# The importance of vegetation functional composition in mediating climate change impacts on ecosystem carbon dynamics in alpine grasslands

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UNIVERSITY OF BERGEN

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"In all things of nature there is something of the marvelous"

— Aristotle —

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To all of you,

Bedankt!

# Contents

# Abstract

Climate is changing around the world, and because temperature and water are key drivers of many ecosystem processes this is expected to have significant effects on ecosystem processes and functioning, including ecosystem carbon cycling. In addition to the direct effects of increased temperature and changes is precipitation, indirect effects of climate-induced shifts in plant dominance can affect ecosystems and their functioning through a complex series of biotic cascades, couplings, and feedbacks (Wookey et al 2009). Alpine ecosystems in particular are expected to be strongly impacted by global warming because of the high temperature-sensitivity of biological and chemical processes and their vulnerability to vegetation shifts.

In this thesis, I investigate the direct and indirect effects of climate change on ecosystem carbon dynamics in semi-natural alpine grasslands. The study design makes use of a systematic climate grid in Western Norway that consists of twelve semi-natural grassland selected along natural climate gradients, where temperature and precipitation vary independently. At each site we performed a fully factorial removal experiment, removing different plant functional groups (graminoids, forbs, bryophytes), to determine their effect on ecosystem carbon cycling and soil physical conditions. In addition, several plant functional traits were measured at each site to assess their contribution in determining ecosystem carbon exchange compared to climate and vegetation structure characteristics. I used a static chamber method to measure ecosystem carbon flux and estimate net ecosystem exchange (NEE), gross primary production (GPP) and ecosystem respiration ($R_{eco}$) across the climatic gradients and removal experiment. Furthermore, I performed a standardized litter bag experiment to investigate the short-term direct effect of annual variability in temperature and precipitation and long-term indirect effect of climate variability along the natural climatic gradients on litter decomposition.

The presence and functional composition of vegetation regulated soil temperature and to an extent soil moisture, which are key controls of ecosystem processes. Vegetation cover reduced maximum soil temperature due to the vegetation's insulating capacity or shading. The strength of this effect depended on vegetation structure, plant functional group cover and vascular and non-vascular vegetation height. Bryophytes had a larger effect on soil temperature than forbs or graminoids, and increased depth of bryophyte mat strengthened the insulating effect of bryophytes. Soil moisture was primarily determined by the amount of precipitation received by a research site. Functional attributes of vegetation will therefore influence ecosystem processes like plant growth and decomposition through their regulating effect on soil temperature and thus influence ecosystem carbon cycling.

Gross primary production was largely determined by vascular plant biomass, while respiration was primarily controlled by temperature and was little influenced by biomass of vascular plants. Bryophytes did not have a significant effect on either gross primary production or ecosystem respiration. Compensation of gross primary production after plant functional group loss was dependent on remaining plant functional groups and their interaction, which again was dependent on climate. In alpine sites, compensation capacity of forbs was stimulated when bryophytes were present, while in boreal sites compensation capacity of gramininoids

seemed to be limited by bryophytes. For ecosystem respiration there was no difference in compensation capacity between plant functional groups nor effects of climate.

We assessed the value of using plant functional traits for predictions of ecosystem C flux in relation to climate change. Climatic effects on gross primary production were related to changes in vegetation structure and plant functional traits, particularly a shift in traits of plant communities from tall, fast-growing species with big, thin leaves and low C:N in warmer drier sites to communities with lower growth, small and thicker leaves and higher leaf C:N cold sites. Plant functional traits were also able to capture additional between-site variation in ecosystem carbon exchange not related to climate, and could even account for appreciable amounts of variability at the within-site scale, which is likely related to smaller-scale driver of vegetation community composition such as topography and soil characteristics.

The decomposition experiment revealed that direct effect of annual variation in temperature and precipitation on decomposition processes are modulated by environmental conditions, including plant diversity. Increasing temperature enhanced decomposition rate $k$ and litter stabilization factor $S$ within each climate regime, while this effect was not found across the different climate regimes for $k$ and even had the reverse effect on $S$, as $S$ decreased with temperature across climate regimes. Increased precipitation reduced $k$ within and across climatic regimes, while increased precipitation decreased S in sub-alpine and alpine sites, but not boreal sites. We speculate that the differences in decomposition between climate regimes can related to differences in microbial community composition and soil structure.

Altogether, this thesis highlight the importance of local environmental conditions and the functional composition of vegetation as modulators of climate change impacts on ecosystem carbon dynamics. This knowledge improves our understanding of how climate-induced changes in the functional composition of vegetation can affect ecosystem carbon cycling, and can possibly help improve predictability of ecosystem carbon exchange under global warming.

# List of individual papers

Paper I    Althuizen, I.H.J., Gya, R., Jaroszynska, F., Lee, H., Telford, R.J., Enquist, B.J., Goldberg, D., and Vandvik, V. Trait shifts affect ecosystem carbon exchange under climate change in alpine grasslands (*in review Global Change Biology*)

Paper II   Althuizen, I.H.J., Jaroszynska, F., Halbritter, A.H., Lee, H., Telford, R.J., Vandvik, V. Contribution and compensation capacity of plant functional groups on ecosystem carbon exchange in alpine grassland across climatic gradients (*manuscript*)

Paper III  Jaroszynska, F., Althuizen, I.H.J., Halbritter, A.H., Lee, H., Klanderud, K., Vandvik, V. Plant functional groups regulate soil microclimate in semi-natural grasslands (*draft of manuscript*)

Paper IV   Althuizen, I.H.J., Lee, H., Sarneel, J.M. and Vandvik, V.
Long-Term Climate Regime Modulates the Impact of Short-Term Climate Variability on Decomposition in Alpine Grassland Soils.
*Ecosystems*

