Climate and biotic interactions – drivers of plant community structure and ecosystem functioning in alpine grasslands

Francesca Jaroszynska

Thesis for the degree of Philosophiae Doctor (PhD)
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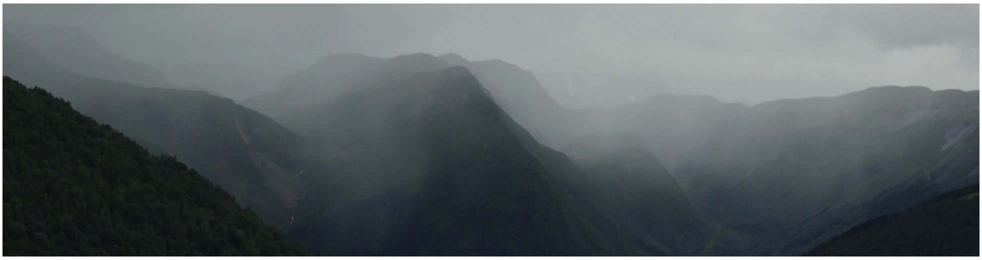
Preface

The governing of biodiversity by climate is profound. Climate as reflected through the major global temperature and precipitation axes determines the distribution of species according to their climatic tolerance, or niche. Interactions among species can mediate strong climate boundaries by expanding the margins of their realised niche through the outcome of positive and negative interactions with other species. However, global climate is undergoing rapid change, not only through increased temperatures and a redistribution of rainfall patterns, but also through a higher frequency of extreme weather events. These ongoing changes have led to a global redistribution of species, the rate of which is most pronounced in alpine regions. The variation in species-specific responses to climate change, according to their climate niche and function in the ecosystem, has consequences for community assembly and the ecosystem's functioning in alpine regions. However, very little is hitherto known about how biotic interactions mediate the combined effects of temperature and precipitation on ecosystem functioning, plant community functioning, and recruitment.

I address these unresolved questions by monitoring biotic and abiotic responses to a fully factorial removal experiment of functionally different plant types – graminoids, bryophytes and forbs – in semi-natural alpine grasslands, replicated along natural climate gradients in southern Norway. I found that although ecosystem functioning and community dynamics were largely determined directly by temperature and precipitation, these effects were strongly mediated by functional group interactions. In particular, bryophytes played a critical role – their facilitative presence increased carbon uptake by forbs at colder alpine sites, whilst limiting carbon uptake by graminoids at warmer boreal sites. Similarly, the strength of soil microclimate regulation was greatest by bryophytes, reducing both growing-season soil temperature on days with high incoming solar radiation, and reducing soil freezing during autumn and winter. Bryophyte presence additionally promoted seedling recruitment by forbs under drought conditions. Finally, graminoids alleviated climate severity for forbs in cold climates but heightened competition for resources in warm and wet climates, resulting in a selection for forb species with competitive trait attributes. The result of this effect is an inevitable reduction in biodiversity of these highly diverse ecosystems. Further increases in temperature and precipitation will increase graminoid dominance, at the expense of forb functioning and cover.

More generally, and consistently across all components of ecosystem functioning addressed in this thesis, the interactive effects of temperature and precipitation point towards non-linear changes in biotic interactions under climate change. Not only was ecosystem functioning regulated by long-term climate at the landscape scale, but also by interannual climate variation and the occurrence of extreme weather events. By conducting macroecological experiments over several years we can conclude that the spatio-temporal variation in climate causes substantial fluctuations in the role of biotic interactions in regulating carbon fluxes, microclimate, and recruitment.

In this thesis I demonstrate that the outcome of biotic interactions is dependent on regional climate, with important consequences for community structure and functioning in semi-natural grasslands. As temperatures and precipitation levels increase, alpine grasslands will become more carbon-rich and with more stable and homogeneous microclimates, whilst simultaneously becoming increasingly species poor and asymmetrical. This loss of biodiversity and change in ecosystem functioning has large consequences not only for species distributions and the persistence of alpine plants, but also more widely for predictions of ecosystem responses to further climate change.



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List of individual papers

Included in the thesis

Paper I: **Jaroszynska, F.**, Olsen, S. L., Gya, R., Klanderud, K., Telford, R. J., and Vandvik, V. Functional trait responses reveal decreasing intensity of whole-community competitive interactions towards colder and drier climates.

Manuscript prepared for Oikos

Paper II: Althuizen, I. H. J., **Jaroszynska, F.**, Halbritter, A. H., Lee, H., Olsen, S. L., Vandvik, V. The effect and compensation capacity of plant functional groups on ecosystem carbon exchange in alpine grasslands under climate change.

Manuscript prepared for *Global Change Biology*.

Paper III: **Jaroszynska, F.**, Althuizen, I. H. J., Halbritter, A. H., Telford, R. J., Lee, H., Klanderud, K., Vandvik, V. Plant functional groups regulate soil microclimate in alpine grasslands.

Submitted to *Functional Ecology.*

Paper IV: **Jaroszynska, F.**, Olsen, S. L., Klanderud, K., Vandvik. V. Functional groups differentially regulate the effect of drought on forb seedling recruitment in alpine grasslands.

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Contributions to other publications during the PhD period

Thomas, H. J. D., Myers-Smith, I. H., Bjorkman, A. D., Elmendorf, S. C., Blok, D., Cornelissen, J. H. C., … **Jaroszynska, F.**, … van Bodegom, P. M. (2019). Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome. *Global Ecology and Biogeography*, *28*(2), 78–95. https://doi.org/10.1111/geb.12783

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Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., … **Jaroszynska, F.**, … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*(7725), 57–62. https://doi.org/10.1038/s41586-018-0563-7

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., … **Jaroszynska, F.**, … Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*(7700), 231–234. https://doi.org/10.1038/s41586-018-0005-6

Specification of author contributions to the individual papers

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Project/experimental design, research ideas	FJ, KK, SLO, VV	IA, FJ, HL, VV	IA, DG, FJ, HL, VV	DG, FJ, KK, SLO, VV
Data collection	RG, SLO	IA, FJ	IA, RG, FJ	AB, FJ, VV, KK
Data preparation	FJ, RT	AH, FJ	IA, RG, FJ	AB, JG, FJ
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Writing	FJ, SLO	FJ, IA	IA, FJ	FJ
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Contents

"Yet in the terrible blasting winds on the plateau

one marvels that life can exist at all"

Nan Shepherd, *The Living Mountain* page 48

Grasslands as a web of interactions

Grasslands in alpine systems are hotspots for species diversity and carbon storage (Graae et al., 2018; Rounsevell et al., 2018), making them globally important for a range of ecosystem services (F. S. Chapin III, Reynolds, D'Antonio, & Eckhart, 1996). These grasslands are maintained by a web of non-static interdependent pathways and feedbacks between plants, the soil, and the climate. These are evident from the basic requirement of light for plants to photosynthesise, to the more complex feedbacks of species diversity on carbon flux to the atmosphere (De Boeck et al., 2007). Disturbance at any point in this web of feedbacks, such as the introduction of a new species or a change in climate, has consequences both for species diversity and carbon storage.

