Disentangling effects and context dependencies of climate change on alpine plants

Ragnhild Gya

Thesis for the degree of Philosophiae Doctor (PhD)
University of Bergen, Norway
2022

UNIVERSITY OF BERGEN

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Date of defense: 02.12.2022

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Year: 2022

Title: Disentangling effects and context dependencies of climate change on alpine plants

Name: Ragnhild Gya

Print: Skipnes Kommunikasjon / University of Bergen

SCIENTIFIC ENVIRONMENT

This PhD dissertation was written at the University of Bergen, the Faculty of Mathematics and Natural Sciences, the Department of Biology in the Between the Fjords research group. I was also affiliated with the Bjerknes Center for Climate Research.

The thesis work was funded by the Research Council of Norway through the INCLINE project (274712) – Indirect climate change impacts on alpine plant communities (PI: Vigdis Vandvik and co-PI Joachim P. Töpper). In addition, I received smaller grants that were used for additional data collection from the Meltzer Foundation, and ‘Olaf Grolle Olsen’s Legat til Universitetet i Bergen med tilførsel av arv etter Miranda Bødker’, and the County Governor of Hordaland. The thesis work was conducted at the Department of Biological Sciences at the University of Bergen, in collaboration with the Norwegian Institute for Nature Research, Bergen.

UNIVERSITAS BERGENSIS

BJERKNES CENTRE
for Climate Research

NINA
Norwegian Institute for Nature Research

INCLINE

The Research Council
of Norway

BETWEEN
THE FJORDS

ACKNOWLEDGEMENTS

First, I thank my supervisors, Prof Vigdis Vandvik and Dr. Joachim P. Töpper for having been the training wheels for me throughout this process. I have learned so much from both of you, and I am very grateful for our collaboration. Vigdis, from the mountains in China to the end of this PhD, you always had something to teach me, both in science and otherwise. Thank you for all the opportunities you have given me, and for believing in me. An extra-large thanks to Joachim for holding my hand through the process of learning how to build a population model, you made that a great experience. I also very much appreciate the fun times we have had together in the field, and hope that this was not the last time.

I want to acknowledge all the other role models I have had throughout my academic career so far, which as a big reason that I did this PhD in the first place. First to the role models that did their PhD while I started to dream about it myself: Mari Jokerud, and Lise Tingstad – you sparked my interest for alpine plants! Then a huge thanks to Francesca Jaroszynska and Inge Althuizen who let me tag along in their PhD as I did my masters next to them. Siri Vatsø Haugum who was just in front of me, who I got to share the experience of the PhD together with, and who is a remarkable researcher. As a PhD candidate, the post docs are always right, and Sonya Geange, Aud Halbritter and Joshua Lynn were always there when I needed help, and showed me what fair, open, and inclusive research looks like. And to Dagmar Egelkraut for the great job that she does, and I really enjoyed having your kindness and excellence right next to me during almost the entire PhD.

Within the Between the Fjords and the greater EECRG research groups, we also have great resources for a developing researcher, and I would not be where I am today if it was not for the writing group (which I started going to in my bachelors), the journal club, and the R club. An especially huge thanks to Richard Telford for teaching me everything I know about coding and R. I am forever grateful for the kind and inclusive environment at EECRG. Further the

bioCEED team has also been important for me through my PhD: both academically to keep my education research interest up, and socially as there was always someone to chat with in the hallway. A big extra shoutout to Oddfrid and Jonathan for being kind, supporting and fun.

I have spent a total of 1348 hours in the field in this PhD. That would not have been the same without my amazing field team. From 2018 to 2021 we have spent a minimum of four weeks in the field, and it has been nice to get to know so many kind and fun people. Thanks to: Joachim, Siri, Kari, Eva, Silje, Inge, Dagmar, Linn, Susanne, Ingrid, Lasse, Gunvor, Camilla, Sherry, Sergio, Alessandra, Solveig, Emma, Regine, Romane, Elia, Sondre, Kengo, Betsabe, and Jana for fun times in the field.

In the last sprint of the marathon of finishing a PhD there are some people that becomes a bigger part of your life. I would like to thank the people who I shared this last part with; teatime, dinners, rants, and walks – thanks to Sonya, Helene, and Ruben for being my sprint team.

Work-life balance can be hard during a PhD. I would like to give a huge shoutout to Crossfit Bryggen and everyone in the gym for keeping me fit and healthy, but also for giving me a mental break form the PhD. It is not easy to think of statistical problems or rejects from journals when you have to do as many burpees as you can fast. Additionally, my friends and family have been a huge support during the PhD. They give me a space to relax and be the other parts of me. I would like to mention the people I studied the teaching program with and give a big thanks to them #Lektorlove. And a big thanks to both Ida in my life who I can talk to for hours on the phone with.

Finally, I need to thank my closest family - my husband, and my dog. First, Nova for giving me something else to focus on, especially during home office. Then, Lars Olav. Thanks for making this *our* project! I would not have been able to do this without your support and help. Thanks for being my safe space, my time-off reminder, and for being so fun. I love you - and I can’t wait to see the next projects for us and see what we accomplish together!

Fieldteam Photos: Ragnhild Gya, Siri Lie Olsen, Eva Lieungh, Dagmar D. Egelkraut

ABSTRACT IN ENGLISH

Climate change poses new challenges for alpine plants, affecting them both directly through altering physiological processes, and indirectly through changes in species' interactions. These indirect effects could be caused by increased intensity of competitive plant-plant interactions among species already present in the current plant community. Additionally, changes in interactions could also be caused by entirely novel interactions emerging as species from lower elevations expand their ranges into the mountains. Such indirect effects of climate change can be important - significantly modifying the magnitude or even reversing the direction of the direct effects. Few studies have explicitly disentangled the contributions of these direct and indirect effects of climate change on alpine plants.

In this thesis I combine different approaches to test the direct and indirect effects of climate change on ecological processes involving alpine plant communities and their individuals and populations. In studies focusing on communities, I used a twelve-site climate grid that varies in temperature and precipitation, where I combined data from an observational study over a ten-year period with site-level functional trait data to look for evidence of change in functional composition of alpine communities, and whether these changes match predictions from the climate gradients. In studies focusing on individuals and populations, I use two common alpine plants with slightly different niches and habitat selectivity: *Veronica alpina*, an alpine generalist and *Sibbaldia procumbens*, a snowbed specialist. I use laboratory experiments to investigate the effect of drought on germination and seedlings of these focal alpine plants. And finally, I use demographic studies in a field experiment to disentangle the mechanisms underlying the direct and the indirect effects of climate change on these focal species. The experiment is designed to explicitly disentangle direct effects of warming from indirect effects operating through either change in current species interactions or in

novel species interactions. Both experiments are conducted along a precipitation gradient to assess context-dependencies in the responses.

As my study region in southwestern Norway has become warmer and wetter, alpine plant communities have shifted towards being more dominated by taller species with more resource-acquisitive leaves. Still, these functional changes in the vegetation were smaller than expected based on the climate response along temperature and precipitation gradients in the same region. The field and lab experiments allowed me to single out two direct effects of climate change: warming and drought. Warming alone seems to impact alpine plants by increasing growth and survival, leading to increased population growth rates. In contrast drought has a negative effect on germination and seedling survival. These results vary between populations along the precipitation gradient, and between species. The alpine generalist (*V. alpina*) had a more positive response to warming than the snowbed specialist (*S. procumbens*). Further, *V. alpina* also showed signs of local adaptations to drought in the driest populations, as opposed to *S. procumbens*, and for both species, populations from drier habitats had a larger positive response to warming.

In this thesis I found that warming alone has positive direct effects on many aspects of the life-histories of alpine plants, but that these effects can in fact be dampened or even reversed by indirect climate change effects operating via species' interactions. The alpine focal plants are affected by competitive (*V. alpina*) or neutral (*S. procumbens*) interactions within the current alpine vegetation and climate. With warming the intensity of competitive interactions within the current alpine vegetation increases. Introducing novel interactions from range-expanding sub-alpine species, especially with more competitive traits, further increases competition and reduces the positive effect of warming. The indirect effects also varied with precipitation, indicating that the negative effect of species interactions is strongest in the wetter sites.

SAMMENDRAG

Klimaendringer byr på nye utfordringer for fjellplanter, og påvirker dem både direkte gjennom å endre fysiologiske prosesser, og indirekte gjennom endringer i interaksjoner mellom planter. Disse indirekte effektene kan være forårsaket av økt intensitet av konkurrerende interaksjoner mellom arter som allerede er til stede i det nåværende plantesamfunnet. I tillegg kan endringer i interaksjoner også være forårsaket av helt nye interaksjoner som dukker opp når arter fra lavlandet utvider sin utbredelse til fjellene. Slike indirekte effekter av klimaendringer kan være viktige – de kan vesentlig modifisere omfanget eller til og med snu retningen på de direkte effektene. Få studier har eksplisitt separert bidragene fra disse direkte og indirekte effektene av klimaendringer på fjellplanter tidligere.

