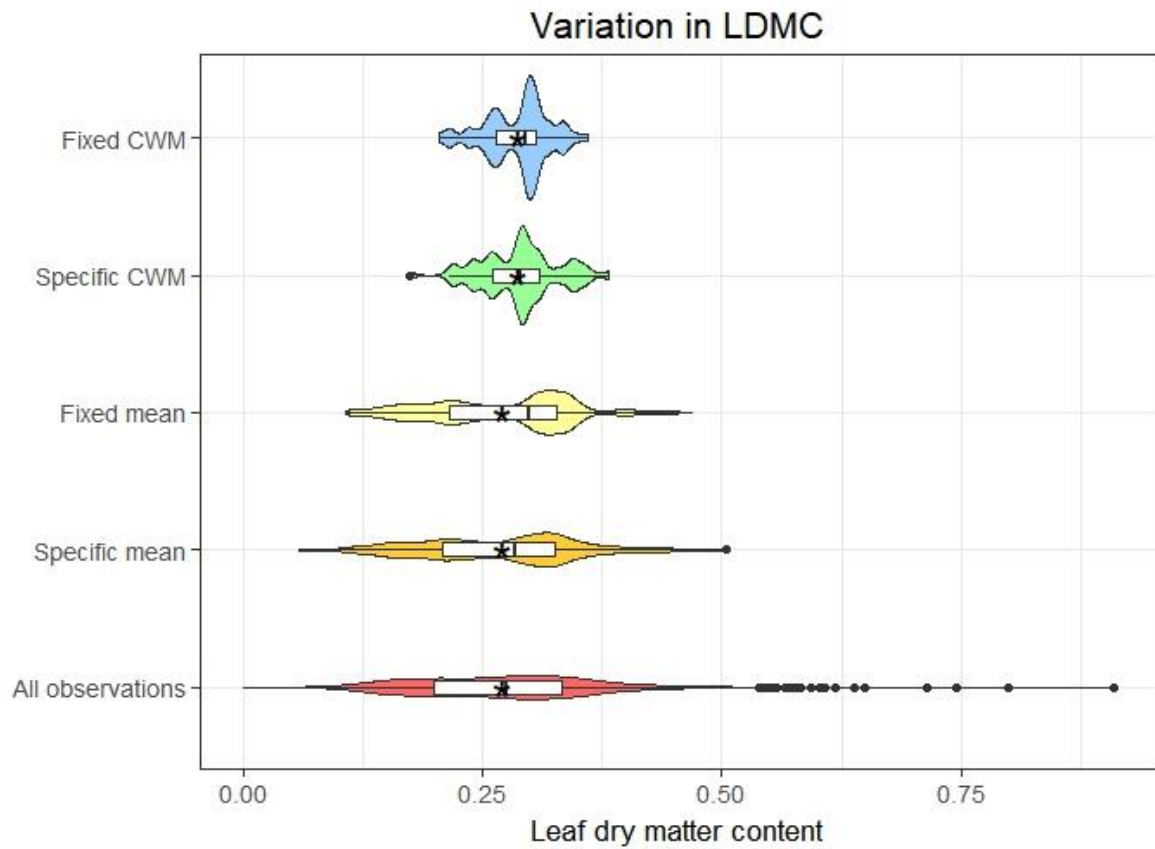


Figure 1: The distribution of leaf dry matter content (LDMC, dry mass (g)/wet mass (g)) with the median, mean (*) and quantiles. This is shown for the all the measurements (all observations), the mean of each species at each site (local mean), the mean of each species across all sites (global mean), the community weighted means calculated for each species at each site they were collected from (local CWM), the community weighted means calculated for each species using data from all locations (global CWM). Leaves were collected from boreal and alpine grasslands in the south-western part of Norway in the summer of 2016.