A fly in the web: climate change

Global climate is currently undergoing rapid change (Hanssen-Bauer et al., 2017; Masson-Delmotte et al., 2018), in terms of temperature rises, shifts in rainfall patterns, and the intensity of extreme weather events. The effects of these changes are perceptible in all biomes across the world (see Parmesan (2006) for a review) but are particularly pronounced in arctic and alpine systems (Gottfried et al., 2012; Post et al., 2009; Steinbauer et al., 2018). Decadal increases in temperature and a redistribution of rainfall patterns directly affects plants through plant physiological changes, and ecosystem processes through increased occurrence rates, such as decomposition (I. H. J. Althuizen, Lee, Sarneel, & Vandvik, 2018; F Stuart Chapin III, Matson, & Vitousek, 2011). The legacy of climate change in the reorganisation of plant growth strategies and plant interactions has been shown to moderate the direct effects of climate on ecosystem processes (Adler et al 2012). These indirect effects of climate change add another complication to interpreting plant-climate interactions, because they are hard to disentangle from the direct effects. However, by not quantifying both the direct and indirect effects we risk wrongly estimating the effects of climate change on ecosystem functioning in grasslands.

The interaction of vegetation and climate

This thesis is part of a project which experimentally disentangles the direct and indirect effects of climate on alpine grassland biodiversity and carbon cycling (see below). The quantification of biotic interactions will provide us with a better understanding of the magnitude of indirect climate effects on alpine grasslands. Indeed, a large number of studies have already revealed that the outcome of biotic interactions varies along environmental gradients (Brooker et al., 2008; Callaway et al., 2002; Callaway & Walker, 1997), demonstrating the potential for shifts in biotic interactions with climate change. The effect of climate on the outcome of biotic interactions has consequences for community assembly processes and ecosystem functioning, such as seed germination and carbon exchange (He, Bertness, & Altieri, 2013; Meineri, Spindelböck, & Vandvik, 2013). However, the majority of these studies are restricted to single species (Cavieres et al., 2014; Kardol et al., 2010), species pairs (Butterfield et al., 2013; Kikvidze et al., 2005; Soliveres & Maestre, 2014), or one benefactor nurse plant (Anthelme, Cavieres, & Dangles, 2014). To my knowledge only a handful of studies are conducted at the population (Siri L. Olsen, Töpper, Skarpaas, Vandvik, & Klanderud, 2016) or community scale (Ballantyne & Pickering, 2015; Klanderud, Vandvik, & Goldberg, 2015; Losapio, De la Cruz, Escudero, Schmid, & Schöb, 2018; Schöb, Armas, Guler, Prieto, & Pugnaire, 2013), and none that experimentally test for the reciprocal effect of climate and biotic interactions on ecosystem functioning at the community level.

One approach to simplify the wide array of functioning in species and communities is to group plant species into functional groups according to their taxonomic, physiological and morphological traits (Dorrepaal, 2007; Harrison et al., 2010; Wright et al., 2004). Distinguishing among plant functional groups when discussing ecosystem processes is crucial firstly because functional groups have been shown to respond in different ways to climate change – e.g., through increased shrub dominance and increases in graminoid abundance (Bjorkman et al., 2018; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012), and large-scale greening of the arctic (Myers-Smith et al., 2019). Secondly, their morphological and growth differences have knock-on consequences for the soil microclimate and ecosystem carbon cycling (Ehrenfeld, Ravit, & Elgersma, 2005; McLaren & Turkington, 2010; Shaw & Pereira, 1982). Thus, the outcome of altered functional group interactions may have consequences not only for community assembly processes, but ultimately the surface energy balance.

The Climate Underdogs: Rain and extremes

Studies testing for the relationship of biotic interactions to climate are predominantly conducted with air temperature as the primary climate predictor. Mounting evidence demonstrates functional group-level responses to climate change such as increases in vegetation height (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012), changes in composition and dominance (Elumeeva, Aksenova, Onipchenko, & Werger, 2018; Klanderud & Totland, 2005), and phenological shifts (Henry & Molau, 1997; Meng et al., 2017). However, there is still debate over the drivers of variation in the consistency of these patterns. For example, variation in soil temperature (Aalto, Roux, & Luoto, 2013; Graae et al., 2012; Scherrer & Körner, 2011) and soil moisture (Kemppinen, Niittynen, Aalto, le Roux, & Luoto, 2019) occurs at a much more local spatial scale, which builds a case for their regulation of locally-occurring processes.

Climate change is responsible not only for ever larger and consistent increases in temperature but also for a redistribution of rainfall patterns and an increase in the frequency of extreme weather events such as drought (Hoegh-Guldberg et al., 2018; Wigley, 2009). There are comparatively few studies testing for the effect of climate variability on biotic interactions and ecosystem functioning. Indeed, most studies that test for the effect of precipitation or climate extremes have hitherto been conducted in warm and arid environments (Maestre, Valladares, & Reynolds, 2005; Metz & Tielbörger, 2016), where water limitation is already extensive. However, drought events are also becoming more frequent in systems not adapted to them, e.g. in areas of typically high rainfall, and in these regions we do not yet know the consequences of fluctuations for short-term feedbacks in the vegetation, such as carbon flux and community assembly processes (Hunt, Kelliher, McSeveny, Ross, & Whitehead, 2004; Reichstein et al., 2003). To address such questions both spatial and temporal climate variation must be considered (De Boeck et al., 2015; Hobbs, Yates, & Mooney, 2007; Metz & Tielbörger, 2016).

Removal experiments

The reciprocal direct and indirect effects of climate on biotic interactions and carbon flux dynamics can be disentangled by replicating removal experiments along climate gradients. Removal experiments are used to disentangle the effect of different plant functional groups on a variety of community and ecosystem-level processes (Díaz, Symstad, Chapin III, Wardle, & Huenneke, 2003; McLaren & Turkington, 2010; Siri L. Olsen et al., 2016). Moreover, by replicating removal experiments along climate gradients we overcome the limitations of single-site experiments (e.g. Roscher et al., 2018).

In summary, very little is known about how biotic interactions mediate the combined effects of temperature, precipitation and climate variability on plant community and ecosystem functioning. This thesis contributes to the ongoing debate of the direct and indirect effects climate change on biodiversity and ecosystem functioning.

Understanding how plant functional groups interact with each other and their surroundings is key to interpreting and predicting community dynamics and ecosystem functioning in response to climate change. I test for the long-term and short-term effects of climate on plant functional group interactions in semi-natural alpine grasslands, and the implications of their outcomes on ecosystem functioning and processes.

To glean an insight into this rather broad topic, I approach the topic from various perspectives whilst maintaining a central focus on the plant community as either the beneficiary or the driver. In particular, I consider the following components:

1. What is the effect of regional climate on biotic interactions among plant functional groups? (**Chapter I**)
2. Do plant functional groups contribute differently to ecosystem carbon exchange under different climate conditions? Are plant functional groups able to compensate for each other with climate change? (**Chapter II**)
3. What role do plant functional groups play in regulating soil microclimate? (**Chapter III**)
4. To what extent does variation in short-term weather extremes and long-term climate determine recruitment success? Do plant functional groups mediate the effects of extreme weather events? (**Chapter IV**)

In the age of open science (Nielsen, 2011), it is clear that reproducible and transparent documentation of data and data processing is essential (Borregaard & Hart, 2016; Hampton et al., 2015). The data collection protocols for the original data I collected, and subsequent data processing and storage, is therefore outlined in **Chapter V**.