I denne oppgaven kombinerer jeg ulike tilnærminger for å teste de direkte og indirekte effektene av klimaendringer på økologiske prosesser i plantesamfunnene på fjellet og deres individer og populasjoner. I studier med fokus på samfunnsnivå brukte jeg tolv lokaliteter i et klimagrid som varierer i temperatur og nedbør. Jeg kombinerte data fra et observasjonsstudie over en tiårsperiode med funksjonelle trekk for å se etter bevis på endring i funksjonell sammensetningen av plantesamfunn, og om disse endringene samsvarer med prediksjoner fra endringer langs klimagradientene. I studier med fokus på individer og populasjoner bruker jeg to vanlige fjellplanter med litt forskjellige nisjer og habitatselektivitet: *Veronica alpina*, en generalist på fjellet og *Sibbaldia procumbens*, en snøleiespesialist. Jeg bruker laboratorieforsøk for å undersøke effekten av tørke på spiringsprosesser og frøplanter av disse artene. Og til slutt bruker jeg demografiske studier i et felteksperiment for å skille ut mekanismene som ligger til grunn for de direkte og indirekte effektene av klimaendringer på disse artene. Eksperimentet er designet for å eksplisitt skille direkte effekter av oppvarming fra indirekte effekter som virker enten gjennom endringer i nåværende artsinteraksjoner eller i nye artsinteraksjoner. Begge eksperimentene er utført langs en

nedbørsgradient for å undersøke kontekstavhengigheter i disse økologiske prosessene.

Etter hvert som studieregionen min i Sørvest-Norge har blitt varmere og våtere, har plantesamfunnene endret seg mot å bli mer dominert av høyere arter med blader med høy fotosyntesekapasitet. Likevel var disse funksjonsendringene i vegetasjonen mindre enn forventet basert på klimaresponsen langs temperatur- og nedbørsgradienter i samme region. Felt- og laboratorieeksperimentene tillot meg å utforske to direkte effekter av klimaendringer: oppvarming og tørke. Oppvarming alene ser ut til å påvirke fjellplanter ved å øke veksten og overlevelsen, noe som fører til økt populasjonsvekstrate. Derimot har tørke en negativ effekt på spiring og frøplantes overlevelse. Disse resultatene varierer mellom populasjoner langs nedbørsgradienten, og mellom arter. Generalisten (*V. alpina*) hadde en mer positiv respons på oppvarming enn snøleiespesialisten (*S. procumbens*). Videre viste *V. alpina* også tegn på lokale tilpasninger til tørke i de tørreste bestandene, i motsetning til *S. procumbens*, og for begge artene hadde populasjoner fra tørrere habitater en større positiv respons fra oppvarming.

I denne avhandlingen fant jeg at klimaendringer har positive direkte effekter på mange aspekter av livshistorien til fjellplanter, men at disse effektene faktisk kan dempes eller til og med reverseres av indirekte klimaendringer som virker via interaksjoner mellom planter. Fjellplantene i fokus i denne avhandlingen påvirkes av konkurrerende (*V. alpina*) eller nøytrale (*S. procumbens*) interaksjoner i dagens fjellplantesamfunn og klima. Med oppvarming øker intensiteten av konkurrerende interaksjoner innad i fjellplantesamfunnene. I tillegg vil introduksjon av nye, mer konkurrerende interaksjoner via lavlandsarter som flytter seg opp i fjellet, reduserer den positive effekten av oppvarming ytterligere. Igjen var snøleiespesialisten mest sensitiv til økt konkurranse, og de indirekte effektene varierte også med nedbør, noe som indikerte at den negative effekten av økt konkurranse var sterkest i de våtere lokalitetene og for spesialiserte fjellplanter.

LIST OF PAPERS IN THE THESIS

Gya, R, Klanderud, K., Jaroszynska, F., Enquist, B., & Vandvik, V. How interactive effects of temperature and precipitation drives plant size and leaf economic trait shifts in space and time. (manuscript prepared for submission to Global Ecology and Biogeography)

Gya, R., Geange, S. R., Lynn, J. S., Töpper, J. P., Wallevik, Ø., Zernichow, C., & Vandvik, V. A test of local adaptation to drought in germination and seedling traits in populations of two alpine forbs across a 2000 mm/year precipitation gradient. *Ecology and Evolution.* DOI: 10.17605/OSF.IO/H7QAU (Accepted first stage of registered report – Resubmitted full paper July 2022).

Gya, R., Töpper, J. P., Olsen, S. L., Lieungh, E., Berthelsen, S, Skarpaas, O., Vandvik V. You have been warmed: novel interactions cancel out positive effects of warming in alpine plants (manuscript)

Gya, R., Töpper, J. P., Olsen, S., Gaudard, J., Lieungh, E., Zernichow, C., Berthelsen, S., Pico, S., Egeberg, S.M.W., Little, E., Gulbrandsen, R.C.B., Søgaard, L., Dybedahl, M., Dahle, I. J., Uggerud, A., Geange, S.R., Östman, S.A.H., Althuizen, I.H.J., Egelkraut, D. E., Klanderud, K., Skarpaas, O., & Vandvik V. Indirect climate change impacts on alpine plant communities – data from a warming, transplant, and removal experiment (manuscript prepared for *Scientific Data*)

Contributions to other relevant papers during the PhD period

Birkeli, K., **Gya, R.,** Haugum, S., Velle, L.G., & Vandvik, V. (2021 – Accepted first stage of registered report). How resilient is *Calluna vulgaris* to drought during germination and its seedling stage? *Ecology and Evolution.* DOI: 10.22541/au.161365878.82553639/v1 (Co-supervised the master student who is the first author of the report)

Dahle, I., **Gya, R.,** Töpper, J. P. & Vandvik, V. (2021 - Accepted first stage of registered report). Are subalpine species' seedling emergence and establishment in the alpine limited by climate or biotic interactions? *Ecology and Evolution.* (Co-supervised the master student who is the first author of the report)

Gya, R., Bjune, A. E. (2021). Taking practical learning in STEM education home: examples from do-it-yourself experiments in plant biology. *Ecology and Evolution.* 11 (8), 3481-3487, DOI: 10.1002/ece3.7207 (Paper reporting on Covid adaptation of my teaching duties during the PhD. First author responsible for writing and editing)

Halbritter, A. H., … **Gya, R.,** … & Vandvik, V. (2019). The handbook for standardised field measurements in terrestrial climate-change experiments and observational studies (ClimEx). *Methods in Ecology and Evolution.* 11 (1), 22-37, DOI: 10.1111/2041-210X.13331 (Part of a group of students screening initial protocols + author of one protocol + helped organize workshop in 2018)

Vandvik, V., … **Gya R.,** ... & Halbritter, A. H. (2022). The role of plant functional groups mediating climate impacts on carbon and biodiversity of alpine grasslands. *Scientific Data*, 9(1), 1-19. DOI: 10.1038/s41597-022-01559-0 (Data paper from an experiment in the climate grid where I did my PhD. I contributed to collected one data set and edited the manuscript)

SPECIFICATION OF AUTHOR CONTRIBUTIONS TO THE INDIVIDUAL PAPERS

Table 1: Author contributions for the different papers in this thesis. We use the CRediT categories to divide the different contributions to the papers. If one or more initials are bolded it means they were the lead of the task in that paper, while the non-bolded people where support in said category. If no one is bolded in that category for that paper all authors contributed equally.

Contribution	Paper I	Paper II	Paper III	Paper IV
Conceptualization	**RG,** VV, FJ	**RG,** VV, JPT, SRG, JSL	VV, JPT	RG, **VV, JPT,** SLO, KK, OS
Data curation	**RG**	**RG**	**RG**	RG, JG, SB, IJD, LS, MD
Formal analysis	**RG**	**RG,** JSL, JPT	**RG,** JPT, SB	
Funding acquisition	**VV,** RG	VV, JPT	**VV, JPT,** SLO, OS	**VV, JPT,** SLO, KK, OS, RG, JG
Investigation	**RG**, VV, KK	**RG**, SRG, JSL, ØW, CZ, JPT	**RG**, JPT, SLO, EL, SB	All authors
Methodology	**RG,** VV, FJ	**RG,** VV, JPT, SRG, JSL	VV, JPT, RG, SLO	RG, VV, JPT, SLO, JG, SB, LS, IJD, SRG
Project administration	**RG,** VV	**RG**	**RG**	**RG,** VV, JPT
Supervision	**VV**, FJ	VV, JPT, SRG, JSL	**VV, JPT,** SLO	**VV, JPT,** SLO, SRG, KK, OS, RG
Validation	**RG**	RG, JSL	**RG, JPT**	RG, JPT, JG, SB, LS, MD, IJD, SRG
Visualization	**RG**	**RG**	**RG,** EL	**RG,** EL
Writing – original draft	**RG**	**RG,** JSL, SRG, JPT, VV	**RG**	**RG,** JPT, SLO, JG, EL, CZ, SB, LS, IJD, AU, SRG, SAHÖ, IHJA, VV
Writing – review & editing	VV, FJ, KK, BJE	VV, JPT, SRG, JSL	VV, JPT, SLO, EL, OS, SB	All authors
Corresponding author	**RG**	**RG**	**RG**	**VV, RG**