## Specification of contributions to the individual papers

| Contributions | Paper I | Paper II | Paper III | Paper VI |
|---|---|---|---|---|
| Project/experimental design | VV, HL, BE, DG | VV, HL | VV, HL, IA, FS | VV, HL, JS |
| Data collection | IA, FJ, RG | IA, FJ | IA, FJ, AH | IA, JS |
| Data preparation | IA, FJ, RG | IA | FJ, AH | IA |
| Statistical analysis | IA, RT | IA | FJ | IA |
| Writing | IA | IA | FJ, IA | IA |
| Commenting/ Editing | VV, RG, FJ, HL, BE, RT, DG | FJ, AH, SO, HL, VV | AH, KK, HL, VV | VV, HL, JS |

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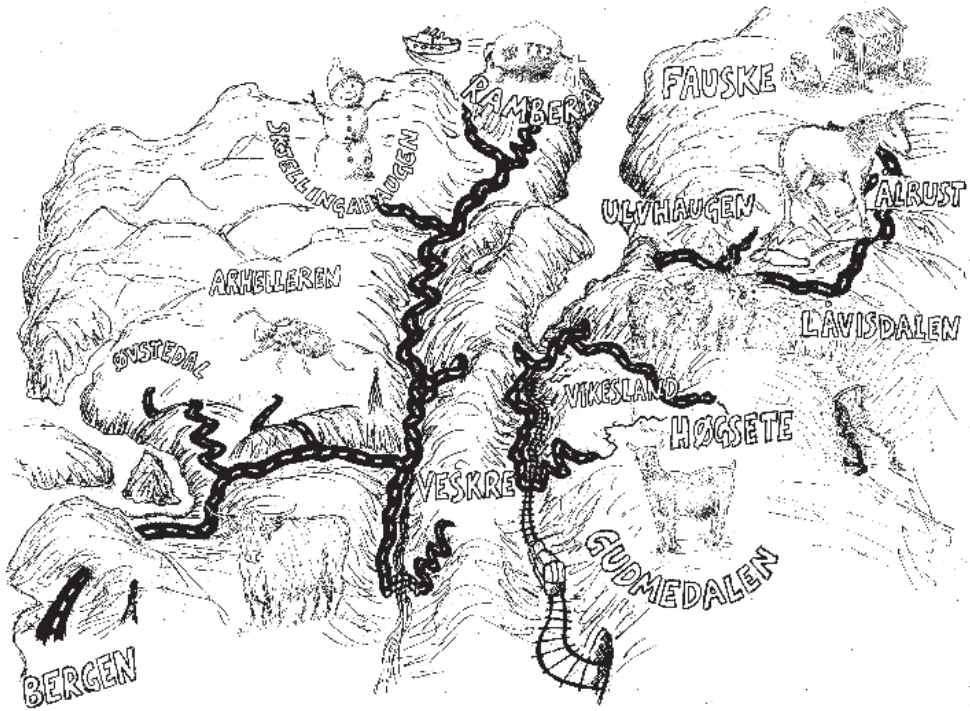
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# Synopsis

# Introduction

Climate is changing around the world, and because temperature and water are key drivers of many ecosystem processes this is expected to have significant effects on ecosystem processes and functioning, including ecosystem carbon cycling. In addition to the direct effects of increased temperature and changed precipitation, indirect effects of climate-induced shifts in plant dominance can affect ecosystems and their functioning through a complex series of biotic cascades, couplings, and feedbacks (Wookey et al 2009). The overall global impact of projected future climate change on terrestrial ecosystem carbon storage and potential feedbacks to climate remains uncertain, as models reveal large differences in the magnitude and even direction of the net change in global NEE and the geographic distribution of carbon sources and sinks (Ahlström, Schurgers, Arneth, & Smith, 2012; Friedlingstein et al., 2006). Therefore, it is important to improve our understanding of the terrestrial carbon cycling processes and particularly disentangling the direct and indirect effects of climate change on these processes.

The net exchange of $CO_2$ between terrestrial ecosystems and the atmosphere (NEE) is the balance between $CO_2$ uptake during photosynthesis (gross primary productivity; GPP) and $CO_2$ emissions associated with plant and soil respiration (ecosystem respiration; ER). This balance determines whether an ecosystem is a carbon source or a carbon sink. Temperature and precipitation have significant effects on ecosystem CO2 exchange, as they are important drivers of GPP by affecting vegetation growth (Beer et al., 2010) and ER by affecting litter decomposition processes and thus heterotrophic respiration (Aerts, 1997).

The effects of climate change on ecosystem carbon dynamics are complex. Changes in temperature and precipitation will directly affect the rate at which ecosystem processes occur, while shifts in aboveground and belowground community composition and interactions between organisms will have indirect effect on ecosystem processes. Alpine ecosystems are expected to be strongly affected by global warming because biological and chemical processes are more temperature-sensitive in colder environments (Kirschbaum, 1995; Shaver et al., 2000). In addition, alpine biomes are highly vulnerable to vegetation shifts (Gonzalez, 2010), and changes in vegetation composition are already evident in alpine and arctic ecosystems (Steinbauer et al., 2018; Walker et al., 2006).

Plant species strongly influence the responses of ecosystems to climate change, because of their effects on carbon cycling through differences in physiology, morphology, and physical and chemical properties of their living and dead tissues (Dorrepaal, 2007). Therefore, shifts in vegetation community composition could have significant effects on ecosystem carbon cycling. In addition, vegetation may have significant and potentially species-specific impacts on soil temperature and hydrology by reducing thermal extremes and evaporative moisture losses through shading, which can again feedback on plant growth and ecosystem functioning (Ehrenfeld et al 2005). In order to improve future predictions we need to improve our understanding of climate change impacts on ecosystem carbon dynamics, not only through

direct effects of temperature and precipitation, but more importantly also take into consideration the indirect effects of climate-induced changes in community composition on ecosystem processes both physical and biogeochemical.