This thesis combines biotic and abiotic data from a four-year removal experiment with a nine year-long comprehensive dataset of biotic and climate variables, both collected along independent and orthogonal temperature and precipitation gradients. The combination of these two complementary datasets augments the capabilities of disentangling direct and indirect impacts of climate and climate change on biodiversity and ecosystem functioning. The thesis therefore builds on a variety of experiments, datasets and data sources, some of which I have had responsibility for, while others which have been conducted and collected by others. The details of these different roles and responsibilities are referred to in **chapter V**, in the contributions table of this thesis, and in each publication.

Study location and site set-up

A macroecological climate experiment was established in 2008 in southern Norway (Figure 1). This experiment comprises a collection of twelve semi-natural grasslands situated along large-scale natural temperature and precipitation gradients in a topographically diverse fjord landscape. Harnessing the steep elevation range inherent in the landscape, the temperature gradient stretches from low elevation sites with a high mean summer temperature, to high elevation sites with a low mean summer temperature (three levels: alpine 6.5°C, intermediate 8.5°C and lowland ca. 10.5°C). Similarly, the natural precipitation gradient extends from a coastal climate with high annual precipitation, to a continental climate with low annual precipitation (ca. 600, 1200, 2000 and 2700 mm). These orthogonal gradients create a climate grid, where the solitary and combined effects of temperature and precipitation on biotic interactions can be tested. All twelve sites are located in species-rich calcareous semi-natural grasslands (Figure 1), with similar south-facing slopes of ~20°. The sites are fenced and grazing is simulated annually by mowing inside the fence. For further details on site selection, see Klanderud et al (2015) and Meineri et al (2013).

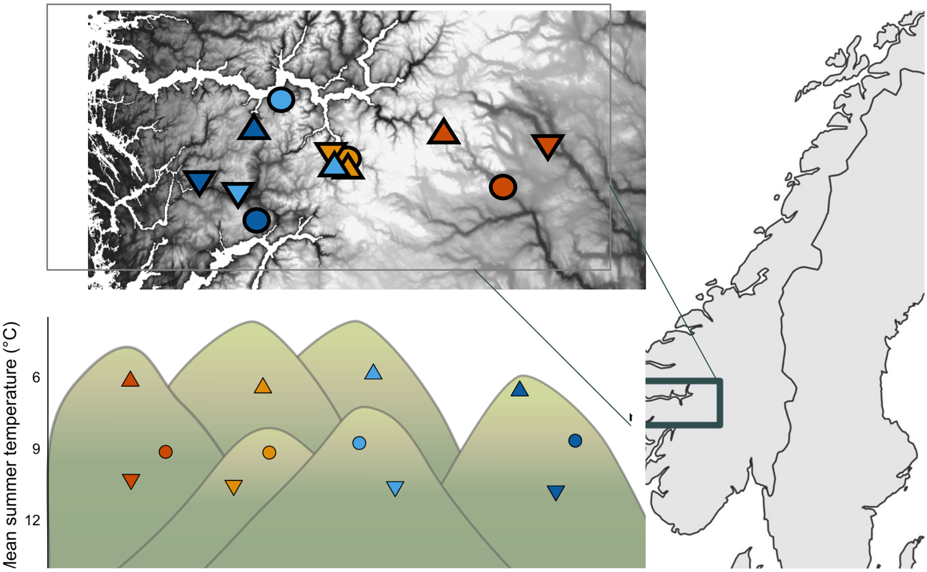

Figure 1: Locations of twelve alpine grasslands, situated along landscape-scale temperature and precipitation gradients in southern Norway. Sites were situated so that the climate axes varied independently from warm (inverse triangle) to cold (triangle), and from dry (red) to wet (dark blue).

Experimental set-up and maintenance

In **paper I** I test for the effect of climate on the interactions of the dominant functional group with the subordinate functional group in determining community properties and functioning. In 2011 a graminoid removal experiment was set up and conducted by establishing five blocks of two 25 × 25 cm plots at each of the twelve sites (**Experiment I,** Siri Lie Olsen, 2014). Each year the above-ground biomass of graminoids was removed in one plot in each block twice during the growing season. The other plot was left untouched.

To determine how plant functional groups regulate ecosystem carbon flux and microclimate (**papers II** and **III**) and seedling recruitment (**paper IV**) we set up four blocks of eight 25 × 25 cm plots at each of the twelve sites in 2015 (**Experiment II**). This experiment is the core experiment of the thesis, which I set up in collaboration with Inge Althuizen. Aboveground biomass of each functional group was removed twice every year in a fully factorial design (Figure 3) except in 2015 when unusually late snowmelt resulted in only one round of removals at 4 alpine sites.

Finally, to investigate the effects of extreme weather events on recruitment success I used an existing experiment where five blocks of two 25 × 25 cm plots were established at each of the twelve sites in 2009 (**Experiment III**). All above-ground biomass was removed once in 2009 in one plot per block.

Species composition

In **experiments I** and **II** the presence and cover of all vascular plant species and vascular and non-vascular functional groups was recorded in each plot before initial removal treatment (2011 by Olsen (2014) for **experiment I** and 2015 by myself for **experiment II**), and all non-treated vascular plant species in subsequent years (see Figure 3). The abundance of each species per plot was visually estimated as the percentage cover at peak growing season. I used these data to calculate species richness and diversity (Shannon Index), derive evenness according to Hill (1973), and calculate community-weighted mean traits (see below). Species were identified according to Lid (2005).

Community functioning

To estimate the difference in resource-acquisition strategy for the vascular functional groups (**papers I** and **II**) we weighted the functional group compositions by the physiological and morphological characteristics of each species. In 2016 traits were measured locally at each site for ~85% of the total number of plant species (Gya, 2017). Where trait data were missing for a particular species at a particular site, a mean trait value was imputed for the species in question. If this was not possible, a mean trait value was computed for all species in that functional group. For further specification of the Bayesian model used to generate these trait imputations, see the supplementary material for **paper II.**