RG = Ragnhild Gya[1,2], VV = Vigdis Vandvik[1,2], JPT = Joachim P. Töpper[1,3], FJ = Francesca Jaroszynska[1,2,4], KK = Kari Klanderud[5], BJE = Brian J. Enquist[6,7], SRG = Sonya R. Geange[1,2], JSL = Joshua S. Lynn[1,2], ØW = Øystein Wallevik[1], CZ = Camilla Zernichow[1], SLO = Siri L. Olsen[5,8], EL = Eva Lieungh[9], SB = Susanne Berthelsen[1], OS = Olav Skarpaas[9], JG = Joseph Gaurdard[1,2], LS = Lasse Søgaard[1], MD = Madeleine Dybedahl[10], IJD = Ingrid J. Dahle[1], AU = Alessandra Uggerud[1], SAHÖ = Silje A. H. Östman[1], IHJA = Inge, H. J. Althuizen[1,2,11], DDE = Dagmar, D. Egelkraut[1,2]
«All authors» in paper 4 also include these people: Solveig Myrstad Wøllo Egeberg[1], Regine C. B. Gulbransen[1], Emma Little[12], Sergio Picó[13]

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SYNOPSIS

Photo: Joachim P. Töpper

INTRODUCTION

ALPINE PLANTS AND THEIR FUTURE CHALLENGES

Alpine[1] plant communities at northern latitudes are experiencing climate change at a rate faster than the global average (Nogués-Bravo *et al.*, 2007; Rangwala and Miller, 2012; Pepin *et al.*, 2015). Climate change leads to changes in alpine communities through direct morphological and physiological responses to for example, warming, increased intensity or frequency of drought events, or changes in the overall amount of precipitation (Fu *et al.*, 2015; Sumner and Venn, 2021). Additionally, climate change can affect alpine species indirectly through changes in species interactions, which may result from either changes in performance of extant species (Klanderud *et al.*, 2015; Hu *et al.*, 2021), or novel interactions introduced by range-expanding species from lower elevations (Alexander *et al.*, 2015; Steinbauer *et al.*, 2018). These indirect effects can be important, and have been found to modify or even reverse the direct responses of plants to climate change (Suttle *et al.*, 2007; Adler *et al.*, 2009).

Alpine plants are characterized by their many stress tolerant strategies and poor competitive ability (Onipchenko *et al.*, 1998, 2021; Grime, 2006), and current plant-plant interactions in alpine ecosystems are often identified as facilitative (Callaway *et al.*, 2002; Anthelme *et al.*, 2014). As climate is warming, the intensity of competitive interactions within alpine communities increases (Callaway *et al.*, 2002; Anthelme *et al.*, 2014; Olsen *et al.*, 2016), partly because of increased growth of the current alpine community but also because species from lower elevations, many of which have more competitive traits, are moving into alpine habitats (Alexander *et al.*, 2015; Steinbauer *et al.*, 2018). Because of the poor competitive ability of many

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[1] I define "alpine" as habitats above the tree line and under the nival zone, globally (Körner, C., Urbach, D., & Paulsen, J. (2021). Mountain definitions and their consequences. Alpine Botany, 131(2), 213-217.). I acknowledge that the phrase "alpine" is considered a Eurocentric phrase in some parts of the world, but I do not refer to the Alps specifically when I use the term in this thesis.

alpine plants, we expect the increased intensity of plant-plant competitive interactions due to the indirect effects of climate change to affect alpine plants negatively (Nomoto and Alexander, 2021). The question than remains; what are the overall impacts of these direct and indirect effects of climate change?

THE DIRECT AND INDIRECT EFFECTS

Alpine ecosystems are characterized by their low mean annual temperatures ranging from 5.8 to -20 °C in alpine habitats across the world (Testolin *et al.*, 2020). Most alpine plants are temperature limited, as seen by an increase in growth or metabolic rate when warmed (Fu *et al.*, 2015). Hence, when temperature increases, alpine plants generally tend to grow taller and produce more leaves (Elmendorf *et al.*, 2012; Fu *et al.*, 2015; Bjorkman *et al.*, 2018).

Warming can also lead to drought which hinders vegetative growth due to water limitation (Dolezal *et al.*, 2020; Fazlioglu and Wan, 2021). Drought events are becoming more common across the world (Spinoni *et al.*, 2018; IPCC, 2022), even in areas of the world where precipitation is projected to increase (Cook *et al.*, 2018). Drought is commonly studied in arid regions of the world (e.g. Adams (1999) and Cochrane *et al.* (2014)), while little is known about drought on species that live in areas that are not thought of as water limited. Alpine plants might be tolerant of drought events because of their adaption to the highly fluctuating alpine environment (Graae *et al.*, 2018; Haynes *et al.*, 2021), including their morphological adaptation to tolerate the cold climates such as hairiness, thick cuticula, cushion growth and stress tolerant traits (Körner, 1999; Testolin *et al.*, 2021). These adaptations in adult individuals might be redundant if the recruitment stage is sensitive, influencing the overall populations (Briceño *et al.*, 2015). Hence, the timing of drought events might be crucial to determine the effect on alpine plants.

Alpine systems worldwide span a large climatic range in annual precipitation from desert-like conditions of <50 mm/year to over 4000 mm/year (Testolin *et* *al.*, 2020). For plants, precipitation translates to a lot of biologically important factors other than just the amount of rainfall. Firstly, plants use water from the soil, hence soil moisture is the most direct component from precipitation that plants actively use. Generally, soil moisture increases with precipitation, but there is not a direct link between the amount of precipitation and soil moisture, as soil moisture also depends on temperature, soil texture, soil depth, vegetation etc. (Daly and Porporato, 2005). Secondly, in alpine areas a lot of the precipitation comes as snow, impacting important ecological processes through snow depth, snow melt-out, and growing season length (Slatyer *et al.*, 2022).

As climate change affects plant growth and performance, and since species differ in individualistic ways to different climatic factors, climate change can also affect interactions among coexisting species. The stress-gradient hypothesis predict more competitive interactions in low-stress environments, and more facilitative interactions in high-stress environments (Maestre *et al.*, 2009). The harsh environments in alpine areas commonly result in facilitative plant-plant interactions (Callaway *et al.*, 2002; Anthelme *et al.*, 2014), and the general expectation is that with climate change interactions within alpine communities might become more competitive (Anthelme *et al.*, 2014; Alexander *et al.*, 2015; Olsen *et al.*, 2016). Observations indicate that warming leads to a change in species composition (Steinbauer *et al.*, 2020; Lynn *et al.*, 2021), which often leads to a shift in functional group dominance (Walker *et al.*, 2006; Fazlioglu and Wan, 2021). In addition, there are many records across the world of plants moving to higher elevations as climate becomes more benign for lower elevation species (Lenoir and Svenning, 2015; Steinbauer *et al.*, 2018; Rew *et al.*, 2020). These changes in species interactions, i.e. indirect effects of climate change, have a large influence on the alpine plants (Adler *et al.*, 2009; Farrer *et al.*, 2014; Klanderud *et al.*, 2017). However, the direct and the indirect effects impact alpine plant communities in concert. In this thesis I disentangle the direct and the indirect effects of climate change, as well as investigate them in concert, to better understand the mechanisms behind the changes we see in alpine plant communities due to climate change.

DIFFERENT QUESTIONS – DIFFERENT METHODS – DIFFERENT LIMITATIONS

Disentangling the direct and indirect effects of climate change requires combining several different approaches. To understand the direct effects of climate change alone I experimentally manipulate climate in the field by means of open-top chambers and in the lab using climate chambers. Further the indirect effects can be investigated by manipulating species interactions. Specifically, in the field, I combine the climate manipulations with transplant and removal experiments to isolate the species or mechanism of interest and remove indirect climate effects. I also use climate gradients, and observations in time to answer the aims of this thesis. There are many ways to address ecological questions, and they all have advantages and disadvantages.

Testing specific questions in a controlled lab experiment can give detailed knowledge about the underlying physiological, morphological, or genetic processes. Laboratory experiments are effective approaches for quantifying physiological limits of species (e.g., drought limits, and minimum and max temperatures), and exploring ecological interactions between individuals (e.g., coexistence and competition). However, laboratory experiments will never be able to incorporate all the factors in nature and can therefore never give the full insight to real-world ecological processes. For example, Blossey *et al.* (2017) found that laboratory germination tests did not reflect seedling emergence in the field. On the other hand, Vandvik *et al. (*2017), found that germination in the lab accurately predicted microsite selectivity in the field, but not seasonal timing of germination.

Moving some ecological experiments into nature and conducting field experiments can help get us closer to the complexity of real-world ecological processes. Experimental field ecology can be used to test for both direct and the indirect effects of climate change. For example, open-top chambers can be used to test the effect of warming (Marion *et al.*, 1997), and rain-out shelters can be used to investigate drought effects on plant communities (Yahdjian and Sala, 2002). Transplanting individual plants or turfs with intact plant communities to warmer, drier, or wetter conditions are commonly used to test for climate change impacts (Nooten and Hughes, 2017).

To assess indirect effects, we similarly need approaches that enable us to isolate these effects and study the response(s) of interest between communities with and without that effect. For example, to study biotic interactions, we can either i) construct communities that differ in species composition, and hence in the intensity of biotic interactions, we can ii) add a target species (i.e., a competitor) to an extant community (Alexander *et al.*, 2016), we can iii) create whole communities with predetermined pairs or groups of species (Roscher *et al.*, 2004), or we can iv) remove one or more species or functional groups from a community (Díaz *et al.*, 2003). Further, by conducting experiments in the field, we can incorporate more of the context dependency by including them in the experimental design – such as testing for warming effects in different habitats (Kudo and Hirao, 2006; Fazlioglu and Wan, 2021), or along climate gradients (Vandvik *et al.*, 2020a). Conducting similar experiments across many sites and under many different climatic conditions can help to understand the generality of patterns we detect. Many researchers are creating standardized protocols (e.g. Yahdjian and Sala, 2002; Pérez-Harguindeguy *et al.*, 2013; Halbritter *et al.*, 2020) with the goal of having more comparable experiments.