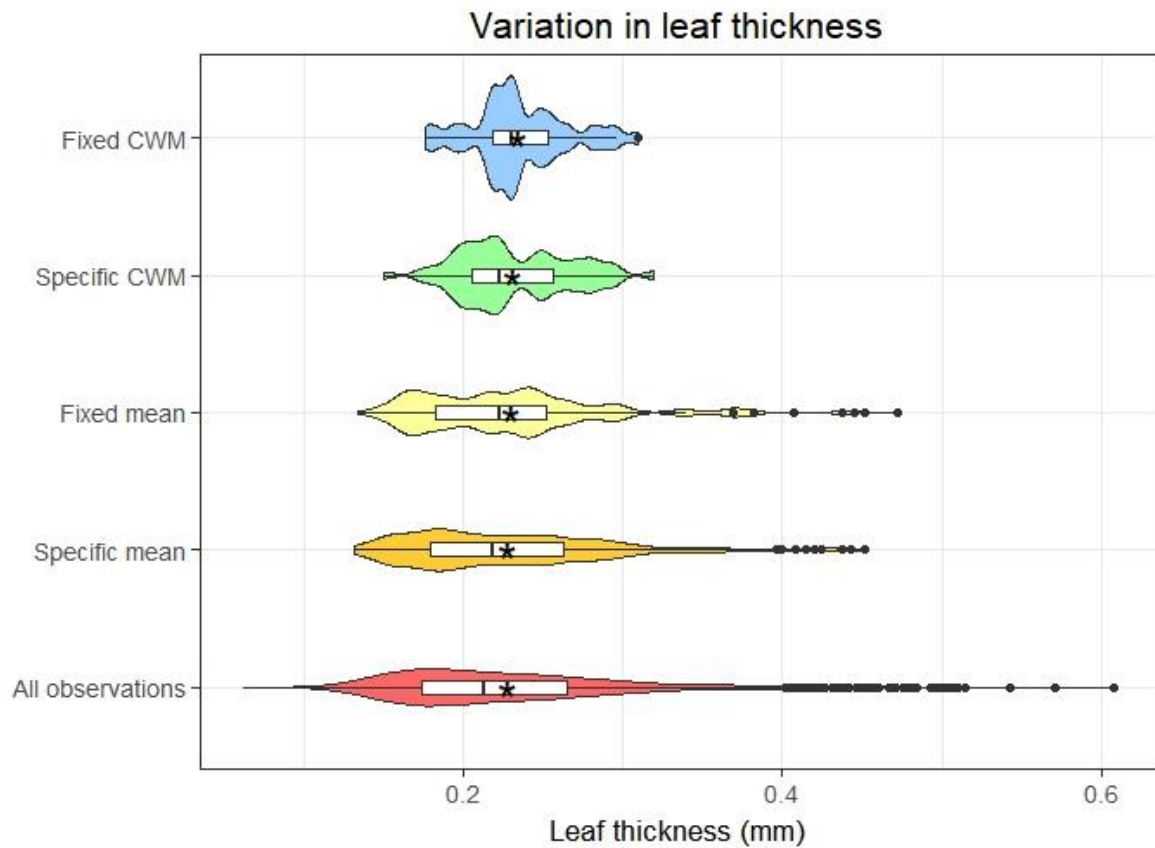


Figure II: The distribution of leaf thickness (mm) with the median, mean (*) and quantiles. This is shown for the all the measurements (all observations), the mean of each species at each site (local mean), the mean of each species across all sites (global mean), the community weighted means calculated for each species at each site they were collected from (local CWM), the community weighted means calculated for each species using data from all locations (global CWM). Leaves were collected from boreal and alpine grasslands in the south-western part of Norway in the summer of 2016.

Variation in height of forbs

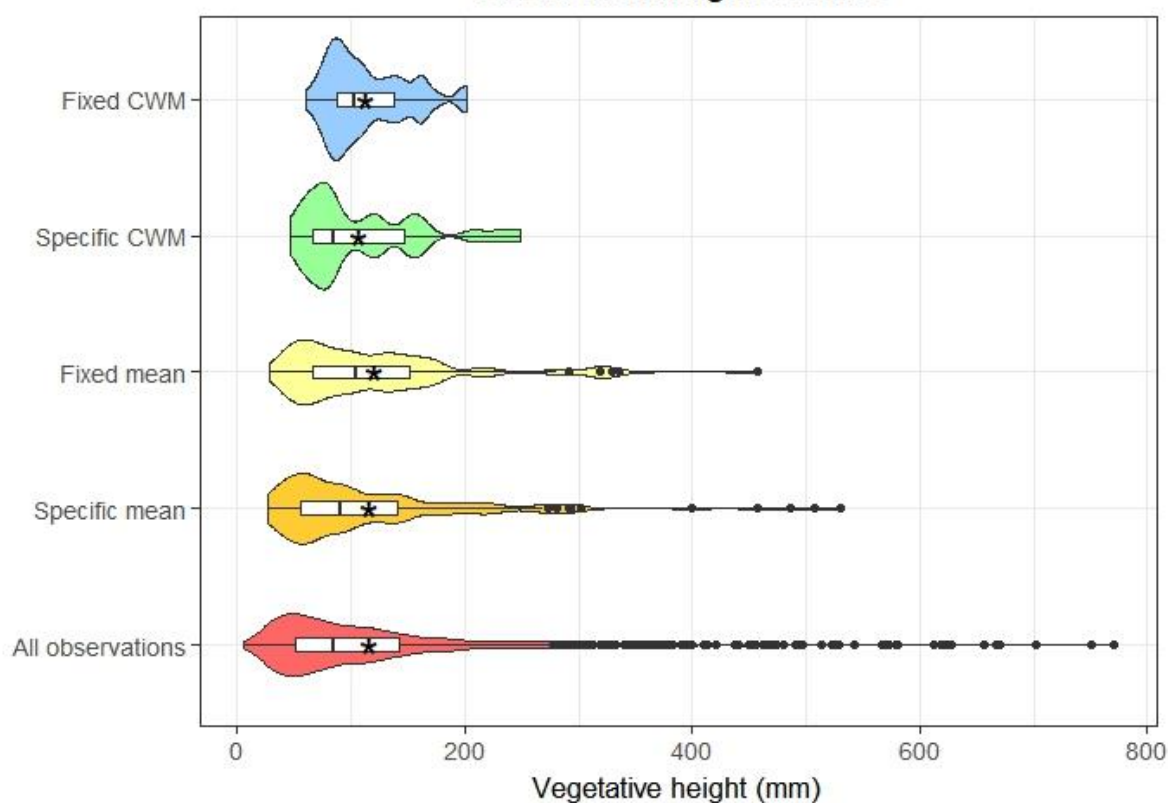


Figure III: The distribution of vegetative height of forbs (mm) with the median, mean (*) and quantiles. This is shown for the all the measurements (all observations), the mean of each species at each site (local mean), the mean of each species across all sites (global mean), the community weighted means calculated for each species at each site they were collected from (local CWM), the community weighted means calculated for each species using data from all locations (global CWM). Leaves were collected from boreal and alpine grasslands in the south-western part of Norway in the summer of 2016.