Plant functional groups (growth forms) provide a useful framework to study vegetation responses to, and effects on, multiple environmental factors and ecosystem processes (Chapin et al., 1997). Plant functional groups consist of plant species that share many morphological and physiological features and show similar responses to variation in environmental conditions or have similar effects on ecosystem processes (Chapin, Bret-Harte, Hobbie, & Zhong, 1996; Gitay & Noble, 1997). For example, distinguishing vascular plants and non-vascular plant (including bryophytes) is essential for all carbon cycling processes, because of differences between these functional groups in growth, production and decomposability (Dorrepaal, 2007). In addition, bryophytes are important ecosystem engineers that influence soil hydrology and soil temperature and thus substantially impact on ecosystem processes (Beringer, Lynch, Chapin, Mack, & Bonan, 2001). Vascular plants can be further divided into 'narrow' functional groups (i.e. evergreen shrubs, deciduous shrubs, graminoids, forbs), which are commonly used in cold, northern biomes (Chapin et al., 1996; Dorrepaal, 2007; Elmendorf et al., 2012).

Recent studies indicate that changes in plant functional group composition and their interactions play an important role in the response of ecosystem processes to climate change and net ecosystem carbon exchange (Chen et al., 2017; Fry et al., 2013; Peng et al., 2017; Suttle, Thomsen, & Power, 2007). However, we lack a comprehensive view on how climate change will affect the contribution and relative interactions between plant functional groups. The effect of vegetation changes on ecosystem properties and functioning can depend on both the response of the remaining vegetation as well as the identity of the vegetation that is lost (Bret-Harte et al., 2008; McLaren & Turkington, 2010; Suding, Miller, Bechtold, & Bowman, 2006). In addition, the nature of relationships between different plant functional groups have been shown to vary along environmental gradients (Callaway et al., 2002; Choler, Michalet, & Callaway, 2001; Olsen, Töpper, Skarpaas, Vandvik, & Klanderud, 2016). This could mean that effect of plant functional groups on ecosystem processes in response to climate change can vary across environments, dependent on the relative interactions between different functional groups.

The role of a specific functional group in ecosystem functioning can be determined by removal experiments, where the functioning of a community with a full array of species is compared with a community where that particular group of species is removed. This method can determine the direct effect of a functional group on ecosystem properties, but also its indirect effects on ecosystem properties through interactions with other groups (McLaren & Turkington, 2010). Using removal experiments in natural communities are promoted for biodiversity–ecosystem functioning studies as the communities have been formed through natural assembly processes and contain species at their natural abundance and allow for compensatory growth by the remaining community (Díaz, Symstad, Stuart Chapin, Wardle, & Huenneke, 2003). By performing the removal experiment along climatic gradients, we can

assess whether the role and interactions between functional groups are constant or vary with climate, and how this affects ecosystem carbon cycling.

More recently, the use of plant functional traits has been suggested as a way to predict ecosystem functioning from changes in vegetation composition due to environmental change (Lavorel & Garnier, 2002). Functional traits are defined as morpho-physio-phenological traits of species which can vary along environmental gradients and can affect ecosystem functioning by influencing physiological processes (Violle et al., 2007). Environmental pressures affect community composition by selecting for individuals with appropriate response traits, while ecosystem processes are affected though effect traits of the vegetation community (Chapin et al., 2000; Lavorel & Garnier, 2002). The biomass ratio hypothesis of Grime (1998) states that ecosystem properties are driven by the traits of the dominant species in the plant community, though functional diversity might provide additional information on community assembly, interactions and complementarity effects (Cadotte, 2017; Cadotte, Carscadden, & Mirotchnick, 2011). A trait-based, causal view of community diversity has gained support and believed to be more meaningful than simple measures of species richness or composition (McGill, Enquist, Weiher, & Westoby, 2006). Furthermore, it could offer additional insight into ecosystem functioning and improve ecosystem modelling compared to classical approaches based on the use of plant functional types (Butler et al., 2017; Reichstein, Bahn, Mahecha, Kattge, & Baldocchi, 2014; Van Bodegom et al., 2012).

Altogether, the functional composition of vegetation plays a significant role in ecosystem carbon cycling, and could modulate the impact of climate change and the feedback of greenhouse gas emission to the climate system. In order to better predict the impacts of global change on terrestrial ecosystem functions and to examine their feedbacks to climate change it is of great importance to understand the processes and controls over photosynthesis and respiration. This thesis addresses the role of direct and indirect effects of climate change on ecosystem carbon cycling in alpine grasslands, with a primary focus on how vegetation composition modulates gross primary productivity, ecosystem respiration and decomposition across natural temperature and precipitation gradients.

## Aims of the thesis

The overall aim of this thesis is to investigate the direct and indirect effects of climate change on ecosystem carbon dynamics in alpine grasslands. The impact of indirect, climate-induced changes in vegetation composition on ecosystem carbon cycling was studied by using natural climate gradients in combination with a removal experiment. To determine the effect of vegetation changes on carbon cycling we distinguished between different plant functional groups and made use of plant functional traits. Furthermore, the short-term direct effect of climate and long-term indirect effect of climate on litter decomposition was studied in a standardized litter bag experiment. The studies presented in this thesis address the climate and climate-change effects on carbon cycling processes along both temperature and precipitation gradients, because it has been stressed that the combination of these two climatic factors is crucial to study interactive effects of climate change (Luo et al 2008, Wu et al 2011).

The specific questions addressed in this thesis are:

- Do plant functional traits that reflect the leaf economics spectrum provide additional predictability of ecosystem carbon exchange along regional climatic gradients in alpine grasslands? (**paper I**)
- What is the contribution and compensation capacity of the different plant functional groups to ecosystem carbon exchange under climate change? (**paper II**)
- How do different plant functional groups affect soil microclimate? (**paper III**)
- What are the direct and indirect effects of climate on decomposition processes? (**paper IV**)