Field experiment gets closer to the real-world ecological processes than the lab experiments as the experimental setting is conducted with natural soil conditions, nutrients, weather, and climate (Nooten and Hughes, 2017). Still, field experiments can’t avoid background noise from other, often unknown, variables or processes, even with the best of experimental designs. For example, when experimentally changing species assembly we ignore important biological information about processes creating species composition, like the environment filters, as well as processes of facilitation or competition during establishment, (Díaz *et al.*, 2003; Lepš, 2004). Studies have found that field experiments might not give the same responses as real-world climate change. For example, Kröel-Dulay *et al.* (2022) found that drought experiments only showed half of the effect on aboveground biomass compared to the effect from observational studies of natural droughts. Experiments are important and powerful but does not give “the one true answer”. Measuring and understanding covariates and side-effects is important. Also, comparing experiments, gradients, and temporal change can help us set experiments into perspective, and thus gain additional insights.

Another approach is to simply observe what happens in nature over time in response to environmental changes or human induced changes and try to explain the patterns detected through different parameters. To answer questions on how ecosystems change over time observational studies that resample the same locations over time, or space-for time gradients that use spatial gradients to estimate changes over time can be used. Some resampling efforts have mapped changes in plant communities over decades to centuries due to drivers such as climate change (Kapfer and Grytnes, 2017; Steinbauer *et al.*, 2018), and pollution and grazing (Britton *et al.*, 2017; Vuorinen *et al.*, 2021). Space-for-time gradients on the other hand, are used to explain changes that might happen in the future of both human induced changes such as climate change, and habitat fragmentation, as well as natural processes like succession (Fukami and Wardle, 2005). It is common to use elevation or latitudinal gradients as space-for-time gradients to predict changes that might happen as climate is warming (Frenne *et al.*, 2013; Sundqvist *et al.*, 2013). However, natural gradients often vary in more than the climatic variable(s) we are interested in (Damgaard, 2019). Additionally, the processes of adapting to the climate variable we are interested in have happened over a much longer time in the natural gradient than what is predicted to happen with climate change. Hence, the processes behind changes could be different, and additional aspects like local adaptation and genetic changes play different roles. However, Blois *et al.* (2013) found that space-for-time estimations were about 70% similar to temporal observations over long time scales.

By combining different methods, we can exploit the strength of the different approaches to better understand ecological processes and effects of environmental change, and to make more accurate predictions for changes in time. We can use observational studies to identify patterns that we want to investigate further. Then conduct field or lab experiments to test different hypotheses. Or we can use field or lab experiments to push the ecological limits and explore scenarios we have not seen in nature yet. Combining field experiments along climatic gradients (Dunne *et al.*, 2004; Yang *et al.*, 2018) or conducting experiments with similar questions in the field and in the lab can give us unique insight on a specific topic. Well designed experiments are needed to disentangle the direct and indirect effects of climate change (Alexander *et al.*, 2016).

DIFFERENT RESPONSE VARIABLES – DIFFERENT ANSWERES

In addition to using several methods, we can also investigate distinct response variables to answer different questions. Some variables can give answers about the underlying mechanisms behind changes, while others can help shed light on the potential broader consequences. Climate change affects alpine plants in many different life stages, including changing the phenology of species (Kudo and Hirao, 2006), seed production and germination establishment (Briceño *et al.*, 2015), and eventually growth and survival of adult individuals (Töpper *et al.*, 2018). In this thesis, I use functional traits, germination responses and demographic population models to answer my questions about direct effects of warming and drought and the indirect effects of species interactions.

The critical recruitment stages

Seed regeneration is a critical stage in the life-histories of plants, affecting species' abilities to maintain local populations, evolve, and disperse to new sites. Hence, regeneration from seeds is an important aspect to investigate in climate change studies. Alpine plants have adapted to the cold alpine climate and its specific challenges in many ways, including through timing of germination processes and optimizing resource allocation (Fernández-Pascual *et al.*, 2021). Many boreal and northern alpine species are dormant when shed and need cold stratification before they will germinate, a process/need that helps avoid germinating directly after seed shed so that seedlings are exposed to the metabolic costs and environmental stressors imposed by the long northern alpine winter (Fernández-Pascual *et al.*, 2021; Graae *et al.*, 2022). After cold stratification, alpine plants also have a high temperature cue for germinating to avoid germinating too early in the spring when late-spring frost events may occur (Fernández-Pascual *et al.*, 2021). These finely tuned germination processes could be threatened by climate change that alters the temperature, growing season length and snowmelt (Mondoni *et al.*, 2012). With climate change also comes more frequent drought events, which has been found to impact alpine plant germination negatively (Orsenigo *et al.*, 2015), and affect the functional traits of seedlings produced during drought (Larson *et al.*, 2020) in dry habitats. Germination is also highly linked to biotic interactions with surrounding vegetation, which can vary between sites (Klanderud *et al.*, 2017; Guittar *et al.*, 2020). The combined effects of warming, increased drought, and more competitive interactions in alpine plant communities could lead to a net negative effect of climate change on alpine plant seed regeneration (Briceño *et al.*, 2015; Mondoni *et al.*, 2022). The effects of climate change on the regeneration stage could have cascading effects into species populations and plant communities, leading to larger shifts in the alpine vegetation.

Population dynamics

We often observe changes in abundance of different species or functional groups as a response to climate change, but we rarely know the underlying reason(s) behind this change in abundance. For instance, whether a reduction in abundance is driven by a decrease in survival and fecundity has different long-term consequences than a decline due to a decrease in plant growth (Hylander and Ehrle, 2013). Monitoring populations over time gives a detailed overview over the mechanisms and we can get a better understanding of which vital rates are driving abundance changes, whether that is growth, survival, clonality or fecundity. A tool that is often used to understand the mechanisms behind population change and project future changes in response to environmental change is demographics and modelling of population dynamics, for example matrix models in cases where size or age is reflected as classes (Caswell, 2001), or integral projection models where size or age are better reflected as a continuous state variable (Easterling *et al.*, 2000).

Functional traits

Plant functional traits are easily measured proxies for an individual's fitness (Textbox 1). Plant functional traits are often used in climate change studies because they can answer questions both about the species' response to environmental changes and about the effects that changes in the vegetation have on ecosystem processes (Suding *et al.*, 2008). As described previously, alpine plants are, generally speaking, poor competitors for light, but rather well adapted to the stressful alpine environment (Onipchenko *et al.*, 2021). Across the world, alpine plants generally possess resource conservative traits as an adaptation to the harsh alpine climate, with some variation in different alpine systems (Testolin *et al.*, 2021). Climate warming does however create a response in community traits towards taller plants with larger leaves and more resource acquisitive traits (Hudson *et al.*, 2011; Guittar *et al.*, 2016; Bjorkman *et al.*, 2018; Fazlioglu and Wan, 2021). These changes in functional composition of the plant community are further linked to ecosystem processes like carbon flux, carbon content in soil, and decomposition (Carbognani *et al.*, 2014; Happonen *et al.*, 2022).

Plant functional traits

Traits are “any morphological, physiological or phenological features measurable at the individual level”, and are referred to as functional traits when they indirectly impact an individual’s fitness through growth, reproduction, or survival (Violle *et al.*, 2007). Traits are used as a proxies for underlying plant functions like leaf construction costs, growth potential, protection, stress tolerance, productivity and photosynthetic rate, which makes it possible to study questions on the indidivual, population, community or ecosystem level (Wright *et al.*, 2004; McGill *et al.*, 2006; de Bello *et al.,* 2010; Perez-Harguindeguy *et al.*, 2013; Diaz *et al.,* 2016).

Key ecological strategies are linked to the size of the plant, the seed mass, and the leaf economic spectrum (Westoby 1998; Díaz *et al.,* 2016; Bruelheide *et al.,* 2018). Plant size (height and leaf area), reflects trade-offs linked to growth and competitive ability (Westoby 1998; Díaz *et al.,* 2016). Seed mass relates to germination ability under different stressors (Westoby 1998; Moles & Westoby 2004). The leaf economic spectrum reflects underlying trade-offs in energy-use efficiency; plants can allocate resources to protection and stress tolerance or they can invest in short-lived leaves with high photosynthetic capacity (Wright *et al.,* 2004; Díaz *et al.,* 2016; Onoda *et al.,* 2011, 2017). Leaves with high photosynthetic capacity are thin leaves with high specific leaf area (SLA), low leaf dry matter content (LDMC), and high nitrogen content compared to carbon (Wright *et al.,* 2004; Diaz et al., 2004; Díaz *et al.,* 2016; Onoda *et al.,* 2011, 2017).