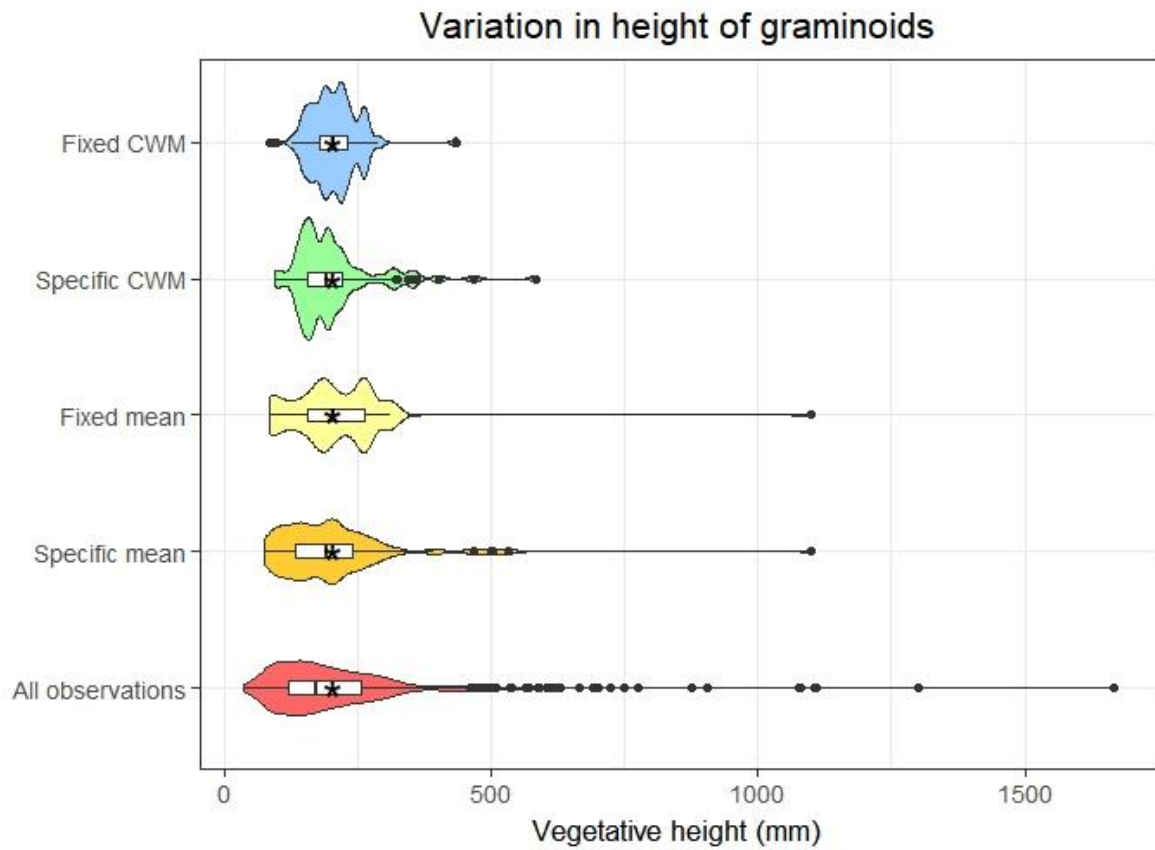


Figure IV: The distribution of vegetative height of graminoids (mm) with the median, mean (*) and quantiles. This is shown for the all the measurements (all observations), the mean of each species at each site (local mean), the mean of each species across all sites (global mean), the community weighted means calculated for each species at each site they were collected from (local CWM), the community weighted means calculated for each species using data from all locations (global CWM). Leaves were collected from boreal and alpine grasslands in the south-western part of Norway in the summer of 2016.

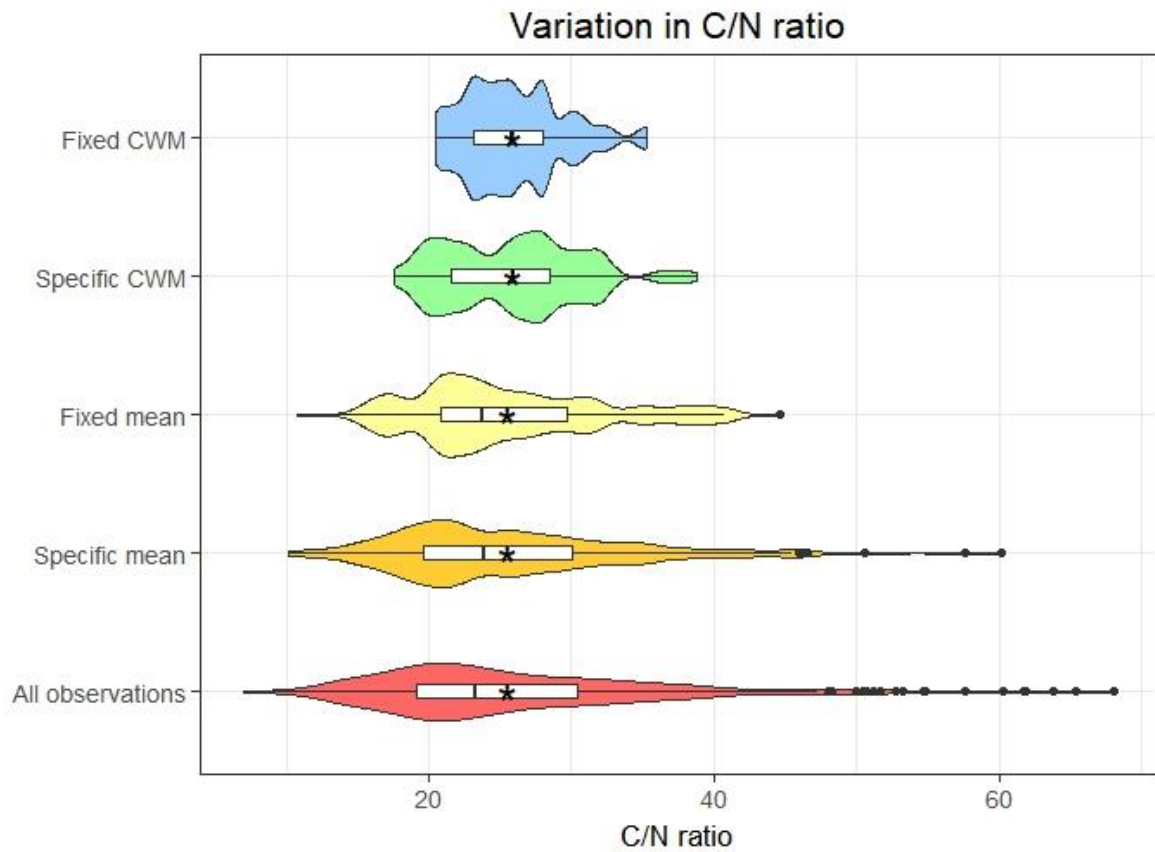


Figure V: The distribution of C/N ratio of the leaves with the median, mean (*) and quantiles. This is shown for the all the measurements (all observations), the mean of each species at each site (local mean), the mean of each species across all sites (global mean), the community weighted means calculated for each species at each site they were collected from (local CWM), the community weighted means calculated for each species using data from all locations (global CWM). Leaves were collected from boreal and alpine grasslands in the south-western part of Norway in the summer of 2016.