## Materials and Methods

*Study locations*

This study was conducted at twelve semi-natural grasslands forming a systematic climate grid located in the fjord landscape of southern Norway. The sites were arranged along natural temperature and precipitation gradients, spanning almost 1000 m in elevation and 175 km in geographical distance, in a way that temperature and precipitation varied independently. The grid combines three levels of summer temperature, *i.e.* the mean of the four warmest months June–September, representing different biogeographic zones (alpine ≈ 6.5°C, sub-alpine ≈ 8.5°C, boreal ≈ 10.5°C) with four levels of mean annual precipitation (1 ≈ 600 mm, 2 ≈1200 mm, 3 ≈ 2000 mm, 4 ≈ 2700 mm; Figure 1). Site selection was based on interpolated climate data from the normal period 1961-1990 with a resolution of 100 m (Norwegian Meteorological Institute, 2010; Tveito, Bjørdal, Skjelvåg, & Aune, 2005). Furthermore all sites are semi-natural grasslands on shallow slopes (5-20°) associated with calcareous bedrock and plant communities within the plant sociological association *Potentillo-Festucetum ovinae* (Fremstad, 1997) and other factors were kept as similar as possible; including aspect and land use (for more details see (Klanderud, Vandvik, & Goldberg, 2015; Meineri, Spindelböck, & Vandvik, 2013). To prevent animal disturbance of the experimental installations sites were fenced in summer and mowed annually to mimic past disturbance regimes. At each site, we continuously measured temperature at 2m and 20 cm above ground with UTL-3 version 3.0 temperature loggers (GEOTEST AG, Zollikofen, Switzerland) and at ground level and 5 cm below ground with MT2-05 Temperature sensors (Delta-T Devices, Cambridge, UK). Soil moisture was measured continuously with two SM200 moisture sensors (Delta-T Devices, Cambridge, UK).
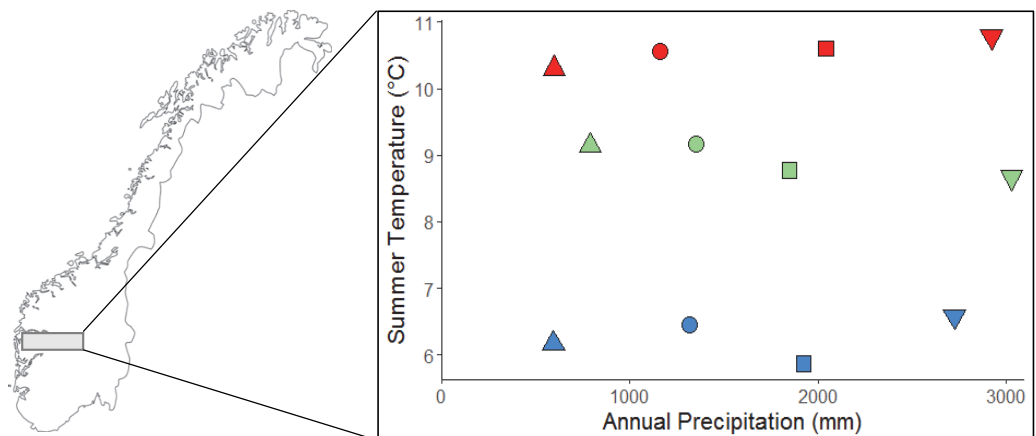


Figure 1. Map showing the location of the climate grid in south-west Norway and schematic overview of the different sites of the climate grid positioned along temperature and precipitation axes based on normal period 1961–1990. Colors correspond to temperature level; alpine = 6.5°C (blue), sub-alpine = 8.5°C (green) and boreal = 10.5°C (red). Different shapes correspond to precipitation level; 1 = 600mm (▲), 2 = 1200mm (●), 3 = 2000mm (■) and 4 = 2700mm (▼).

*Removal experiment*

To investigate the relative roles of three dominant plant functional groups on ecosystem functioning we performed a factorial removal experiment, where we removed above-ground biomass of graminoids, forbs, and mosses with hand scissors in a reciprocal removal experiment. In 2015, we established four blocks of eight 25 x 25 cm plots (n = 32) at each site for the removal experiment. The biomass removal was done twice during the growing seasons of 2015-2017. Due to unusually long-lying snow only one round of removals was done at the alpine and sub-alpine sites in 2015. The removed biomass of each plot was separated by functional group, dried at 60 ºC for 48 hours and weighed. In 2016, four additional plots were added per site, and all the above ground biomass was harvested at towards the end of the 2016 growing season and sorted into the three functional groups and litter, forbs were sorted to species. All biomass was dried at 65°C for 72 hours and weighed. To determine the effect of plant functional group removal on soil temperature, we installed Ibutton sensors (Maxim Integrated, San Jose, USA) at each plot 5 cm below soil surface.
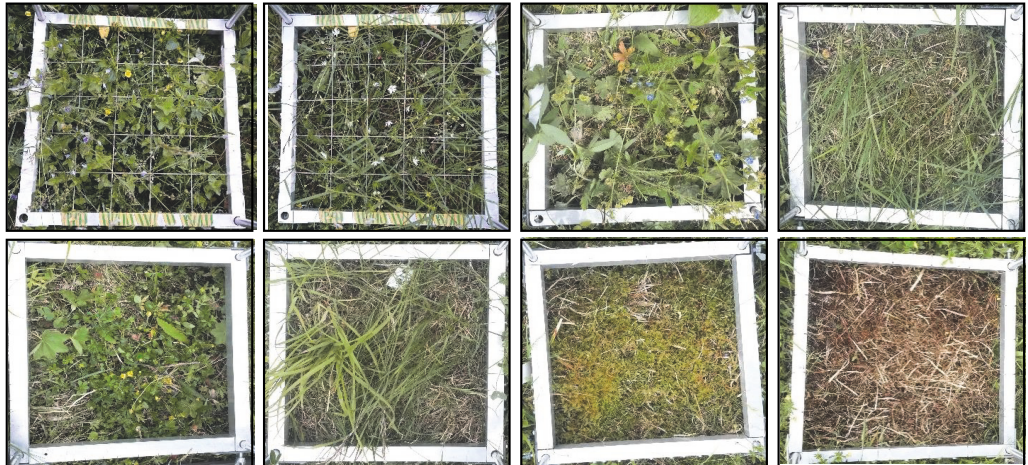


Figure 2. Removal treatments were treatment names indicate plant functional groups removed. Top row left to right; C, B, G, F. Bottom row left to right; GB, FB, GF, FGB. C = controls with no removals, G = graminoids removed; F = forbs removed; B = bryophytes removed.