Textbox 1: Plant functional traits

DIFFERENT PLACES

The direct and indirect effects of climate change can also vary across different alpine areas. Alpine habitats of the world span a large climatic range (Testolin *et al.*, 2020), they have different topography (Elsen and Tingley, 2015), and they have different geological and biogeographical history (Huang *et al.*, 2019). Climate warming is also variable, for example, it generally happens faster at higher elevations (Pepin *et al.*, 2015). Observations of climate change induced shifts in alpine plant populations and communities also vary. For instance, Elmendorf *et al.* (2012) found that the effect of warming on tundra vegetation differed based on the summer temperature and soil moisture of the site. Likewise, the temperature and precipitation of the experimental site have been identified as important in that these context variables can explain variation in responses to climate change in everything from seed germination (Meineri *et al.*, 2013), plant-plant interactions (Olsen *et al.*, 2016), and colonization of sub-alpine species and extinction of alpine species (Vandvik *et al.*, 2020a). The degree of range expansion into the mountains of warm-loving species (a process called thermophilization) also differs between regions (Gottfried *et al.*, 2012). Due to some of these differences between places it has been proposed that some alpine regions are more sensitive to change than others, and that they are sensitive to different aspects of climate change (Engler *et al.*, 2011; Seddon *et al.*, 2016). Hence, replicating experiments and observational studies across different places might help disentangle the context dependencies of climate change effects on alpine plant communities.

DIFFERENT SPECIES

Alpine species can be divided into those that grow in many different habitats (hereafter: alpine generalist), and those that grow in certain microclimates such as snowbeds or ridges (hereafter: alpine specialists). How species are affected by warming and wetting is dependent on the species niches (Lynn *et al.*, 2021). Alpine specialists are generally thought to be some of the largest losers with climate change (Kudo and Hirao, 2006; Rumpf *et al.*, 2018; Niskanen *et al.*, 2019). They are sensitive to the direct effects of warming (Sperduto *et al.*, 2018; Niskanen *et al.*, 2019), and the indirect effects of increased intensity of competitive plant-plant interactions (Schöb *et al.*, 2008; Hülber *et al.*, 2011; Sperduto *et al.*, 2018). Hence, different groups of species in the alpine will likely respond to climate change in different ways.

NORWEGIAN MOUNTAINS ARE BECOMING WARMER AND WETTER – AND PLANTS ARE RESPONDING

From 1900-2014 the mean annual temperature of Norway increased by 1°C, mostly in spring and winter leading to a longer growing season (Hanssen-Bauer *et al.*, 2017). During the same period there has been an increase of 18% in annual precipitation, with the smallest increase in summer (Hanssen-Bauer *et al.*, 2017). The intensity, and frequency of heavy short-duration rainfall, as well as drought periods have also increased, trends that are predicted to continue in the future (Hanssen-Bauer *et al.*, 2017). As a result of this climate warming in Norway, species have moved upslope and colonized mountain ecosystems (Klanderud and Birks, 2003; Odland *et al.*, 2010), and thermophilous species are increasing in cover (Vanneste *et al.*, 2017). There is also a shift in functional group dominance were the more competitive shrubs and graminoids have become more abundant and forbs and lichens decrease in abundance (Michelsen *et al.*, 2011), at the same time as the tree line is moving up in elevation (Bryn and Potthoff, 2018). Over time lichens are decreasing and bryophytes are increasing in cover, most likely linked to increases in precipitation (Vanneste *et al.*, 2017).

AIMS OF THIS THESIS

In this thesis I combine different methods to disentangle direct and indirect effects of climate change, and assess context dependencies in these effects, across alpine regions of southwestern Norway. I compare functional traits composition of the adult plant community, along climatic gradients in a space-for-time study, with an observational study of climate change over a ten-year period (**Paper I**). Further, I use a laboratory experiment to test for drought effects on seedling establishment traits of populations from different precipitation regimes (**Paper II**). And finally, I conduct a field experiment where I combine warming treatments with manipulation of biotic interactions and study the effect on population dynamics (**Paper III; Paper IV**). By using all these methods and investigating different stages in alpine plants' life cycles I disentangle the direct and indirect effects of climate change on alpine plant communities and the mechanisms they act through.

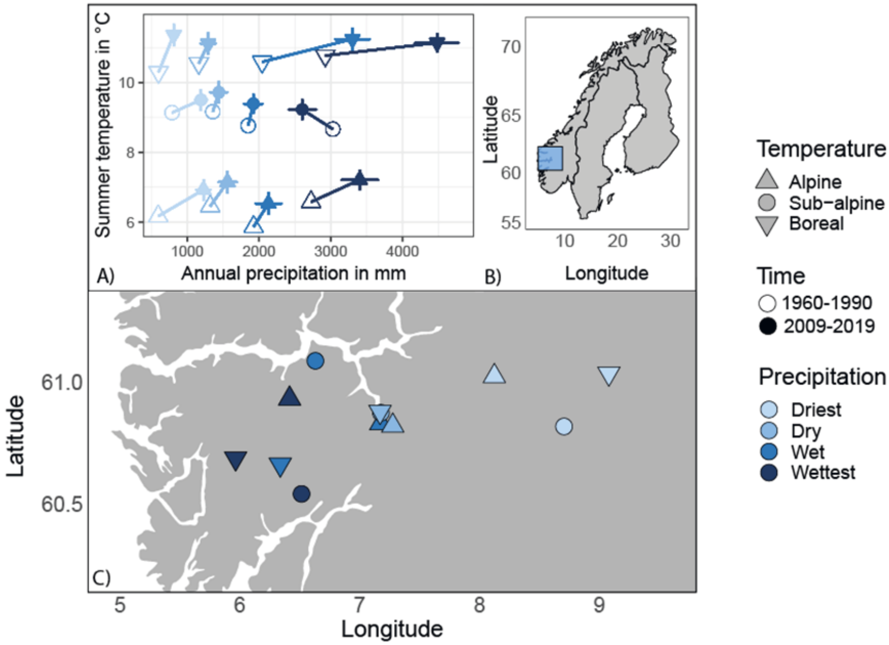
The general aim of this thesis is to disentangle the direct and indirect effects of climate change on alpine plants and investigate context dependencies in these responses. I investigate the direct effects of warming and drought, and the indirect effects through changes in species interactions due to the increased warming. In addition, I shed light on how climatic context may alter these patterns by investigating my research questions along a broad precipitation gradient. The specific research questions addressed in this thesis are:

1) Has the last decade of warming and wetting caused functional trait response in alpine plant communities in Norway? **(Paper I)**
2) To what extent are the direct effects of climate change driving changes in alpine plant individuals, populations, and communities? **(Paper II & III)**
3) How are alpine plants affected by the indirect effects of climate change, due to changes in species' interactions? **(Paper III)**
4) Are there context dependencies in the responses to climate change between species with different niches, and between places with different climates? **(Paper I, II & III)**
5) Building on the insights gained in 1-4, what are the overall impacts of climate change on alpine plant communities in Norway? **(Paper I, II & III)**

METHODS

Study sites – the Vestland Climate Grid

This thesis is based on four papers that are all conducted within or based on material from the field sites of an established climate grid with twelve sites varying independently in temperature and precipitation (Vestland Climate Grid; Figure 1). All the sites are semi-natural grasslands selected to represent a precipitation gradient from the continental, dry inland to the oceanic, humid coast, and using elevation to create a temperature gradient (boreal, sub-alpine and alpine). Mean annual precipitation ranges from 800-4400 mm/year, and mean summer temperature from 6.5-11.5 °C (Figure 1A). The sites were chosen to reflect broad-scale climate gradients, while keeping all other underlying factors similar (i.e., slope, aspect, soil pH, soil type, semi-natural grassland vegetation, and grazing history). The target vegetation type was forb-rich semi-natural alpine grassland vegetation (Klanderud *et al.*, 2015), within the plant sociological association Potentillo-Festucetum ovinae tending towards Potentillo-Poligonium vivipara in the alpine sites (Fremstad, 1998). These sites have experienced climate change over the last decades and become warmer and wetter (Figure 1A and Figure 2).



<u>Figure 1</u>: A) The mean summer temperature and mean annual precipitation of the 12 study sites in western Norway in the normal period 1960-1990 (open symbols) and during the study period 2009-2019 (closed symbols). Lines link 1960-1990 with the 2009-2019 climate centroids per site, error bars for each symbol reflect the standard error. B) The study region in south-western Norway and C) the geographical location of the twelve sites. Summer temperature is calculated as the mean temperature for the four warmest months per year (May-August), and precipitation as the mean annual precipitation. Climate data provided by the Norwegian Meteorological Institute (<u>www.met.no</u>). From **paper I**.

Paper I is an observational study across all the <u>twelve sites</u> in the Vestland Climate Grid, over a ten-year period using data collected in previous projects. For **paper II** we collected seeds at the <u>four alpine sites</u> of the climate grid, to investigate the local adaptation of alpine species to drought, and how that may vary across a precipitation gradient. To further disentangle the effects of direct and indirect effects of climate change we established the INCLINE experiment (further explained below) in the <u>four alpine sites</u> of this climate grid (**Paper III**; **Paper IV**). In this experiment we also sourced species for the transplants part of the experiment from the four sub-alpine sites of the Vestland Climate Grid.

In 2009 permanent plots of 25x25 cm were installed in the 12 sites of the Vestland Climate Grid as part of a climate transplant experiment (Klanderud *et al.*, 2015; Vandvik *et al.*, 2020a). I use the five control plots from each site in **paper I** of this thesis. The sites were fenced in and mowed once every growing season to simulate the natural grazing in the system.