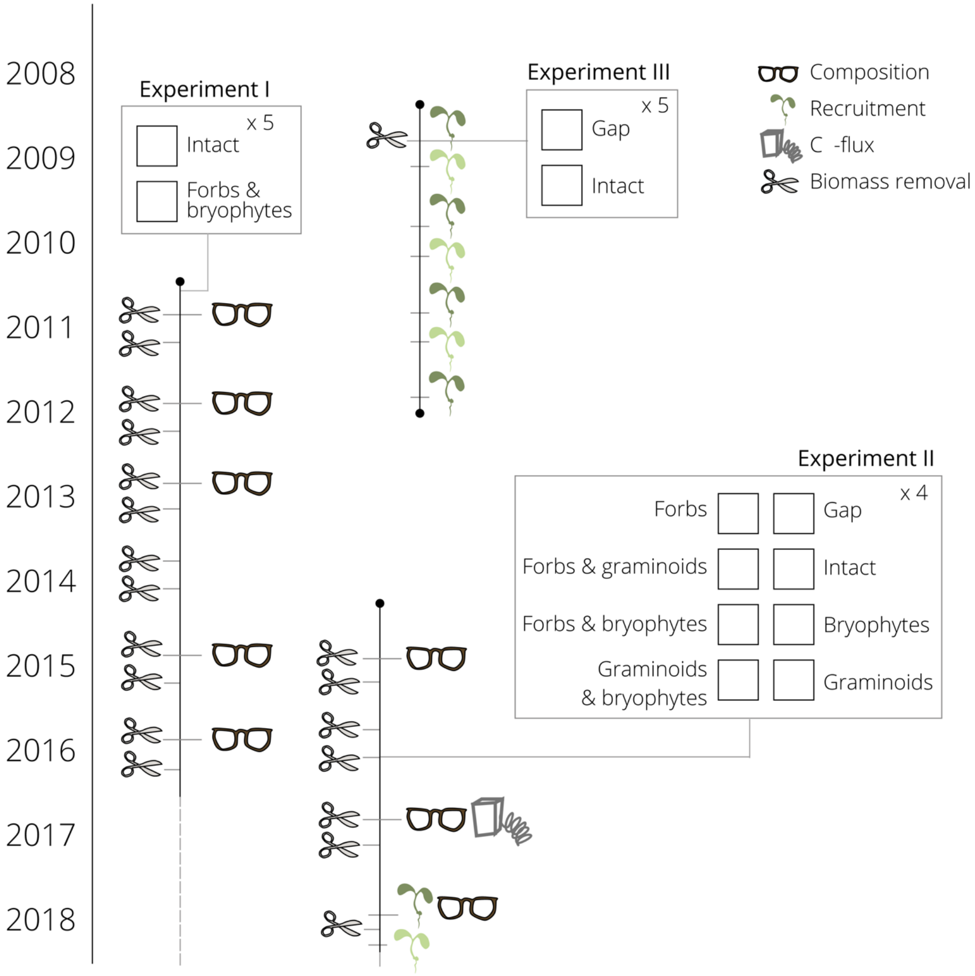

Figure 2: An illustration of the experimental set-up. Three independent experiments were conducted at each of the twelve sites; **Experiment I** ran from 2011-2016, **experiment II** from 2015-2018, and **experiment III** from 2009-2012.

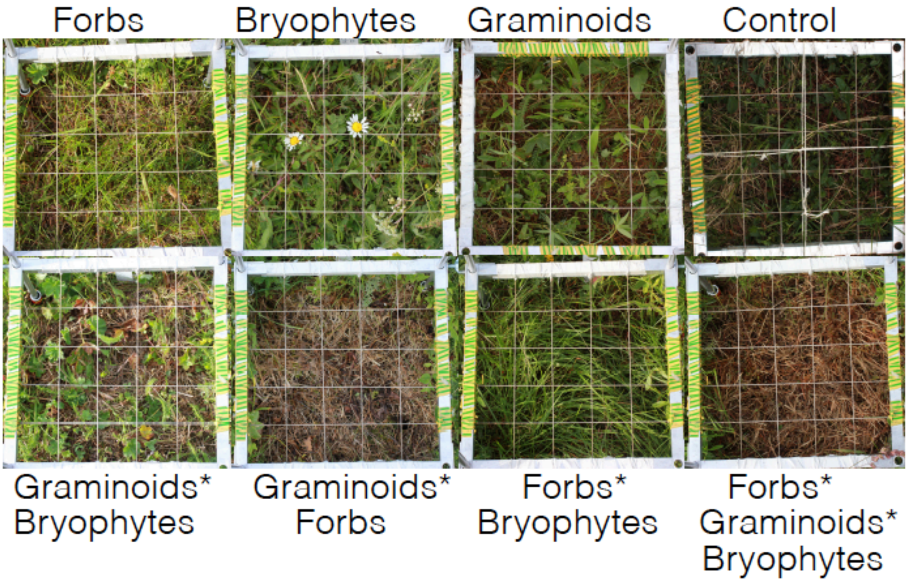

Figure 3: plant functional group removal, where the labels indicate the removed functional groups.

Species recruitment

In **paper IV** the total number of forb seedlings (hereafter referred to as *seedlings*) was recorded in each plot twice each year from 2009 to 2012 (**experiment III**, Berge, 2010) and again in 2018 (**Experiment II,** Jaroszynska**)**. I associated each 'round' of seedling abundance estimation with the deviation in soil moisture and air temperature from the long-term average (2008-2016) at each site.

Ecosystem carbon flux data

For **paper II** we measured net ecosystem exchange (NEE) to estimate ecosystem respiration (R_{eco}) and gross primary production (GPP) using a static chamber method (I. H. J. Althuizen, 2018). Measurements were taken throughout the growing season at ambient light levels. Growing season was considered as the time at which *Agrostis capillaris* flowered at each site. Photosynthetically active radiation and air temperature inside the chamber was monitored throughout the measurements to aid with the standardisation of measurements. We linked these flux measurements with the community vegetation analysis and functional traits.

Climate data

We measured a number of climate parameters at multiple scales. To estimate regional climate effects, we continually measured air temperature at 2 m and soil temperature at -5 cm, soil moisture, and UV-B from 2009 – 2018 at each site. I refer you to the methods chapters in **papers I-IV** for further description of the processing of these variables.

To investigate plant functional group effects on microclimate (**paper III**), we measured soil temperature and soil moisture in each plot. We continually measured soil temperature 3-5 cm below the soil from June 2015 to July 2016. In 2015 and 2016, we measured soil moisture 3-5 times during each growing season by taking the average of measurements at four places in each plot.

Analytical approach

To investigate the interactive effects of graminoid removal and climate on total forb species cover, species richness, evenness, and functionality (**Paper I)** and the effect of functional group identity on soil microclimate during peak growing season (**Paper II**) I used linear mixed effects models and generalised linear mixed effects models fitted with Maximum Likelihood. For each response variable in **paper I** the models tested the interactive effects of graminoid removal, climate (interactive effects of temperature and precipitation) and time (fixed effects) for plots nested within sites (random effects). All models were run with a *gaussian* error distribution (lmer), except for species richness where we used a *poisson* error distribution (glmer). I tested for significance by extracting model estimates and 95% confidence intervals and deemed models as significant where the confidence intervals did not include zero.

To estimate the effect of plant functional groups on summer soil temperature and moisture, and winter soil freezing (**paper III**), I ran generalised mixed effects models. I modelled the response of maximum daily soil temperature and soil moisture to functional group removal, and the 1970-2010 interpolated mean annual precipitation and mean summer temperature, using a nested random effect structure to account for variation among block replicates and among sites. The effect of plant functional groups on soil temperature was analysed separately for sunny and cloudy days due to the principal effect of solar radiation on soil temperature (Figure 6).