APPENDIX 4

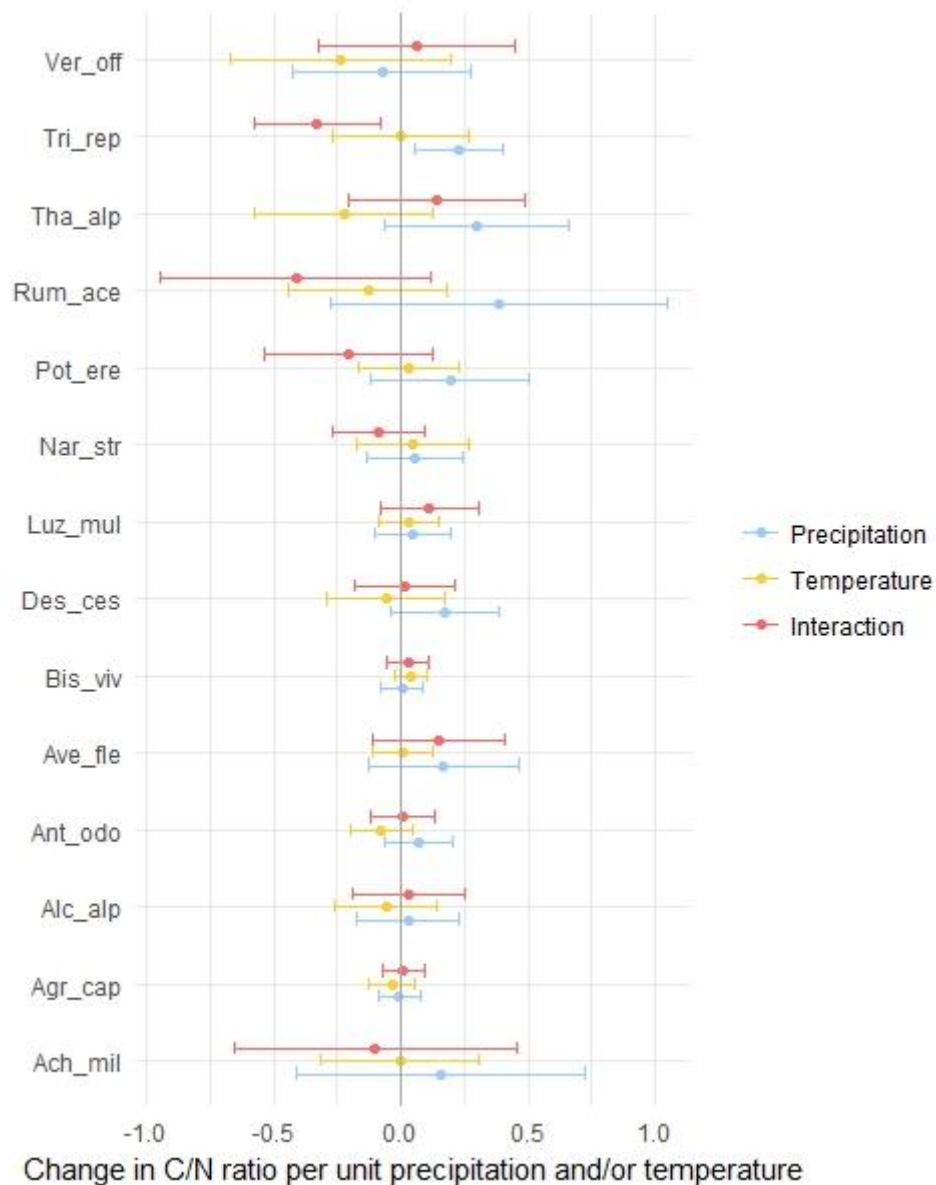


Figure VI: Changes in C/N ratio (log) of the leaves per unit precipitation and/or temperature (scaled values) for each of the 15 most common species that were collected in an alpine and boreal grassland in south-western Norway over the summer of 2016. The point shows the estimate of the change in C/N ratio per unit precipitation and/or temperature, the whiskers show the 95% confidence interval.

Ach_mil = *Achillea millefolium*, Agr_cap = *Agrostis capillaris*, Alc_alp = *Alchemilla alpine*, Ant_odo = *Anthoxanthum odoratum*, Ave_fle = *Avenella flexuosa*, Bis_viv = *Bistorta vivipara*, Cam_rot = *Campanula rotundifolia*, Des_ces = *Deschampsia cespitosa*, Luz_mul = *Luzula multiflora*, Nar_str = *Nardus stricta*, Pot_ere = *Potentilla erecta*, Rum_ace = *Rumex acetosa*, Tha_alp = *Thalictrum alpinum*, Tri_rep = *Trifolium repens*, Ver_off = *Veronica officinalis*.