## Vegetation composition and structure

Vegetation composition was determined by recording the vascular species present and estimating their relative abundance in each plot at peak growing season. The percentage cover of each species was estimated visually. Because vegetation is layered, the total cover for a plot could exceed 100%. In addition, a visual estimation of the total cover of each functional group was made, which could not exceed 100% for vascular plant vegetation. Vegetation height was determined by measuring the average height of the vegetation (mm) at four points in each plot and taking the average value of these measurements. Vegetation analysis was done before removals at the start of the study in 2015, while in 2016 and 2017 the analysis was done after the first round of removals. Vegetation structure was characterized by these measurements of community composition, plant growth and calculations of community richness, evenness and diversity.

## Plant functional traits

We measured plant traits at each site for the most abundant vascular species that collectively made up close to 80% of the cumulative abundance of the community at each particular site (Garnier et al 2004). For each of these species, one leaf was sampled locally from ten individuals in peak growing season of 2016, following the protocol of Pérez-Harguindeguy et al. (2013). The following leaf traits were measured: leaf area (LA; $cm^2$), leaf thickness (LT; mm), fresh leaf mass and oven-dry leaf mass (g; after 72h drying at 65°C) (Gya, 2017). We calculated specific leaf area (SLA; $cm^2/g$) by dividing LA by oven-dry mass, and leaf dry matter content (LDMC) as the ratio of oven-dry to fresh leaf mass. Leaf carbon (LC; g/kg) and nitrogen (LN; g/kg) content and leaf C:N ratio (LCN) was measured for three individual leaves of each species (minimum weight 5 mg), or if leaves were too light, several leaves combined into one sample. Leaves were milled using a ball mill (MM400, Retsch Gmbh, Haan, Germany) and subsequently LC, LN and LCN was measured using a Vario MICRO cube elemental analyzer (Elementar Analysesystem GmbH, Germany).

## Ecosystem carbon flux

We measured ecosystem C fluxes to estimate net ecosystem exchange (NEE), ecosystem respiration ($R_{eco}$) and gross primary production (GPP) using a static chamber method. In 2015, we measured ecosystem C fluxes for all the plots at each site before removal treatment, and in 2016 we measured all the control plots and the plots used for biomass harvest. In 2017, we measured the effect of the removal treatment on ecosystem C flux.

Ecosystem C fluxes were measured using a clear plexiglas chamber (25 x 25 x 40 cm) connected to an infrared gas analyzer (Li-840, LI-COR Biosciences, Lincoln, NE, USA) and equipped with two fans for air circulation. Wind-air mixing was prevented by a windshield attached to the bottom of the chamber that was weighed down on the ground by a heavy chain, as we did not use collars to prevent cutting of roots and disrupting of water flow. Measurements were taken throughout the growing season, but for consistency measurements at each site were taken around the time *Agrostis capillaris* flowered, as this is a common

species across the grid that flowers at peak growing season (boreal; June-early July, sub-alpine; early-mid July, alpine; late July-early August). As removal of aboveground vegetation has been shown to result in a small flush of $CO_2$ from the soil surface over the first 24h after clipping (Grogan & Chapin, 1999), we always waited at least 24 hours before taking C flux measurements.

Ecosystem C flux measurements were taken under ambient light and dark conditions. Measurements under ambient light were used to estimate NEE, a combination of photosynthetic $CO_2$ uptake and respiratory $CO_2$ release from the ecosystem (NEE= GPP-$R_{eco}$). Measurements under dark conditions were made by covering the chamber with a light impermeable material to exclude sunlight and represent $R_{eco}$, autotrophic and heterotrophic respiration. For measurement of $R_{eco}$ we covered. For each measurement, $CO_2$ concentration was recorded at 5 second interval over a period of 90-120 seconds. Other environmental conditions were monitored during the C flux measurements. Light intensity was measured as photosynthetically active radiation (PAR, $\mu mol\ m^{-2}\ s^{-1}$) using a quantum sensor (Li-190, LI-COR Biosciences, Lincoln, NE, USA) placed inside the chamber. Temperature inside the chamber was measured using an iButton temperature logger (DS1922L, Maxim Integrated, San Jose, CA, USA). Surface soil volumetric water content ($m^3\ m^{-3}$) was measured from the average of four measurements with a soil moisture sensor (SM300, Delta-T Devices, Cambridge, UK) at each plot. NEE was calculated from the temporal change of $CO_2$ concentration within the closed chamber according to the following formula:

$$NEE = \frac{\delta CO_2}{\delta t} \times \frac{PV}{R \times A \times (T + 273.15)}$$

where $\delta CO2/\delta t$ is the slope of the $CO_2$ concentration against time ($\mu mol\ mol^{-1}\ s^{-1}$), P is the atmospheric pressure (kPa), R is the gasconstante ($8.314\ kPa\ m^3\ K^{-1}\ mol^{-1}$), T is the air temperature inside the chamber (°C), V is the chamber volume ($m^3$) and A is the surface area ($m^2$).

*Decomposition*

Decomposition parameters, initial decomposition rate (*k*) and stabilization factor (*S*; amount of labile litter stabilizing), were quantified for all 12 sites using the Teabag Index method (TBI) method (Keuskamp, Dingemans, Lehtinen, Sarneel, & Hefting, 2013) for the summers of 2014, 2015 and 2016. For each site and year, air-dried, weighed Lipton green tea and Lipton rooibos tea–bags with a nylon mesh were buried in pairs directly after snowmelt at a depth of 8 cm and collected after an *in situ* incubation period of 60-98 days, depending on the duration of the snow–free season. After collection, adhering soil particles and roots were removed and the tea–bags were dried (48h at 60°C) and weighed. Three additional tea–bags of each type of tea were not buried but handled and dried the same way as the experimental tea–bags to allow correction for weight loss during transport and drying.

Figure 3. Photos of fieldwork. Top left: Ecosystem carbon flux measurement with static chamber method. Top right: Markings of buried litter bags. Bottom: Vegetation analysis and ecosystem carbon flux measurements at the driest boreal site (Fauske).