Similar models were constructed for the effect of plant functional group cover and height and their interaction with mean summer temperature and mean annual precipitation on soil temperature on sunny days, soil moisture, and frost days. Models fitted with the lme4 package for soil temperature and moisture (Bates et al., 2016) and the glmmTMB package for soil freezing (Brooks et al., 2017).

Finally, to investigate climate and functional group effects on recruitment success (**paper IV**), I employed a Bayesian approach. To test for the effect of temperature and soil moisture deviations from the long-term average on seedling abundance, I set up a negative binomial model, using seedling counts from experiments **II** and **III**. Seedling abundance varied in response to treatment, temperature and soil moisture deviations, season, long-term temperature and precipitation, and the interaction among treatment and the two climate deviations (temperature and soil moisture).

Next, I tested whether any one particular functional group drives the difference between recruitment success in gaps and closed vegetation. I constructed a similar model to the one described above, except only for 2018 and for the functional group removal treatments (**experiment II** only) and without the climate anomalies, allowing seasonality to account for the occurrence of the extreme weather during the first seedling census. Lastly, to test for the effect of drought on seedling mortality in 2018, I ran a beta-binomial model, where survival varied in response to removal treatment, regional temperature and precipitation, and their interactions.

All models were fitted with a site-level random intercept structure to account for differences among sites that are unexplained by site-level temperature or precipitation. We ran model checking of the posteriors using the Dharma package (Florian Hartig, 2019). All models were run with 5 chains and 20 000 iterations. JAGS code and model-checking results for the models are provided in *supplementary material* (Figures S6-S8 of **paper IV**). Models were implemented using JAGS (Plummer, Stukalov, Denwood, & Plummer, 2018) and the R2jags package (Su, Yajima, Su, & SystemRequirements, 2015).

In **paper I** we ask what the effect of climate is on biotic interactions in semi-natural grasslands. Dominant functional group interacts competitively with the subordinate functional group at warmer and wetter sites. Further warming and wetting will increase this dominance, at the expense of forb trait functionality and cover. We demonstrate that the outcomes of biotic interactions along temperature gradients, previously illustrated at the population level in our system (Siri L. Olsen et al., 2016), can be scaled to the community for biomass and for resource economic strategies.

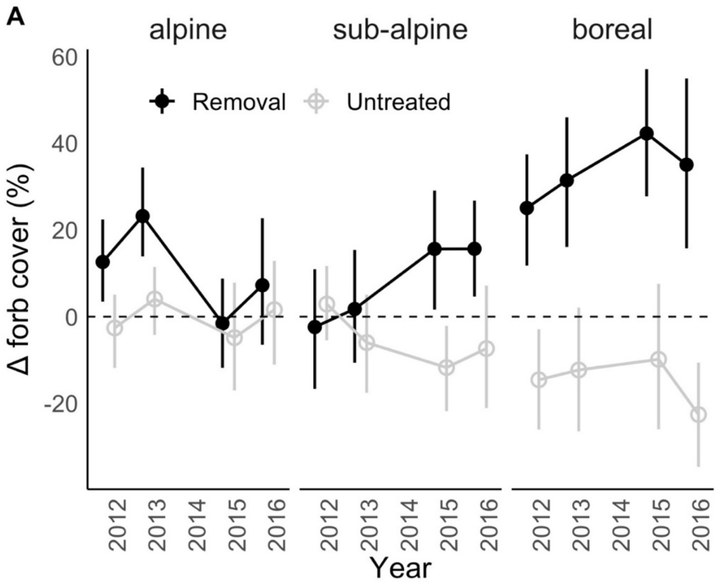

Figure 4: Mean difference in forb species cover from pre-treatment levels (2011) to each subsequent year in alpine, sub-alpine and boreal grasslands. Values above the zero line indicate higher forb cover or diversity than in the pre-treatment year, while values below the zero line indicate lower forb cover or diversity than in the pre-treatment year, ±1 SE.

Paper II illustrates that plant functional groups contribute differently to ecosystem carbon exchange. We found that graminoids and forbs both contribute substantially to gross primary production (GPP) and ecosystem respiration, whereas the non-vascular functional group does not (Figure 2AB in **paper II**). Forb and graminoid presence is equally important as regional temperature in regulating GPP. Ecosystem respiration, on the other hand, is largely determined by temperature and not by functional groups. Precipitation is unimportant for both GPP and ecosystem respiration.

Temperature and functional group interactions influence the capacity of plant functional groups to compensate for the loss of neighbours (Figure 5). For example, at cold temperatures forbs poorly compensate in GPP for neighbour removal except in the presence of bryophytes. Bryophytes somewhat inhibit the compensation capacity of graminoids.

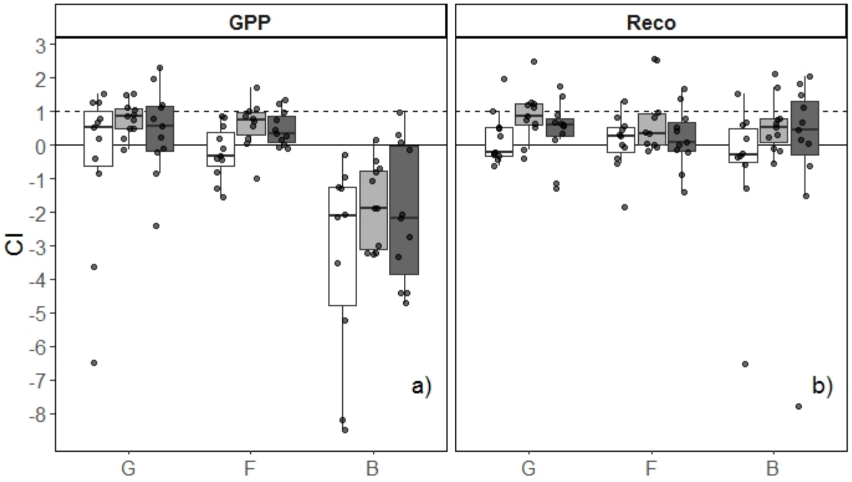

Figure 5: compensation in gross primary productivity (GPP) and ecosystem respiration (Reco) in alpine (white), sub-alpine (light grey) and boreal (dark grey) grasslands.

In **paper III** we further investigated the role of plant functional group identity on regulating soil temperature and soil moisture in summer, and soil freezing in winter.

In general plant functional groups differentially moderate the strong effect of solar radiation and ambient summer air temperature on soil microclimate (in line with e.g. (Isard, 1986; Scherrer & Körner, 2011; Wundram, Pape, & Löffler, 2010). This regulation was largely driven by bryophyte presence. On sunny days, functional groups reduced daily maximum soil temperatures by as much as ~1°C compared to bare soil, an effect that was comparable to the effect of regional climate itself. The functional group effect was not seen on overcast days (Figure 2A).