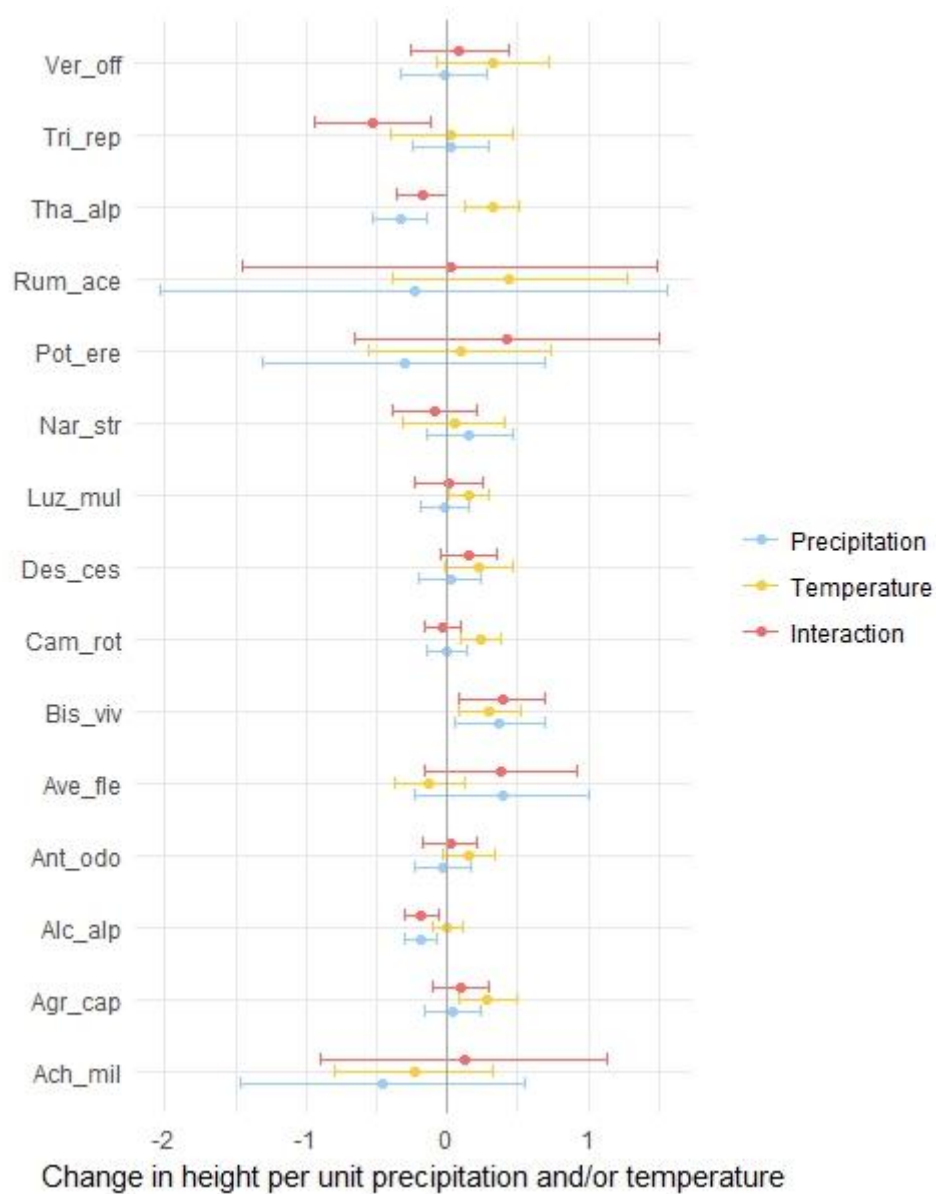
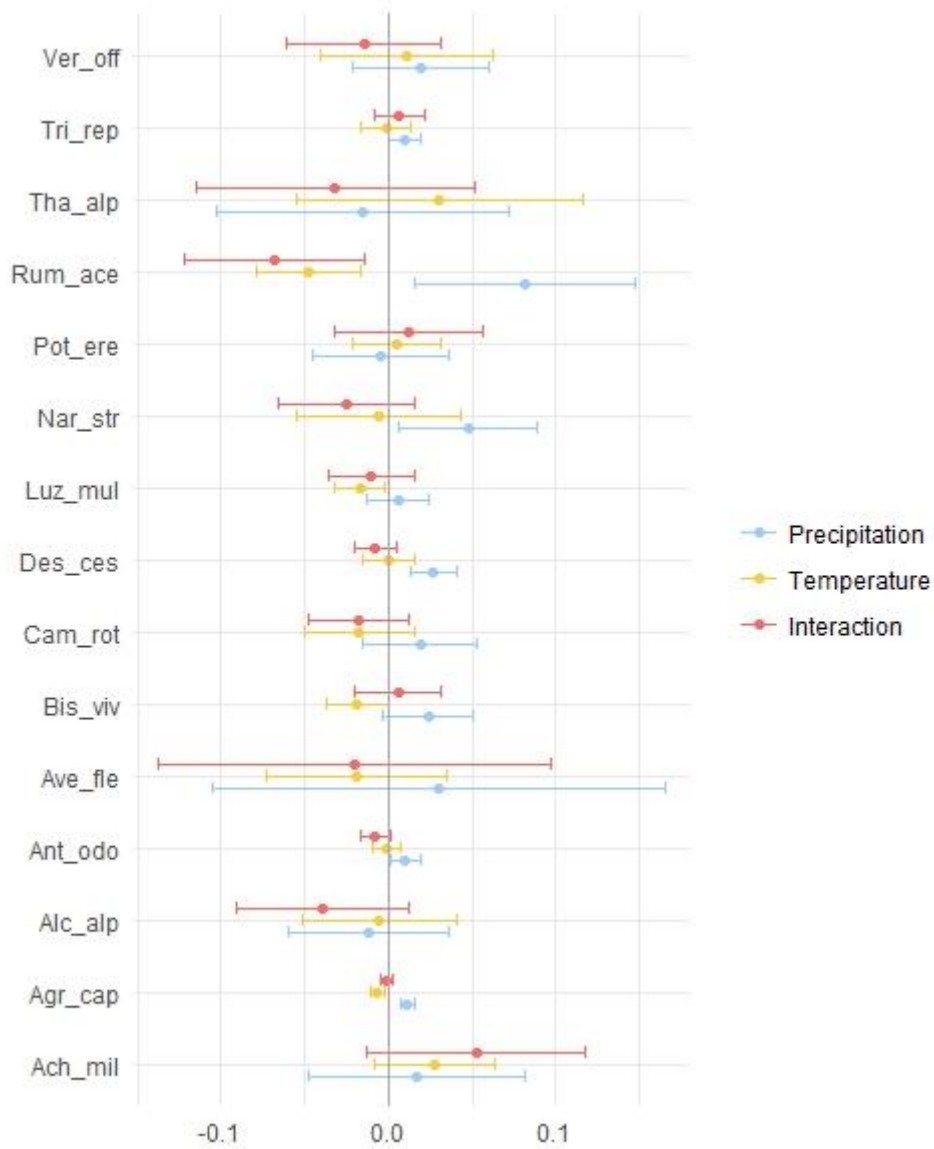


Figure VII: Changes in vegetative height (log mm) of the leaves per unit precipitation and/or temperature (scaled values) for each of the 15 most common species that were collected in an alpine and boreal grassland in south-western Norway over the summer of 2016. The point shows the estimate of the change in vegetative height per unit precipitation and/or temperature, the whiskers show the 95% confidence interval.