## Analytical approaches

*Plant functional traits as predictors of ecosystem carbon exchange*

In **paper I**, the relative contribution of climate, vegetation structure and plant functional traits to the predictability of ecosystem carbon exchange is determined at the between and within site scale. We determined the relationship of individual climate, vegetation structure, and trait variables with GPP and $R_{eco}$ using mixed effect models. Next, we built three separate multiple linear regression models using only predictors of a single group of variables (climate, vegetation structure characteristics or plant functional traits) for both ecosystem carbon fluxes. Then we determined the respective distinct and joint effect of climate, vegetation structure and plant functional traits at the between- and within site scale using variance partitioning. The total between-site variation was determined by constructing a model with site as the only explanatory factor.

*Compensation capacity of plant functional groups*

In **paper II**, we assessed the effect and compensation capacity of different plant functional groups for ecosystem carbon exchange. First, we determined the effect of the different removal treatment on each ecosystem carbon flux using mixed effect linear models with treatment as fixed effect and block nested within site as random effect. A similar model was used to determine the relative effect of climate and plant functional groups on ecosystem carbon flux, where mean summer temperature, mean annual precipitation and functional group biomass were specified as fixed effects. The compensation capacity of the different functional groups was evaluated by calculating a compensation index (Pan et al 2016). Difference in compensation capacity between PFG and temperature level were tested using two way ANOVA followed by pairwise T-tests.

*Plant functional groups effects on soil physical conditions*

In **paper III**, the effects of different plant functional groups on soil properties was determined by assessing the effect of different removal treatment on number of frost days, daily amplitude of soil temperature, maximum temperature anomaly, and soil moisture. The effect of removal treatments on soil temperature was evaluated separately for cloudy and sunny days, because solar radiation had a significant effect on soil temperature. Anomalies from total bare ground (removal of all plant functional groups) were calculated for both soil temperature and soil moisture, and used as response variables in mixed effects models. We determined the effect of plant functional group cover and plant functional group height on soil temperature by specifying a model with daily max temperature during peak growing season as response variable, plant functional group cover or height and their interaction with sunniness as fixed factors and site as random factor. For soil moisture, point measurements throughout the 2016 growing season were specified as response variable, and treatment, precipitation and temperature as fixed effects and site as a random effect.

*Climate effects on decomposition processes*

In **paper IV**, we studied the impact of short-term direct effects and long-term indirect effects of climate on decomposition processes. Direct effects of climate change were investigated through the response of decomposition processes to short-term inter-annual climate variation, whereas indirect effects were studied through the use of spatial climate gradients that represent long-term climate which is an important state factor shaping ecosystem structure and functioning. Environmental characteristics of each site were quantified by measuring soil properties and vegetation characteristics. The effect of temperature and precipitation on decomposition processes was assessed using linear regression. Next multiple linear regression models and variance decomposition were used to assess the relative effects of short-term direct effects of climate and long-term indirect effect of climate.

# Results

*Trait shifts affect ecosystem carbon exchange*

**Paper I** demonstrates that changes in gross primary production along climatic gradients are paralleled by a trait-shift in plant communities. Mean summer temperature explained almost half (13.5%) of the between-site variation in GPP (28.2%). The effect of climate on GPP was mediated by changes in vegetation structure and plant functional traits (Figure 2a, paper I). Furthermore, vegetation structure and plant functional traits were also able to explain remaining amounts of variation in GPP not related to climate at the between-site scale and an appreciable amount of variation at within-site scale (Figure 2a, paper I). In contrast, for ecosystem respiration much less of the variation could be explained by either climate, vegetation structure or plant functional traits (Figure 2b, paper I). Except for leaf quality (leaf C:N), plant functional traits were generally poor predictors of ecosystem respiration (Table 2, paper I).

*Effects and compensation capacity of plant functional groups on ecosystem carbon exchange*

**Paper II** demonstrates that plant functional groups differ in their contribution to ecosystem carbon exchange. Forbs and graminoids both contribute significantly to gross primary productivity and ecosystem respiration, unlike bryophytes (Fig 2ab, paper II). The effect of graminoids and forbs on GPP is large compared to temperature, while ecosystem respiration is primarily controlled by temperature, with plant functional group biomass only have minor effects on $R_{eco}$ (Fig 2ab, paper II). Compensation of gross primary production after plant functional group loss was dependent on remaining plant functional groups and their interaction, which again was dependent on climate. Compensation capacity of forbs was stimulated in the presence of bryophytes in alpine sites, while graminoid compensation capacity seemed to be limited by bryophytes in lowlands (Figure 3a, 4a paper II), implying facilitation by bryophytes in cold alpine climates (Callaway et al., 2002; Choler et al., 2001; Kjær, Olsen, & Klanderud, 2018; Olsen et al., 2016) and recruitment limitation by bryophytes in warmer climate (Soudzilovskaia et al., 2011). For ecosystem respiration there was no difference in compensation capacity between plant functional groups nor effects of climate.

*Regulation of soil microclimate by vegetation*

**Paper III** shows that vegetation composition significantly modifies soil temperature in summer and soil freezing in winter. Vegetation cover significantly reduced daily soil temperature amplitudes compared to bare ground on days in summer with high solar radiation and in winter it reduced the cumulative frost sum (Fig 1bc, paper III). Bryophytes in particular had a strong regulating effect on soil temperature. Bryophyte cover increases soil temperature compared to bare ground on cloudy days and keeps the soil cooler on sunny days (Fig 2a, paper III), and this effect is strengthened with increased depth of bryophyte mat (Fig 2b, paper III). They also strongly reduced the amount of frost experienced by the soil (Fig 1b, paper III). Vascular plants have much less pronounced effects on soil temperature and cumulative frost

sum. Soil moisture was primarily determined by climate regime, as soil moisture increased towards sites with higher mean annual precipitation (Fig 3a, paper III). Vegetation did not have a significant effect on soil moisture, although intact vegetation did tend to decrease soil moisture towards warmer sites, while presence of only bryophytes tended to increase soil moisture towards warmer sites (Fig S2, paper III).