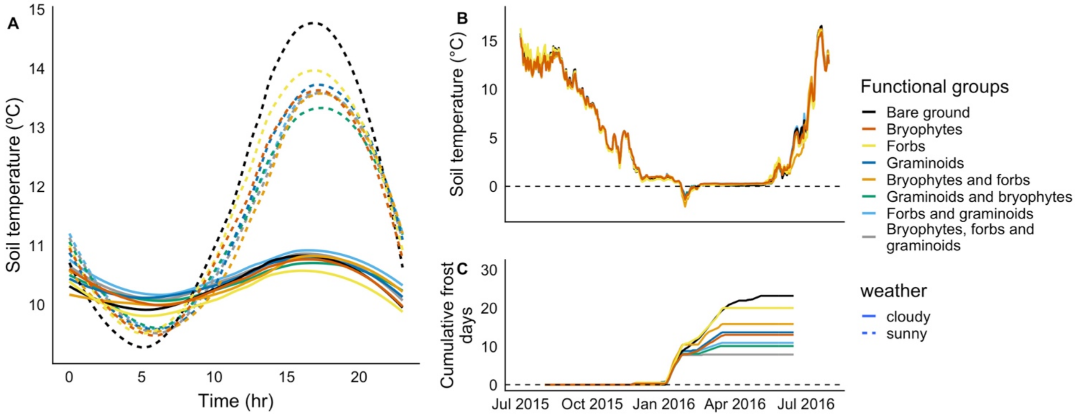

Figure 6: Illustration of the effect of different plant functional groups on soil temperature at the sub-alpine sites (n = 4). (A) Average diurnal temperature fluctuation for August and September 2015 on sunny (dashed lines) and cloudy (solid lines) days, (B) seasonal trends in daily maximum soil temperature from July 2015 to July 2016, and (C) the cumulative frost day sum. Colours indicate presence of plant functional groups (i.e., the remaining functional groups in the factorial removal experimental plots, see legend).

In **Paper IV**, we demonstrate that seedling recruitment is primarily regulated by climate extremes. In general, seedling abundance is higher in seasons with above-average soil moisture and air temperature (Figures 3 and S3 in **paper IV**). Below-average temperatures and wetter soils reduced seedling numbers more so in gaps than in intact vegetation.

Upon further investigation of a year with a drought event (2018), I found seedling abundance to be greatest at typically cold and wet sites and lowest at typically warm and dry sites (see Figure 7 where '*early'* is ubiquitous with *drought*). This trend is reversed after drought. In general, this trend in seedling abundance was marginally increased in forb-only plots than in closed vegetation.

Finally, survival over the growing season during a drought year is not improved by the presence of any particular functional group. However, survival is lower in gaps. Survival is lower at warm sites than at cold ones.

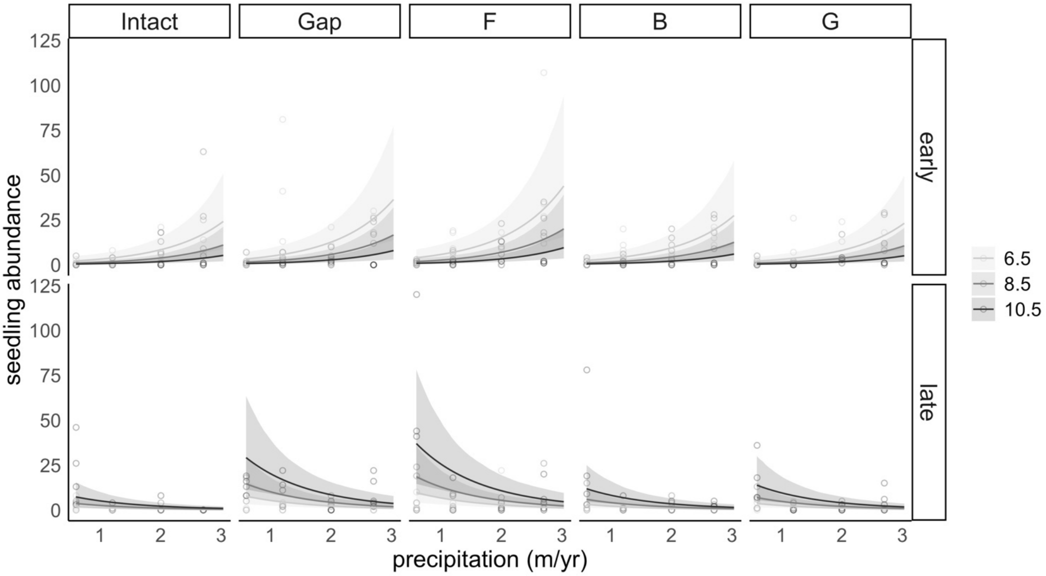

Figure 7: The effect of plant functional groups on seedling abundances in early summer (during drought) and late summer (after drought) in alpine (pale grey), sub-alpine (mid grey) and boreal (dark grey) grasslands. Letters indicate the functional groups present in the plot, where F = forb, B = bryophyte, and G = graminoid.

In concert, **papers I-IV** demonstrate that climate has profound effects on biotic interactions and ecosystem functioning, and that plant functional group interactions in turn have reciprocal mediating effects on microclimate, carbon flux, and community assembly processes. Where the scale and duration of the climate event and biotic response vary across different ecosystem functions, the overall trend is toward increased ecosystem carbon fluxes and competition with increased warming, at the expense of diversity and microclimate heterogeneity.

Biotic interactions respond to climate

Across arctic and alpine systems, a number of large-scale shifts of species in direct response to climate change has already been documented (Gottfried et al., 2012; Post et al., 2009). Furthermore, climate drives change in biotic interactions (Siri L. Olsen et al., 2016; Tylianakis, Didham, Bascompte, & Wardle, 2008), which acts to moderate the direct effects of climate change. This is supported by my findings of multi-directional shifts in biotic interactions along both temperature and precipitation gradients – graminoid-forb interactions tended towards increased competition with increasing temperature (**paper I**), whilst bryophyte-forb interactions are predominantly facilitative with lower temperatures (**paper II**). These findings support the general consensus that climate warming in cold regions will result in increased competition. Our results support evidence that forbs, rather than graminoids or bryophytes, are most affected by biotic interactions (Klanderud et al 2015).

Although temperature is the dominant driver of some aspects of ecosystem functioning, plant functional groups are arguably as important for functions such as carbon flux (**paper II**) and soil microclimate regulation (**paper III**). Functional group regulation of biomass (Dormann & Woodin, 2002) and aboveground net primary production has been observed along temperature gradients in grasslands (Mowll et al., 2015) although the authors conclude that there are complex interactions with precipitation that could explain some of the variation in biotic outcomes. Interactive temperature and precipitation effects have been observed for root biomass (Bai et al., 2010), phenological shifts (Lesica & Kittelson, 2010), and community composition (Klanderud et al., 2015). This thesis also finds that precipitation plays a crucial role in determining species dominance patterns for forbs (**paper I**), in addition to recruitment success during transient climate events such as droughts (**paper IV**). Increases in the intensity and time between rainfall events, more so than annual precipitation, reduces carbon cycling and species diversity (Knapp et al., 2002). Intermittent precipitation has also enabled a shift in species dominance (Hobbs et al., 2007), which may enable grassland invasion when under climate stress.