Ach_mil = *Achillea millefolium*, Agr_cap = *Agrostis capillaris*, Alc_alp = *Alchemilla alpine*, Ant_odo = *Anthoxanthum odoratum*, Ave_fle = *Avenella flexuosa*, Bis_viv = *Bistorta vivipara*, Cam_rot = *Campanula rotundifolia*, Des_ces = *Deschampsia cespitosa*, Luz_mul = *Luzula multiflora*, Nar_str = *Nardus stricta*, Pot_ere = *Potentilla erecta*, Rum_ace = *Rumex acetosa*, Tha_alp = *Thalictrum alpinum*, Tri_rep = *Trifolium repens*, Ver_off = *Veronica officinalis*.



Change in leaf thickness per unit precipitation and/or temperature

Figure VIII: Changes in leaf thickness (mm) of the leaves per unit precipitation and/or temperature (scaled values) for each of the 15 most common species that were collected in an alpine and boreal grassland in south-western Norway over the summer of 2016. The point shows the estimate of the change in leaf thickness per unit precipitation and/or temperature, the whiskers show the 95% confidence interval.

Ach_mil = *Achillea millefolium*, Agr_cap = *Agrostis capillaris*, Alc_alp = *Alchemilla alpine*, Ant_odo = *Anthoxanthum odoratum*, Ave_fle = *Avenella flexuosa*, Bis_viv = *Bistorta vivipara*, Cam_rot = *Campanula rotundifolia*, Des_ces = *Deschampsia cespitosa*, Luz_mul = *Luzula multiflora*, Nar_str = *Nardus stricta*, Pot_ere = *Potentilla erecta*, Rum_ace = *Rumex acetosa*, Tha_alp = *Thalictrum alpinum*, Tri_rep = *Trifolium repens*, Ver_off = *Veronica officinalis*.

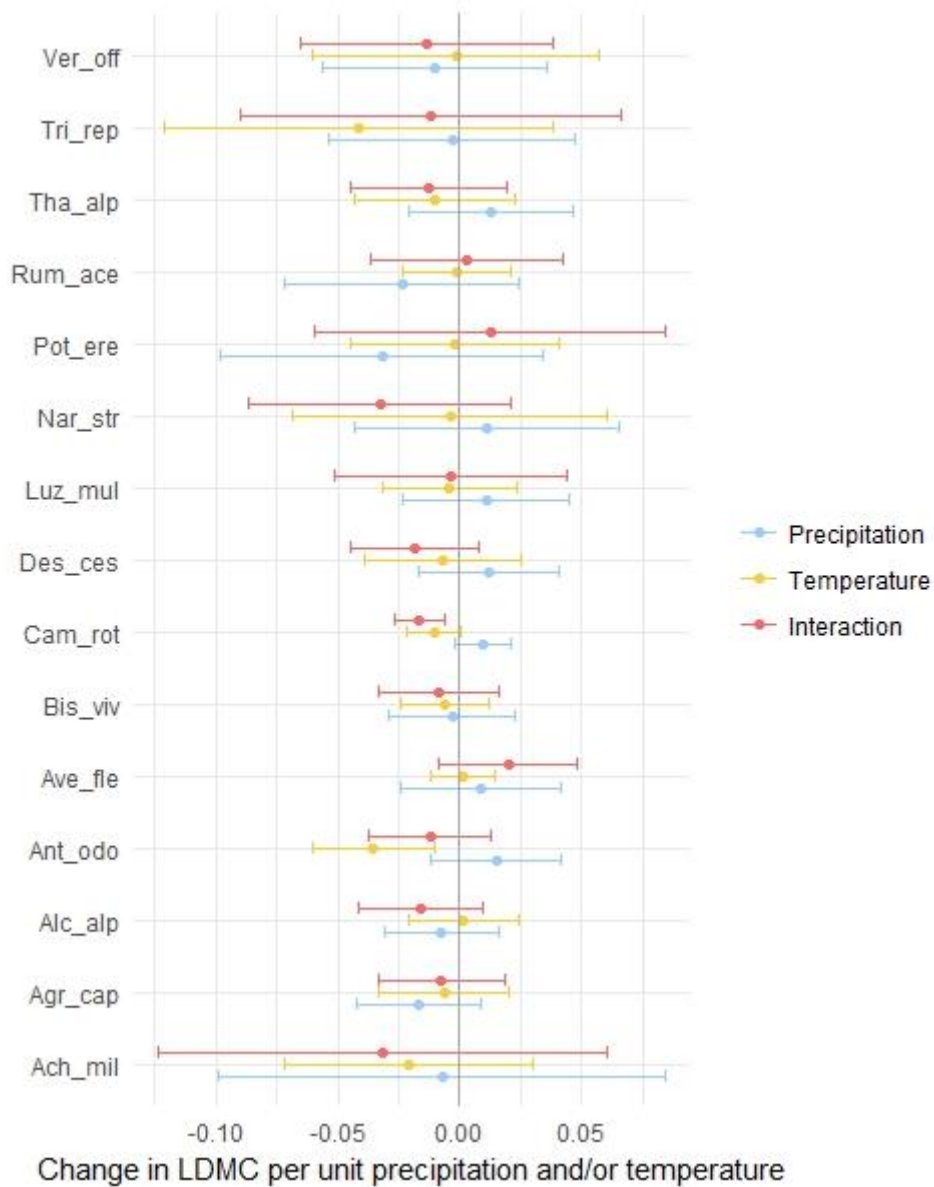


Figure IX: Changes in leaf dry matter content (LDMC) of the leaves per unit precipitation and/or temperature (scaled values) for each of the 15 most common species that were collected in an alpine and boreal grassland in south-western Norway over the summer of 2016. The point shows the estimate of the change in LDMC per unit precipitation and/or temperature, the whiskers show the 95% confidence interval.