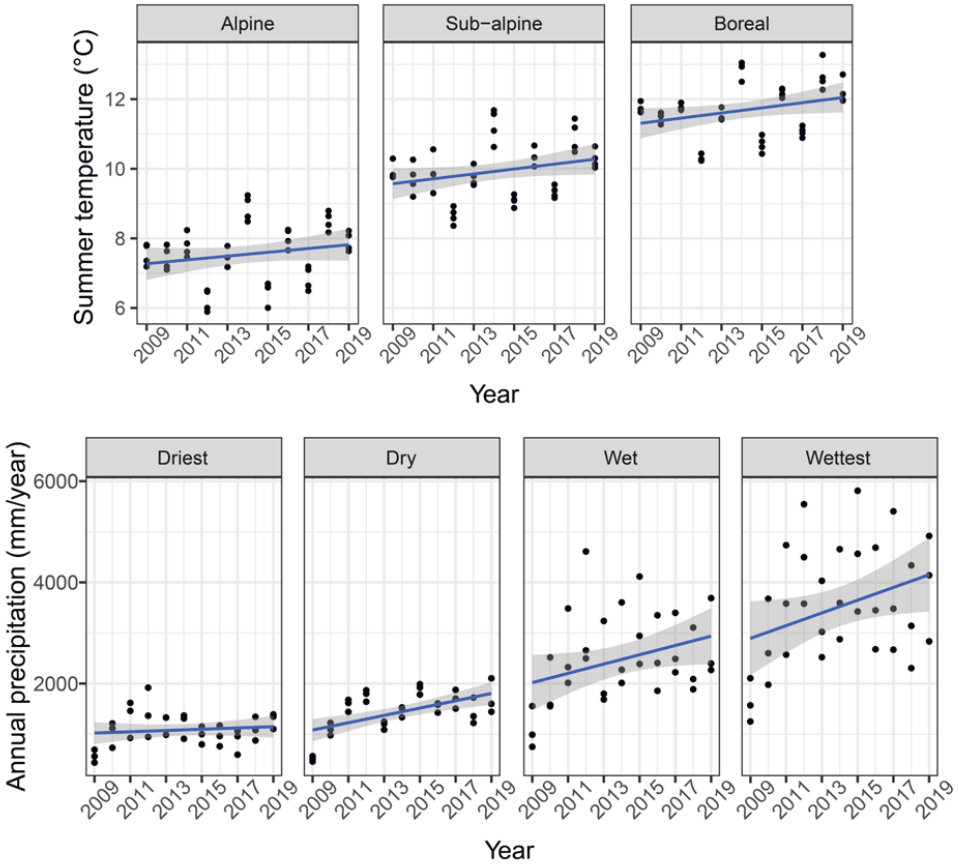


Figure 2: Summer temperature (May-July) and annual precipitation (m/year) in the Vestland Climate Grid sites in south-western Norway from 2009-2019. Summer temperature is split into the alpine, sub-alpine and boreal sites, and the precipitation is split into the driest, dry, wet, and wettest sites. Trendline is from a linear model estimated from geom_smooth in ggplot. Figure adapted from appendix figure 1 and 2 in **paper I**.

The INCLINE experiment

In 2018 we started the INCLINE experiment in the four alpine sites of the Vestland Climate Grid (Figure 1). We installed permanent plots of 25x35 cm with five replicates of each treatment, and all plots were fenced during the growing season to avoid disturbance from grazing animals or humans. See more detailed description in **paper IV**.

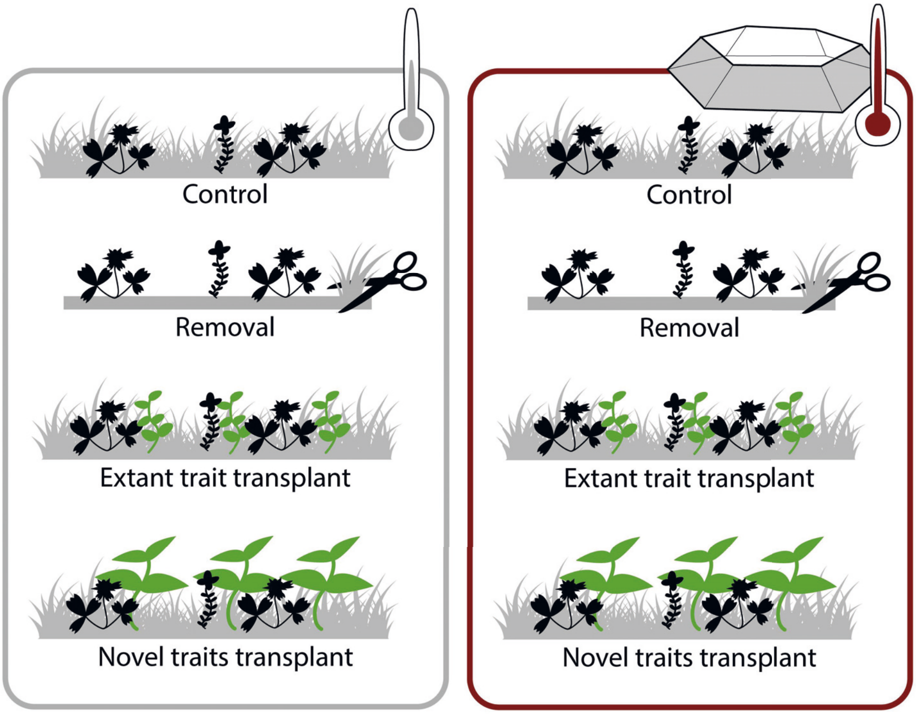


Figure 3: Overview of the treatments in the INCLINE experiment. To test the effect of warming we used open top chambers, and further combined the ambient alpine climate and the warmed climate with additional treatments. Both climates have a control, a removal experiment removing all above ground biomass except two focal species, and two transplant treatment with sub-alpine species with extant traits (similar to the alpine plant community), and novel traits (more competitive than the alpine plant community).

The INCLINE experiment has eight treatments (Figure 3); one control, one removal and two transplant treatments, and all of them a crossed with a warming treatment. The removal treatment entails removing everything but the alpine focal species from plots (Figure 4 g-h), to test for facilitative or competitive effect from the extant alpine plant communities on the focal alpine species. To test the effect of novel interactions from range-expanding species on the alpine plants we established two transplant treatments, introducing sub-alpine species with ‘extant’ and ‘novel’ traits (Figure 4 a-e). The two transplant treatments enabled me to not only test for effects of range-expanding species but also to what extent their functional traits mattered for these effects. In the control treatments we conducted local transplants within plots, using small turfs of the same size and position as the range-expanding plants into transplants plots, to control for the disturbance effect on the transplant plots experienced (Figure 4 a). We used open-top chambers to obtain the warming treatment (Figure 4 j). The experiment was conducted in the four alpine sites of the Vestland Climate Grid, thus enabling an assessment of if and how responses changed along a precipitation gradient. Note that our study system that is much wetter than most other alpine habitats globally, which also adds uniqueness to the study (as illustrated by expanding the boarders of the climatic overview of global biomes; Figure 5).

Figure 4 (on next page): Pictures from the field of the different treatments etc. in the INCLINE experiment. a) S 25x35 cm plot with the six subplots used for transplant cut out. b) Six transplant individuals (form the left: *Carex pilulifera*, *Viola canina*, and *Veronica officinalis*) that is about to be transplanted into the alpine vegetation. c) A *Succisa pratensis* individual that successfully came back after the first winter, thriving in the alpine vegetation. d) *Succisa pratensis* flowering. e) *Carex pallescens* flowering. f) Seeds glued to toothpicks installed in the bare ground (forefront of the picture) and in vegetation (in the background of the picture) to estimate germination success. g) Removal treatment with removing all above ground biomass. h) A removal plot with all above ground biomass removed except *Veronica alpina* and *Sibbaldia procumbens*. i) An overview of a vegetation plot of 25x35 cm with 35 subplots of 5x5 cm, and a data collection sheet for species inventory. j) An open-top chamber. Photos by Ragnhild Gya and Siri Lie Olsen.

For each site there are five replicates of each treatment. The five replicates were spread out across seven blocks due to space constraints inside each open-top chamber. After the first year of data collection (2018) we randomly assigned the treatments to plots, with some adjustments to make sure we had spread the treatments across vegetation types and had enough of the alpine focal species for **paper III** in each treatment (see **paper IV** for details about the adjustment).