*Direct and indirect climate effects on decomposition processes*

In **Paper IV**, the effect of increasing temperature on decomposition rate ($k$) and stabilization factor ($S$) across the grid and within temperature levels revealed Simpson's paradoxes. This means that the trend within different climatic regimes disappeared or reversed when looking across the entire climate grid. Increasing temperature enhanced $k$ and $S$ within each climate regime, while this effect was not found across the different climate regimes for $k$ (Figure 3a, paper IV) and even had the reverse effect on $S$, as $S$ decreased with temperature across climate regimes (Figure 3c, Paper IV). Increased precipitation reduced $k$ within and across climatic regimes, while increased precipitation decreased S in sub-alpine and alpine sites, but not boreal sites. The impact of short-term climate variability on decomposition processes is modulated by environmental factors such as soil pH, soil C:N, litter C:N and plant diversity, which are shaped by the long-term climate regime (Table 2, paper IV). These indirect effects are as important as or even more important than direct climate effects as environmental factors could explain 44% and 32% of the variation in k and S respectively, versus 22% and 33% by direct effects of climate.

# Discussion

Climate change is leading to shifts in the functional composition of plant communities and these changes in plant dominance will have significant, but complex effects on ecosystem processes (Wookey et al., 2009). Together **paper I-IV** give insight into the controlling factors of ecosystem carbon dynamics in alpine grasslands and how both direct and indirect effects of climate change will affect carbon cycling processes. Temperature and precipitation are important drivers of ecosystem processes, including plant growth (**paper I**) and decomposition (**paper IV**). Functional composition of vegetation also plays a key role in regulating ecosystem carbon dynamics in response to climate change, not only through the effect of functional traits on ecosystem carbon exchange (**paper I**) and the capability of different plant functional groups to compensate for the loss of other groups (**paper II**), but also by regulating soil microclimate (**paper III**). Furthermore, environmental conditions modulate the response of decomposition processes to the direct effects of temperature and precipitation (**paper IV**). This thesis shows that functional composition of vegetation plays important roles in ecosystem C fluxes, arguably more important than direct effects of climate, and therefore that understanding these relationships can help improve predictions of ecosystem carbon dynamics in response to climate change. However, I also find that local environmental conditions add complexity to these responses and need further attention, as they also play an role in shaping plant communities and can thus influence biotic interactions, aboveground as well as belowground (Brooker, 2006; Classen et al., 2015).

*Vegetation functional composition and Earth system modelling*

Terrestrial vegetation is a key component in the biogeochemical and biophysical dynamics of the Earth system, and among the largest sources of uncertainty in climate change predictions by Earth system models (Friedlingstein et al., 2006). However, there is much debate as to how plant diversity and function should be represented in these models as static plant functional types might misrepresent vegetation by ignoring important variation in traits related to carbon, water and nutrient cycling (Wullschleger et al., 2014).

I show that plant functional traits play an important role in mediating effects of climate change on ecosystem carbon exchange, particularly gross primary production (**paper I**). Plant communities exhibited a trait-shift along climatic gradients, from communities with fast-growing species with high vegetative height, big and thin leaves with high SLA and low C:N in warmer drier sites to communities with lower growth, small and thicker leaves and higher leaf C:N cold and wet sites (Gya, 2017). Similar changes in plant community structure have also been observed in warming studies (Debouk, de Bello, & Sebastià, 2015; Fridley, Lynn, Grime, & Askew, 2016). Plant functional traits showed limited relation to ecosystem respiration (**paper I**) although the effects of leaf quality on $R_{eco}$ reflects the importance of leaf quality as a control of litter decomposition (Aerts, 2006) and thus heterotrophic respiration. My findings demonstrate that taking into account plant functional traits can improve our understanding of the effect climate-induced changes in vegetation composition has on ecosystem carbon cycling. The importance of functional composition of vegetation for

ecosystem carbon exchange is demonstrated from a different point of view in **paper II**. I found that graminoids and forbs were able to compensate for the loss of other plant functional groups regarding GPP because of their relatively comparable photosynthetic capacity, while bryophytes were not due to their negligible contribution to GPP (**paper II**). For ecosystem respiration, compensation capacity did not vary between plant functional groups. On the other hand, bryophytes more important regulators of soil microclimate, as they dampen temperature extremes experienced by the soil in summer and reduce the number of frost days in winter more effectively than graminoids or forbs (**paper III**). Bryophytes in particular can therefore influence belowground ecosystem processes including decomposition by their effect on soil temperature (Gornall, Jónsdóttir, Woodin, & Van der Wal, 2007; Turetsky et al., 2012, **paper IV**). This findings support the need for including bryophytes into earth system models because of their effect on carbon, water and nutrient cycling (Wullschleger et al., 2014), and differentiation between bryophytes and vascular plants when estimating gross primary production from normalized difference vegetation index (NDVI) data (Yuan et al., 2014).

*Environmental context and biotic interactions*

In addition to broad-scale climatic patterns, soil conditions and local topography have also been identified as small-scale drivers of plant community structure (de Bello et al., 2013). A considerable amount of between- and within-site variation in ecosystem C exchange was explained by vegetation structure and plant functional traits that was not related to climate (**paper I**), implying that these small-scale drivers can have important influence on ecosystem C cycling by shaping vegetation structure across these heterogeneous alpine landscapes.

Observations in this thesis also support previous findings that have shown plant-plant interactions to change from competition to facilitation along environmental gradients within the climate grid (Olsen et al., 2016), following the stress-gradient hypothesis (Bertness & Callaway, 1994; Grime, 1998). Plant communities were observed to alter their investment strategies from more competitive strategies in warmer sites to more stress tolerant in colder wetter sites (Gya, 2017, **paper I**). Furthermore, compensation capacity of forbs in alpine sites was stimulated in the presence of bryophytes, while bryophytes seemed to limit compensation capacity of graminoids in lowland sites (**paper II**). This indicates facilitation (Callaway et al., 2002; Choler et al., 2001; Kjær et al., 2018; Olsen et al., 2016) of forb growth by bryophytes in cold alpine climates and recruitment limitation by bryophytes (Soudzilovskaia et al., 2011) in warmer climate.