Ach_mil = *Achillea millefolium*, Agr_cap = *Agrostis capillaris*, Alc_alp = *Alchemilla alpine*, Ant_odo = *Anthoxanthum odoratum*, Ave_fle = *Avenella flexuosa*, Bis_viv = *Bistorta vivipara*, Cam_rot = *Campanula rotundifolia*, Des_ces = *Deschampsia cespitosa*, Luz_mul = *Luzula multiflora*, Nar_str = *Nardus stricta*, Pot_ere = *Potentilla erecta*, Rum_ace = *Rumex acetosa*, Tha_alp = *Thalictrum alpinum*, Tri_rep = *Trifolium repens*, Ver_off = *Veronica officinalis*.

APPENDIX 5

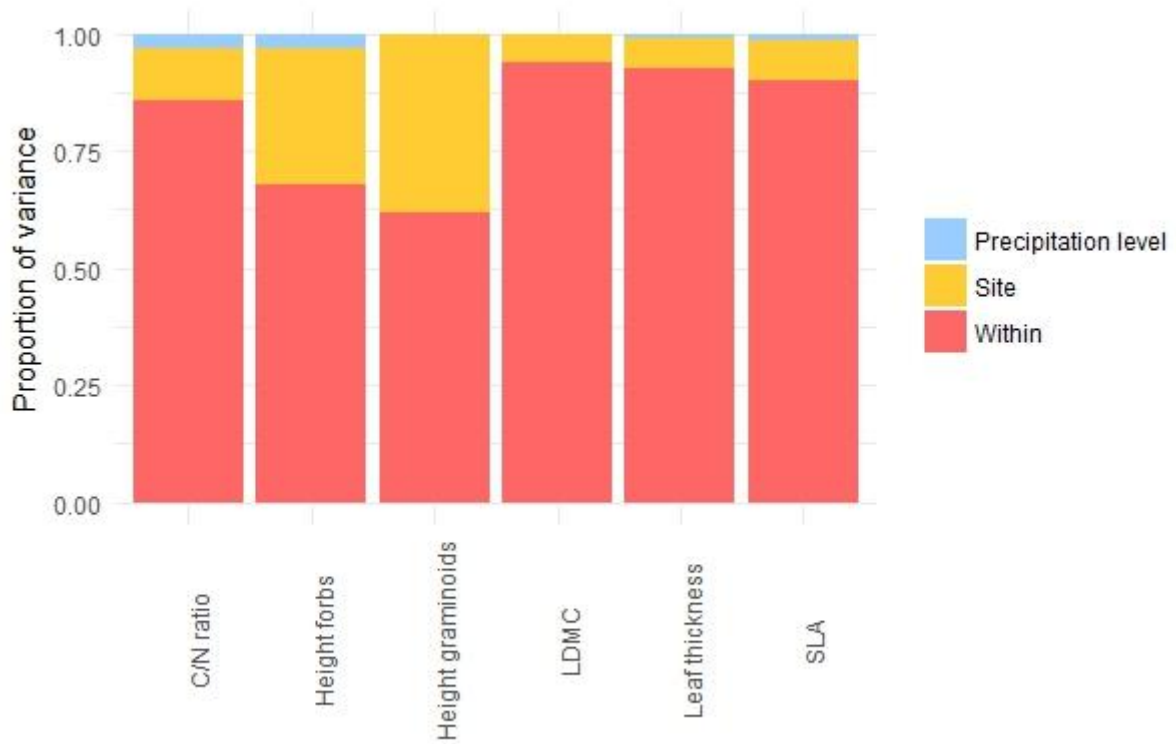


Figure X: Variance partitioning of traits between levels of within site, between site and between precipitation level in which several sites are nested in. These variance partitionings are approximate, using the total variance in the trait measurements to calculate the partitioning. Traits were collected from boreal and alpine grasslands in south-western Norway over the summer of 2016.

APPENDIX 6

Table III: Proportion of competitive, stress-tolerant and ruderal strategies for species sampled in the thesis “The role of intraspecific variability in driving community trait shifts along temperature and precipitation gradients in alpine and boreal semi-natural grasslands”. Strategies were calculated using leaf trait values and the StrateFy protocol from Pierce et al. (2017). Table goes over four pages.

Species	C (%)	S (%)	R (%)	CSR-strategy
<i>Achillea millefolium</i>	27.2	33.5	39.4	CSR
<i>Agrostis capillaris</i>	8.8	53.1	38.1	SR
<i>Alchemilla alpina</i>	16.4	66.5	17.0	S/SR
<i>Alchemilla sp</i>	27.1	38.2	34.6	CSR
<i>Antennaria dioica</i>	2.3	51.6	46.1	SR
<i>Anthoxanthum odoratum</i>	10.7	50.0	39.4	SR
<i>Astragalus alpinus</i>	21.1	29.3	49.6	R/CSR
<i>Avenella flexuosa</i>	4.8	76.5	18.7	S/SR
<i>Bistorta vivipara</i>	19.7	33.3	47.0	SR/CSR
<i>Campanula rotundifolia</i>	3.3	57.0	39.7	SR
<i>Carex bigelowii</i>	9.8	68.1	22.1	S/SR
<i>Carex capillaris</i>	4.3	59.4	36.4	SR
<i>Carex flava</i>	9.6	58.3	32.1	S/CSR
<i>Carex leporina</i>	11.3	59.4	29.3	S/CSR
<i>Carex nigra</i>	10.2	59.5	30.4	S/CSR
<i>Carex norvegica</i>	10.1	67.2	22.7	S/SR
<i>Carex pallescens</i>	13.5	54.0	32.5	S/CSR
<i>Carex panicea</i>	9.5	65.9	24.6	S/SR
<i>Carex pilulifera</i>	8.1	60.8	31.0	S/SR
<i>Carex vaginata</i>	14.6	62.4	23.0	S/CSR
<i>Dactylis glomerata</i>	29.4	50.5	20.1	S/CSR
<i>Deschampsia cespitosa</i>	16.5	66.0	17.5	S/SR
<i>Dianthus deltoides</i>	0.2	69.3	30.5	S/SR
<i>Empetrum nigrum</i>	0.0	85.8	14.2	S
<i>Epilobium anagallidifolium</i>	6.0	42.8	51.2	SR