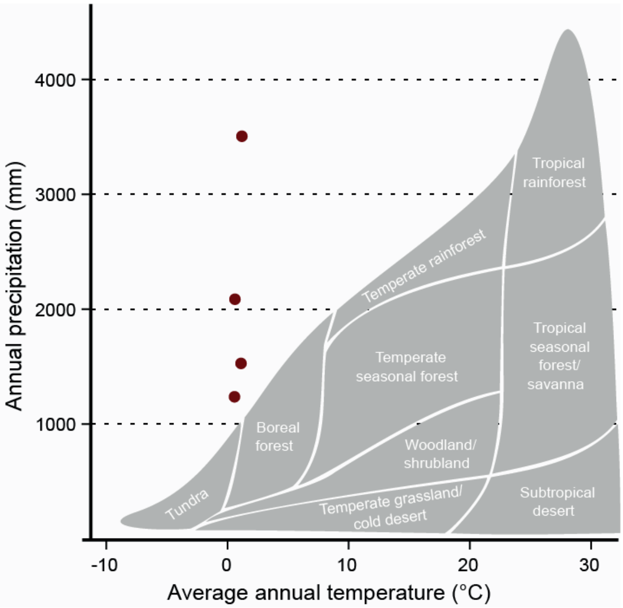


Figure 5: The worlds biomes and how they are distributed in climatic space. The four red points are the four alpine sites of the INCLINE experiment, visualizing that we cover a climatic space that is not very commonly studied. Adapted from Whittaker (1970), figure available from: https://commons.wikimedia.org/w/index.php?curid=61120531

The effect of range-expanding species on alpine species may differ depending on species' functionality, or functional trait expression. To test this hypothesis, we chose two groups of sub-alpine species for the transplant experiment: i) extant traits species (with similar traits to the alpine plant community), and ii) novel trait species (with more competitive traits than the alpine plant community) (Figure 3; **Paper IV**). An individual's competitive ability, including invasive potential, can be indicated by performance metrics such as growth and light capture, that are in turn characterized by key functional traits such as vegetative height, specific leaf area (SLA) and leaf area (Van Kleunen *et al.*, 2010; MacLean and Beissinger, 2017; Dolezal *et al.*, 2019). Consequently, we selected our species for transplanting by comparing height, SLA and leaf area. Species representing the extant traits groups were chosen if their trait-expression did not vary from alpine community in at least two of three traits (**Paper III**; **Paper IV**). In contrast, the novel traits group were selected to be taller, have larger leaves and/or higher SLA in comparison to the alpine plant community (**Paper III**; **Paper IV**), with species differing from the alpine plant community in at least two of the three traits. The trait measurements used to define both extant and novel groups were collected on individuals within our study sites, as is described below. The species used as focal alpine species were *Sibbaldia procumbens* and *Veronica alpina*, the extent traits species were *Viola canina, Veronica officinalis*, and *Carex pilulifera*, and finally the novel traits species were *Hypericum macculatum, Succisa pratensis* and *Carex pallescens* (see **paper IV** for more details about the species).

Data collection

Species composition

For **paper I** we collected species composition data in all the twelve Vestland Climate Grid sites (**Paper I**). In sampled plots all vascular plants were identified to species, and percent cover was visually estimated for each vascular plant species (Figure 4 i). The community species composition was recorded in the permanent plots of the twelve sites in the Vestland Climate Grid for analysis of **paper I**, during the peak of the growing season (late June for boreal sites, July for sub-alpine sites and late July/early August for alpine sites) in 2009, 2011, 2012, 2013, 2015, 2016, 2017, and 2019. The species composition data were predominantly registered by Vigdis Vandvik and Kari Klanderud with help from Siri Lie Olsen (see author contribution and acknowledgements in thesis and **paper I**). Taxonomy followed the species name list of the Norwegian Biodiversity Information Center (Artsdatabanken, 2015). *Deschampsia alpina* was included in *D. cespitosa* and *Anthoxanthum* *nipponicum* was included in *A. odoratum* since these species are hard to distinguish in vegetative form (Rothera and Davy, 1986; Lid and Lid, 2007). In addition, we only identified species to genus level for species of *Alchemilla spp.* (excluding *A. alpina)*, *Euphrasia spp., Salix spp. (*excluding *Salix herbacea),* and *Taracaxum spp.*

Trait collection

For **paper I**, I also measured functional traits of the most common plants in the plant community at all the twelve sites of the Vestland Climate Grid during the peak growing season of 2016. At each site we collected ten individuals for the most abundant species at each site, selected to ensure that at least 80% of the vegetative cover in the plots were represented. To avoid variation caused by phenological and developmental stages, we chose flowering individuals; if species/individuals were not flowering at the time, we chose mature vegetative individuals avoiding juveniles and wilted plants. Where possible, individuals were collected at least two meters apart to ensure that they were not from the same genet. We measured size and growth-related traits: vegetative height (mm), leaf area (cm^2), leaf dry and wet mass (g), and leaf carbon (%). The leaf economic traits: leaf thickness (mm), specific leaf area (SLA cm^2/g, leaf area (cm^2)/dry mass (g)) and leaf dry matter content (LDMC, dry mass (g)/wet mass (g)), leaf nitrogen (%), and carbon to nitrogen ratio (leaf C%/ leaf N%). All traits were collected following a standardized protocol (Pérez-Harguindeguy *et al.*, 2016). See **Paper I** and Gya (2017) for a more detailed description of the data collection.

Demographic data collection

In the INCLINE experiment we conducted demographic studies of two alpine focal species (*Sibbaldia procumbens* and *Veronica alpina* – Figure 6) to understand the underlying mechanisms of the direct and indirect effects of climate change (**Paper III**). For each species, all individuals within the experimental plots were tagged and monitored during the peak growing season (August) every year from the pre-treatment year 2018 until 2021. We monitored survival of individuals over the years, and registered new individuals from seeds, or clonal reproduction. We measured different attributes of the individuals, such as number of leaves and reproductive units and shoot height, to estimate growth and fecundity.

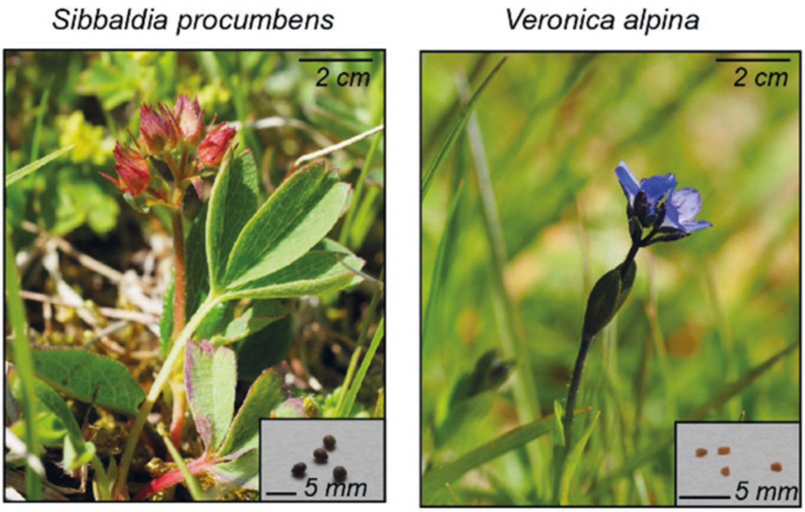


Figure 6: The two alpine focal species: the snowbed specialist *Sibbaldia procumbens* and the alpine generalist *Veronica alpina*. *Adapted from figure in **Paper II**.*

To estimate biomass we used the attributes measured at individual level by calculating biomass regressions. The biomass regressions used to calculate the size and biomass of plants were based on samples from *S. procumbens* collected in 2019 (Dybedahl, 2020), and previous data of *V. alpina* from our system from 2009 (Olsen *et al.*, 2016; Skarpaas *et al.*, 2016; Töpper *et al.*, 2018). We then estimated the relationship between biomass and attributes measured in the field using linear models. To estimate the number of seeds per capsule we collected ten flowering individuals per species per site in 2020. We then counted the number of seeds per capsule and tested if this varied between population, which it did not so we used the average number of seeds per capsule across populations. To calculate germination success, we sowed 20 seeds of each species in five replicates of warmed and unwarmed plots in the field, with and without vegetation (Figure 4 f) in 2019 and surveyed them in 2020. Finally, to estimate the survival of seeds in the seedbank, across five replicates of warmed and unwarmed plots, we buried 20 seeds of each species in nylon socks about 5 cm below ground, in 2019. After one year in the ground, we retrieved the seeds and registered viability. Further details about the methodology for all these data collections can be found in the INCLINE data paper (**Paper IV**). These data were collected by me, Joachim P. Töpper, and Siri Lie Olsen with assistance from technicians and interns (see author contributions and acknowledgements in **Paper III and IV**).

Germination experiment

In **paper II**, we tested how germination in the two alpine species *S. procumbens* and *V. alpina* is affected by water availability. To assess if there were any local adaptation to drought from populations of different precipitation regimes, we collected mature seeds of both species from the four sites in the INCLINE experiment, during August-September 2019. The seeds were cold stratified for nine weeks at 4 °C in a moist and dark environment to break dormancy. Then we germinated the seeds across ten different water potentials in an Agar medium in the range between -0.25 (only agar) and -1.7 MPa. We used polyethylene glycol (PEG, molecular weight 8000; Sigma, St Lois, MO, USA) to alter the osmotic water potential.

The germination experiment was conducted in a controlled climate growth chamber, with varying temperature and light conditions simulating day and night. We monitored seed germination, cotyledon development and leaf emergence at a minimum of twice a week (more frequently during the start of the experiment). After seedlings had developed true leaves, they were harvested and dried to measure above ground and below ground biomass, which was then used to calculated root:shoot ratios. The data collection was run by me with assistance from researchers, technicians, and students (see author contributions and acknowledgements in **Paper II**). See **Paper II** for a more detailed description of the methods.