The many and contrasting hats of plant functional groups

There is variation in the function that stands either to lose or gain in the outcome of biotic interactions. For example, whilst the interaction between forbs and graminoids at high temperatures is predominantly competitive when the function in question is diversity, the interaction is rather neutral for carbon flux. The stability of these interactions suggests that under long-term climate equilibrium, the outcomes of biotic interactions would likely remain constant. What we observe, however, is temporal variation in biotic interactions in response to climate (as in **papers I and IV**). Hollister et al. (2005) found differences in short- and long-term responses of plant communities to climate warming (Arft et al. 1999, Walker et al. 2006), indicating that the effect of climate-driven changes in biotic interactions may change in the long term.

Climate extremes

This thesis demonstrates that temperature and precipitation variability are more important for recruitment (**paper IV**) and to some degree diversity (**paper I**) than mean summer temperature or total precipitation. Similar responses have been observed for recruitment (Lloret, Peñuelas, & Estiarte, 2005), decomposition (I. H. J. Althuizen et al., 2018), and carbon cycling processes (Knapp et al., 2002) variation within climate band drove changes in decomposition rates, not so much between climate bands. Suggesting that it's the climate you're adapted to. Deviations from that which matters, not really climate per se. this does not bode to well for ecosystem functioning in the future, when rapid changes are making communities and populations lag more… if we use space for time approaches without consideration for transient climate events we risk being overly optimistic about ecosystem-wide abilities to adapt and respond, in agreement with (Elmendorf et al., 2015).

Bryophytes – the unassuming director of ecosystem processes?

A central theme that stands out throughout this thesis has been the unexpected role of bryophytes in almost all processes. I demonstrate that bryophytes regulate soil microclimate (**paper III**) and consequently alleviate drought conditions, they facilitate carbon flux by forbs in alpine regions (**paper II**), and they reduce recruitment success even during drought (**paper IV**). Bryophytes play a critical role in feedback systems in the arctic (Van Der Wal & Brooker, 2004). Some have found bryophytes can exert both positively and negatively on seedling recruitment depending on their depth, cover (Wang et al., 2017), and even diversity (Lett, Nilsson, Wardle, & Dorrepaal, 2017; Lett, Wardle, Nilsson, Teuber, & Dorrepaal, 2018). Similarly, their regulatory capacity for soil heat and carbon fluxes have been demonstrated elsewhere (Blok et al., 2011; Douma, Wijk, Lang, & Shaver, 2007)

Clones and flower power

Where above-ground leaf traits partly illustrate plant resource acquisition strategies, as demonstrated in **paper I**, it may be that clonal traits can provide additional clarity on resource allocation. There is as yet no agreement on the impact of drought on the relative role of clonal growth in determining biotic interactions and resource allocation. This is an omission in our understanding of grassland systems because clonal traits are suggested to be equally as important in determining community responses to climate change as growth-related plant characteristics (Guittar, Goldberg, Klanderud, Telford, & Vandvik, 2016; Klimešová & Herben, 2015), emphasising the urgent need for a better understanding of clonal dynamics. There was a tendency for clonal species to profit from drought conditions (Jaroszynska 2019, *personal* *observation*). Without consideration for clonal dynamics of alpine vegetation it is difficult to conclude on total community resource economy strategy, particularly in response to drought. New analyses should address the response of clonal species to drought.

Implications for ecosystem functioning and biodiversity

Similarly, the increase in competition between forbs and graminoids could result in the eventual decline of forb cover, recruitment capacity, and ultimately diversity. Graminoids consistently limited seedling abundance across the climate gradients (**paper IV**), and heightened competition between graminoids and forbs resulted in reduced forb cover and diversity with increased temperatures (**paper I**). If competition continues at this rate with climate warming, further reductions in forbs could lead to lower seedling abundances. However, in long-lived plant communities like those found in alpine regions, only a small number of successful recruitment events are necessary to maintain populations (Körner, 2003) although the risk of building up an 'extinction debt' is already prevalent in alpine systems in Europe (Dullinger et al., 2012). The implications for species diversity and for their associated pollinators are significant (Wesche, Krause, Culmsee, & Leuschner, 2012). Since mowing and moderate grazing keeps graminoids from over dominating in semi-natural grasslands (Kotas et al., 2017; Lepš, 2014), our findings make a case for the promotion and upkeep of traditional land-use practices for maintaining plant and insect diversity.

Grazing was simulated annually by removing above-ground biomass across all our fenced sites at the end of the growing season, but it may be that this is not sufficient for replicating all the effects that herbivores have on alpine grasslands. Although not formally tested, permanently fenced sites tend to show greater functional and cover responses in the untreated than the treated plots, suggesting that trophic rather than non-trophic interactions may be important for mediating plant community dynamics. Herbivore density has already been shown to be important for species richness and recovery in upland systems in Norway (Speed, Austrheim, Hester, & Mysterud, 2012), and the role of a dominant plant species can be dwarfed in importance by mowing and fertilising regimes (Kotas et al., 2017). However, since all of our sites have been subjected to the same grazing simulation, we can be confident that the variation in response of the forb community to graminoid removal along the climate gradients is genuine. Nevertheless, this raises an interesting question regarding the interplay of climate and land-use.

Concluding remarks

This thesis demonstrates that temperature, precipitation, and climate variability have profound effects on biotic interactions and ecosystem functioning. Furthermore, I show that plant functional groups and biotic interactions are important mediators of climate change effects on microclimate, carbon flux, and community assembly processes in alpine grasslands. The cascading effect of regional temperature and precipitation on biotic interactions toward increased graminoid dominance and reduced forb diversity will result in short-term increases in carbon cycling and reduced recruitment success. Increased occurrences of extreme weather, such as droughts, in combination with climate warming, will likely enhance recruitment limitation and alter carbon cycling. The complex longer-term effects have consequences and feedbacks on a variety of ecosystem functions. Further investigation into the legacy effect of climate variability, microclimate, and the stability of communities following diversity loss, will provide deeper insight into the longer-term implications of climate change on alpine grasslands. In conclusion, while many of the interactions illustrated in this thesis are complex, I demonstrate that climate has generalisable direct and indirect effects on ecosystem functioning that improve our interpretation and prediction of climate change in alpine ecosystems.

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Chapter Five

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V

In this world of meta-analyses and large international collaborations, careful documentation of data collection and processing is an invaluable tool (Halbritter et al., in review). It allows for better and more robust syntheses, which in turn enables us to answer some of the most pressing questions regarding climate change at a much larger scale than the single site or experiment.

In order to achieve such goals data, and the means to derive our findings from those data, need to be publicly available. In the following section I document the relevant procedures used to collect the data I collected. All data are stored on OSF (https://osf.io/4c5v2/). All analyses and data cleaning procedures are documented in open-access github project files (https://github.com/fja062/FunCaB).