Species	C (%)	S (%)	R (%)	CSR-strategy
<i>Euphrasia sp</i>	1.4	52.7	45.9	SR
<i>Festuca ovina</i>	2.3	84.3	13.4	S
<i>Festuca rubra</i>	7.9	67.5	24.5	S/SR
<i>Galium verum</i>	0.0	84.1	15.9	S
<i>Gentianella campestris</i>	14.0	0.0	86.0	R
<i>Geranium sylvaticum</i>	43.5	31.0	25.4	CSR
<i>Hieracium pilosella</i>	32.8	3.7	63.5	R/CR
<i>Hieracium vulgatum</i>	39.5	0.0	60.5	CR
<i>Hypericum maculatum</i>	10.8	45.7	43.4	SR
<i>Knautia arvensis</i>	38.5	25.7	35.8	CSR
<i>Leotodon autumnalis</i>	20.4	0.0	79.6	R/CR
<i>Leucanthemum vulgare</i>	20.9	23.2	55.9	R/CSR
<i>Lotus corniculatus</i>	11.6	43.5	45.0	SR/CSR
<i>Luzula multiflora</i>	11.3	38.1	50.7	SR/CSR
<i>Luzula pilosella</i>	22.5	32.7	44.8	SR/CSR
<i>Melampyrum pratense</i>	13.2	28.6	58.1	R/CSR
<i>Nardus stricta</i>	4.6	95.4	0.0	S
<i>Noccaea caerulea</i>	5.6	45.8	48.5	SR
<i>Omalotheca supina</i>	1.2	40.2	58.6	SR
<i>Oxalis acetosella</i>	18.8	12.2	69.0	R/CR
<i>Oxyria digyna</i>	33.6	0.0	66.4	R/CR
<i>Parnassia palustris</i>	15.1	12.2	72.7	R/CR
<i>Phleum alpinum</i>	9.0	55.8	35.2	SR
<i>Pimpinella saxatilis</i>	15.6	61.9	22.5	S/CSR
<i>Pinguicula vulgaris</i>	14.7	0.0	85.3	R
<i>Plantago media</i>	62.4	12.4	25.3	C/CR
<i>Poa alpina</i>	7.6	64.4	28.0	S/SR
<i>Poa pratensis</i>	12.8	55.5	31.7	S/CSR

Species	C (%)	S (%)	R (%)	CSR-strategy
<i>Potentilla crantzii</i>	14.7	54.3	31.0	S/CSR
<i>Potentilla erecta</i>	9.1	55.4	35.4	SR
<i>Prunella vulgaris</i>	13.5	30.3	56.3	R/CSR
<i>Pyrola minor</i>	19.7	65.3	15.0	S/CS
<i>Ranunculus acris</i>	24.7	22.3	53.1	R/CSR
<i>Rhinanthus minor</i>	16.5	0.0	83.5	R/CR
<i>Rubus idaeus</i>	36.9	38.1	25.0	CS/CSR
<i>Rumex acetosa</i>	35.9	0.0	64.1	R/CR
<i>Rumex acetosella</i>	18.5	0.0	81.5	R/CR
<i>Salix herbacea</i>	7.8	71.2	21.0	S/SR
<i>Saussurea alpina</i>	42.6	7.8	49.6	CR
<i>Sibbaldia procumbens</i>	11.3	59.5	29.1	S/CSR
<i>Silene acaulis</i>	0.0	63.1	36.9	S/SR
<i>Silene vulgaris</i>	19.1	0.0	80.9	R/CR
<i>Solidago virgaurea</i>	20.7	36.6	42.7	SR/CSR
<i>Stellaria graminea</i>	2.2	41.0	56.8	SR
<i>Succisa pratensis</i>	42.6	0.0	57.4	CR
<i>Taraxacum sp</i>	59.8	0.0	40.2	CR
<i>Thalictrum alpinum</i>	8.4	68.1	23.6	S/SR
<i>Tofieldia pusilla</i>	6.6	60.8	32.6	S/SR
<i>Trifolium pratense</i>	20.3	45.0	34.7	SR/CSR
<i>Trifolium repens</i>	21.0	9.7	69.3	R/CR
<i>Vaccinium myrtillus</i>	5.3	76.1	18.6	S/SR
<i>Vaccinium uliginosum</i>	4.0	88.1	7.9	S
<i>Vaccinium vitis-idaea</i>	3.7	96.3	0.0	S
<i>Veronica alpina</i>	6.7	26.8	66.5	R/SR
<i>Veronica chamaedrys</i>	9.6	47.1	43.3	SR
<i>Veronica officinalis</i>	10.2	66.5	23.3	S/SR

Species	C (%)	S (%)	R (%)	CSR-strategy
<i>Vicia craca</i>	17.6	56.3	26.0	S/CSR
<i>Viola biflora</i>	19.6	0.0	80.4	R/CR
<i>Viola palustris</i>	30.3	0.0	69.7	R/CR
<i>Viola riviniana</i>	14.7	40.1	45.3	SR/CSR