Furthermore, long-term climatic regime and environmental conditions shaped by this long-term climate had a large effect on decomposition as they modulated the effect of temperature and precipitation on decomposition processes (**paper VI**). Plant diversity, soil pH, soil C:N and litter C:N were significant predictors of decomposition processes along our climatic gradient, and for both decomposition rate and stabilization environmental factors explained the same amount of variation or more compared to climate (Figure 4). Because these environmental factors have been shown to influence soil microbial community composition (Rousk, Brookes, & Bååth, 2010; Steinauer et al., 2015; Wan et al., 2015; Zak, Holmes,

White, Peacock, & Tilman, 2003), we speculate that differences in decomposition rate across the grid could be partly traced back to differences in microbial community composition between sites (Figure 4). Recently Classen et al. (2015) explore how climatic change affects soil microbes and soil microbe-plant interactions directly and indirectly and discussed the significant changes in microorganism-plant interactions could have for plant community composition and ecosystem function, and suggested areas for future research.
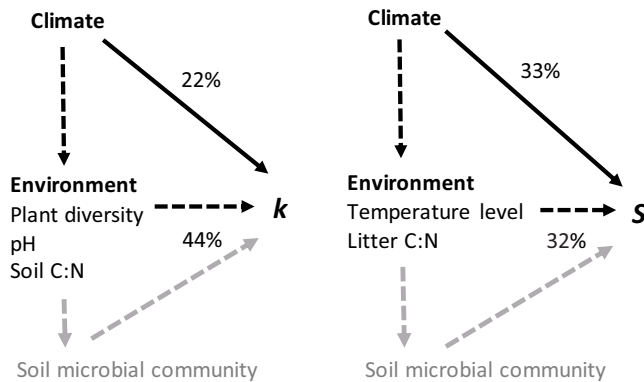


Figure 4. Conceptual diagram indicating the direct (solid arrows) and indirect (dashed arrows) effects of climate and the proportion of variance explained for decomposition processes; *k (left)* and *S (right)*. Grey components indicate proposed effect microbial community composition in mediating decomposition rate

*Plant functional traits vs species diversity*

To explain the influence of plant communities on ecosystem processes two major hypothesis have emerged: the 'diversity hypothesis' which states that the diversity of both the organisms in a community and their functional attributes influences ecosystem processes through mechanisms such as complementary resource use (Tilman et al., 1997), and the 'mass ratio hypothesis' that states that ecosystem processes are determined primarily by the functional traits of the dominant species (Grime, 1998). Studies have provided evidence supporting either hypothesis and fueled the debate as to which of the hypothesis best explains variation in ecosystem properties and processes in natural ecosystems (Mokany, Ash, & Roxburgh, 2008). However, the diversity and mass ratio hypotheses are not mutually exclusive, and it is possible that both community diversity and the functional identity of the dominant species are important in influencing ecosystem processes. In support of the mass-ratio hypothesis, community weighed mean traits and variance in traits were found to be significantly related to ecosystem processes, while measures of species diversity and richness were not (Mokany et al., 2008, **paper I**). The increasing awareness that species' traits influence coexistence and ecosystem function has led to increased interest in the links between traits and ecosystem functioning including the effects of trait variation community (Cadotte et al., 2011). Plant functional trait variance generally had negative effect, so trait variance does not seem to enhance ecosystem carbon exchange. However, the data used in our analysis focusses on

ecosystem carbon exchange and was measured around peak growing season and standardized to represent ecosystem carbon exchange under similar environmental conditions across the sites. Trait variance could be important for supporting different ecosystem functions sustaining ecosystem functioning under highly variable conditions and promote resilience of ecosystem functioning under changing environmental conditions (Jung et al., 2014; Kohler et al., 2017; Wright, 2016).

*Implications for ecosystem carbon dynamics under climate change*
Alpine ecosystems are expected to be strongly impacted by global warming because of the high temperature-sensitivity of biological and chemical processes and because alpine systems are vulnerable to vegetation shifts. Climate change will affect ecosystem carbon dynamics through direct effects of temperature and precipitation on carbon cycling processes (**paper IV**), but I show that indirect effects through climate-induced changes in plant community composition are possibly even more important as mediators of climate change (**paper I, paper II**). Plant communities showed a shift in plant functional traits that explained differences in ecosystem carbon exchange along temperature gradients (**paper I**). However, changes in vegetation composition do not necessarily have to alter ecosystem functioning, as the altered vegetation community could compensate in functioning for the loss of species or functional groups, though this will depend on functional attributes of the species lost and the remaining plant community composition (**paper II**). For example, increased grass abundance at the expense of biomass of sedges and forbs in response to climate warming did not affect net primary production (Liu et al., 2018). Furthermore, biotic interactions could play an important role in mediating climate change effects (Steinauer et al., 2015). In our study, we found indications of facilitative and competitive effects between plant functional groups that can affect compensation capacity for gross primary production (**paper II**), as plant investment strategies change along climatic gradients (**paper I**). In addition, changes in plant community composition can also affect belowground processes through the regulation of soil microclimate (**paper III**), and likely by affecting plant microbial composition (**paper IV**). C Climate-induced changes in vegetation composition therefore affect ecosystem carbon cycling in various ways that need to be accounted for when predicting the overall effect of climate change on carbon dynamics.

*Concluding remarks*
Altogether, this thesis highlight the importance of vegetation functional composition as mediators of climate change effects on ecosystem carbon dynamics. I show that plant shift in functional traits mediated effects of climate change on ecosystem carbon exchange, particularly gross primary production. Ecosystem respiration is largely controlled by direct effects of temperature and precipitation, though vegetation composition can have a modulating effect through regulation of soil microclimate. Furthermore, vegetation composition likely also affects decomposition processes by affecting microbial community composition. Climate-induced changes in vegetation composition do not necessarily have to change ecosystem functioning if the future vegetation composition can compensating for the loss of species and sustain ecosystem processes. This thesis gives important insight into the

indirect effect of climate change through vegetation functional composition, but also indicates that additional research is needed to investigate the complex cascades and feedbacks between plant and soil communities.

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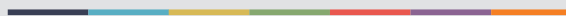
**Paper I-IV**

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