The data were collected at all twelve of the SeedClim project sites. More information on the sites can be found in the SeedClim data documentation: https://docs.google.com/document/d/1RUOqkf8V_TqwZabu8LUjwQvephE5EClyYegV9wPAgfs/edit?usp=sharing

2.5 Biomass harvest/Carbon flux plots (SeedClim/FunCaB)

We established four plots of 25x25 cm at each site in 2016 for biomass harvest linked to carbon flux measurements (see #2.8). Vegetation analysis was performed on each of these plots (see #2.6.1).

The biomass of these plots was harvested towards the end of the season (Aug/Sept 2016) and kept in a freezer at -22°C until processing. The removed biomass of each plot was separated into species and dried at 60 °C for 48 hours and weighed.

2.6 Graminoid Removal (FunCaB)

Within each site we established five experimental blocks, each containing two 25 × 25 cm plots, one control plot with intact vegetation and one dominant removal plot. The dominant removal was carried out once in 2011 and then twice a year, in the beginning and peak of the growing season, in 2012 - 2016. The removal was done with hand scissors by clipping all graminoids, including grasses, sedges and rushes, at the soil surface leaving the rest of the vegetation undisturbed. Biomass removal is a standard method for studying interspecific interactions, and the strengths and limitations of removal experiments have been thoroughly discussed by Aarssen & Epp (1990) and Díaz *et al.* (2003). Although clipping mainly manipulates above-ground interactions, it is a recommended method for experimental biomass removal in grasslands, as it minimizes soil disturbance whereas nutrient-release from decomposing roots has been shown to have minimal effects on the remaining vegetation (McLellan *et al.*, 1995).

The removed biomass was collected, dried at 60 ºC for 48 hours and weighed. The total biomass of graminoids removed decreased in all sites over time, from an average of 52.7±4.7 g per site in 2011 to 15.3±1.6 g in 2013, indicating that the removal treatment successfully suppressed the graminoids in the treated plots (Olsen et al. 2015). Total vascular plant biomass in one additional plot per block was harvested, sorted into functional groups, dried and weighed in 2013 (S. Fariñas, unpublished data). On average graminoids made up 65.3±2.2 % of the total vascular plant biomass in our study sites, with minimal variation along the climate gradients. Mean vegetation height, measured in each plot in 2011 prior to graminoid removal, increased with increasing temperature from 6.5±3.8 cm in the alpine sites to 15.3±8.1 cm in the boreal sites (Olsen et al. 2016).

2.7. Functional Group Removal (FunCaB)

A fully factorial field removal experiment was set up in the 12 sites in 2015. The experiment was set within the SeedClim experiments whenever possible, or in similar grasslands no further than 100m away. We used 25 x 25 cm plots in 4 blocks per site with a total of 384 plots across all twelve sites. Four aluminium pipes were hammered down into the soil in the outer corners of all the 25 x 25 cm treatment plots, ensuring the pipes to fit the corners of the standardized vegetation analysis frame (aluminium frame demarking a 25 x 25 cm inner area, with poles fixed in the corners that fit into the aluminium tubes used for plot demarcation in the field). Each of the three major plant functional groups (non-vascular plants [mainly bryophytes but also including any lichens present], graminoids, and forbs [including any woody plants present]) were removed separately and in all possible combinations, yielding 8 treatments including an intact community control (Table 3). For each treatment, all above-ground biomass of the target functional group(s) was carefully removed using scissors (graminoids, forbs) or tweezers (bryophytes) twice per growing season over three years. In 2015 the biomass was only removed once in the alpine sites because of a late start to the growing season. All removed biomass was dried and weighed, and the plots were photographed before and after removal. In the final year, all plots will be destructively harvested for above-and below-ground biomass.

Table 3. Overview of the experimental design per site for the removal experiments (green = present, blank = removed). Forbs = non-graminoid vascular plants including woody plants if present.

Treatment	Treatment code	Graminoids	Forbs	Non-vascular
1	C	🟩	🟩	🟩
2	B	🟩	🟩	
3	F	🟩		🟩
4	FB	🟩		
5	G		🟩	🟩
6	GB		🟩	
7	GF			🟩
8	FGB			

2.8 Vegetation composition (FunCaB)

In 2015, we conducted full species composition of all plots. In each subsequent year we recorded the community composition of the functional groups that would remain in the plot according to the plot's corresponding treatment. We recorded all species of vascular plants in the central five 5 x 5 cm subplots (Figure 2.7), noting the subplot cover of each species present in each of the five subplots (1-25% = 1, 26-50% = 2, 51-75% = 3, >76% = 4). Additionally, if the individual was fertile (circled if flowers were about to come, flowering, or in fruit), juvenile (J), or a seedling (S) was recorded. We estimated the percent cover (%) of acrocarps and pleurocarps in the subplots where bryophytes were not removed. For the entire 25 x 25 cm plot, any new species not found in one of the central subplots, and their fertility, were noted. The data were collected during the growing seasons in 2015, 2017, and 2018.

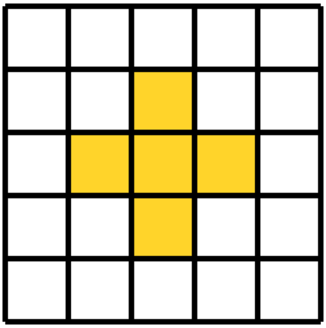

Figure 2.7: the central five subplots (yellow) were analysed for detailed life history traits.

The total number of seedlings was consistently recorded in 2018. At peak growing season, forb seedlings were marked with wooden toothpicks and their coordinates and potential species noted. Toward the end of the growing season, each plot was re-visited and seedling survival established. Any further seedlings were marked.

Other variables that were measured for each plot:

vegetation height (mean of 4 measurements)
moss % cover (pleurocarp and acrocarp)
moss layer depth (mean of 4 measurements)
litter % cover
bare ground % cover
rock % cover
date of analysis
recorder / scribe (if any)
comments
Other variables that were measured for each sub-plot:
moss % cover
litter % cover
bare % ground cover
rock % cover
nomenclature follows Lid & Lid (2005)

8. *How was the data collected and developed (curation, corrections, etc) and where is it stored*

The information from the field data sheets was manually entered into digital worksheets, manually proof-read and stored in Excel files. If possible, missing data and errors were checked and corrected by creating figures of species covers over time. Where data were missing, a mean was generated based on the year previous to, and the year following the missing data. For further details on data cleaning and management, see the cleaning files in the FunCaB github repository.

For each turf in each year we calculated the diversity, richness, evenness, and cover of each functional group. The data are stored and publicly available on OSF.

9. *Other datasets within the project of direct relevance (e.g., predictor data)*

- This dataset shares experimental design with, and can therefore be used in conjunction with, all other SG and TT response variable data.
- All transplant experiment plot-scale environmental data
- All site-scale environmental data

For further details on the sites, experimental set-up, and data availability, I refer you to https://docs.google.com/document/d/1RUOqkf8V_TqwZabu8LUjwQvephE5EClyYegV9wPAgfs/edit#heading=h.j3ecgc8pkwoj. Documentation for seedling recruitment data used in **paper IV** of this thesis is found in section 2.4. Flux data (**paper II**) documentation is available here: https://docs.google.com/document/d/1sxwJefOflidReXDOy0EBzKS-3cD4V3Zyvtg4wFek98I/edit

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