Analytical approaches

In **paper I** I used a novel bootstrapping method to calculate community weighted means for each site-year combination. The advantage over standard approaches being that this new method allows us to keep some of the variation in the data and explicitly account for it in the calculation of community-weighted means and in downstream analyses (Maitner *et al.*, 2021; Telford and Halbritter, 2021). We used the calculated community-weighted means in linear mixed effect models for each trait to test for the effect of temporal and spatial variation in temperature and precipitation. We also made ordinations, using Principal Component Analysis (PCA) (Abdi and Williams, 2010), based on the community weighted means of all the traits for each plot to visualize patterns and identify main axes of variation in multivariate trait space. Additionally, we tested the multivariate trait relationships with temperature, precipitation, and time (year) using redundancy analysis (RDA) (Van Den Wollenberg, 1977). In **paper II**, we used Bayesian modelling to build linear mixed effect models or generalized linear mixed effect models to test how germination responses and seedling traits responded to drought, and if this varied with the precipitation or seed mass of the source population. In **paper III,** we built integral projection models (IPMs) based on regression models of vital rates (survival, growth, clonality, and fecundity) against estimated biomass as a continuous state variable. From the IPMs, we extracted the population growth rate (λ), and calculated life table response experiments (LTREs) to investigate the contribution of each vital rate to the overall λ. **Paper IV** is a data paper reporting on the INCLINE field experiment and does not contain any analyses.

MAIN FINDINGS AND GENERAL DISCUSSION

In the following, I present, contrast, and compare the main findings of the papers in this thesis, and I discuss them in light of existing literature. For detailed discussions of the results and implications each study, see the specific papers.

WARMING AND WETTING HAS CHANGED ALPINE AND BOREAL PLANT COMMUNITIES

RQ1. Has the last decade of warming and wetting caused functional trait response in alpine plant communities in Norway?

In this study system there has been a general warming and wetting across the whole region (Hanssen-Bauer *et al.*, 2017), which has led to changes in plant communities over the last decade (**Paper I; Paper III**). Species that are more adapted to warm habitats have increased in abundance (Lynn *et al.*, 2021), as also seen in other alpine systems in Norway (Framstad *et al.*, 2022), and alpine and Arctic studies worldwide (Gottfried *et al.*, 2012). Additionally several studies find that species are moving up the mountains in response to warming (Chen *et al.*, 2011; Steinbauer *et al.*, 2018). While there's no published evidence confirming range shifts in our specific study region yet, **Paper III** and **Paper IV** show that transplanted adult individuals of species from lower elevations can grow in our alpine habitats. We also found that seeds of these species could germinate in the current alpine climate (Dahle *et al.*, 2022; **Paper IV**), indicating that the climate is currently warm enough for these lower elevation species do establish in the alpine. Further, very few studies have investigated the effect that increased precipitation has on alpine plant communities in already wet habitats. In the same study sites as this thesis is conducted Lynn *et al.* (2021) found that very few species benefit from an increase in precipitation because most species have a niche centre (i.e. climate optimum) that is drier than the climate of these sites. Together, my research and other studies in the same system indicate that after the recent warming and wetting our specific study system has seen an increase in abundance of the more thermophilous species (Lynn *et al.*, 2021), and conditions have become warm enough for lower-elevation species to grow in alpine habitats (**Paper III**; **Paper IV**), while the species composition has not responded to precipitation (Lynn *et al.*, 2021).

As for the functional composition of the alpine plant community, the multivariate trait space has changed over time but these changes are dependent on the current climate of the site (**Paper I;** Figure 7). Plant communities from colder and wetter climates shifted to more resource acquisitive traits over time, whereas the communities from the warm and dry climates became more resource conservative (Figure 7). These trait shifts in colder and wetter climates indicate higher productivity (taller plants with larger leaves and/or more resource acquisitive traits) with climate change, as has also been found in other Arctic and alpine studies (Hudson *et al.*, 2011; Bjorkman *et al.*, 2018; Vuorinen *et al.*, 2021). Additionally, In **Paper III** and **Paper IV,** we transplanted lower-elevation species with more resource acquisitive traits into these alpine habitats, and found that they survived and grew well here, indicating that the current alpine climate does support species with more resource acquisitive strategies than currently present in the alpine community. Further, the shift we found to more conservative leaf economic traits in the warm and dry climates (Figure 7) supports other studies that found the same for certain traits (Hudson *et al.*, 2011; Vuorinen *et al.*, 2021). These are changes in the multivariate trait space, but the only single trait that changed as a response to changes in climate over time was LDMC, which increased in wetter years, but only in the driest sites (Figure 8). We also find that the differences in alpine plant communities' functional composition in response to warming and wetting over time is dependent on the previous climatic conditions of the site (**Paper I**; Figure 7). I discuss different challenges of the high precipitation alpine climates and the consequences for the future in the “Climate change in high precipitation systems” section of this discussion.

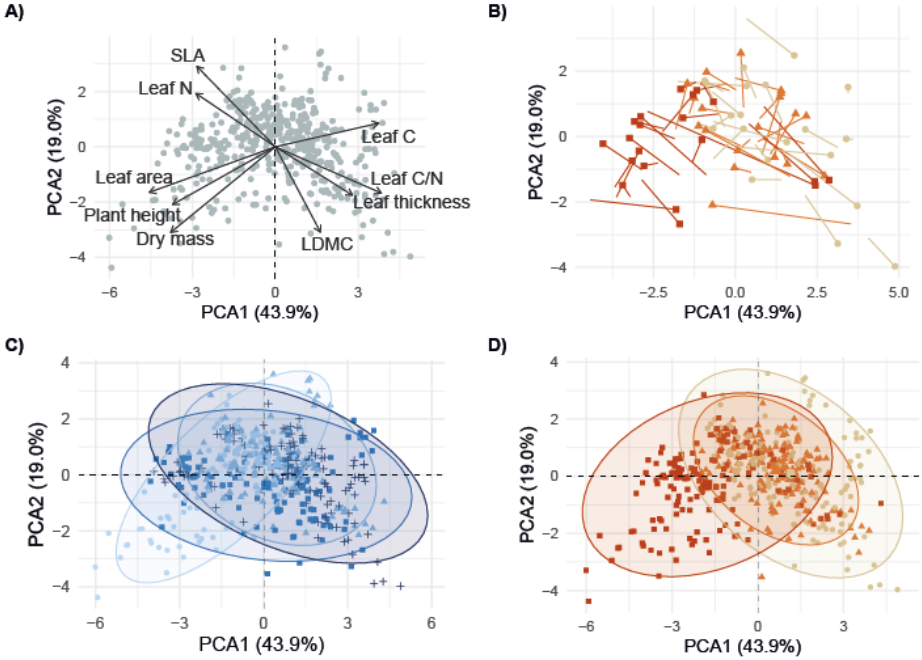


Figure 7: PCA of the community weighted means traits across temperature (three levels) and precipitation (four levels) gradients in boreal, sub-alpine, and alpine plant communities in Norway. Each point is one plot based on the plant community analysis from 2009, 2011, 2012, 2013, 2015, 2016, 2017 & 2019. Each point is one plot-year combination. A) How the trade-off between different traits are across all sites and years, B) change in traits over time for each plot from the first year (2009 - point) to the last year (2019 - end of line) (yellow is the alpine sites, orange is the sub-alpine sites and dark red color are the boreal sites), C) PCA scores four precipitation levels (light blue is the driest site, and dark blue is the wettest site), D) three temperature levels (colors as B). Figure from **paper I.**

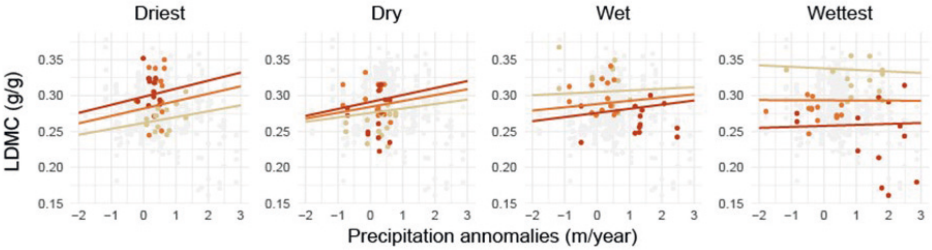


Figure 8: Changes in community weighted Leaf Dry Matter Content (LDMC g/g) in response to precipitation anomalies in time based on their position in the spatial climate gradient. Light grey points are the observed community weighted means. The lines are predicted values from a mixed effect model in cold alpine (light yellow), sub-alpine (orange) and warmer boreal (red) sites. The predictions were made for four different precipitation regimes with 1 m/year (driest), 1.45 m/year (dry), 2.4 m/year (wet) and 3.5 m/year (wettest). Figure from **paper I.**

Finally, the context dependency of shifts in trait values does not necessarily need to be linked to climate differences directly, but could also be indirectly linked to climate through differences in biotic interactions in the different sites (Blonder *et al.*, 2018). As we move from harsh alpine conditions to the less stressful environments in the boreal sites, the intensity of facilitative interactions is expected to decrease (Maestre *et al.*, 2009) and the intensity of plant-plant competition for light is expected to increase (Hulshof *et al.*, 2013). To gain resources from light under increased light competition a plant could either grow taller and produce more leaves, or improve the photosynthetic capacity of the leaves through leaf economic traits (Díaz *et al.*, 2016). Studies have found that warming itself leads to taller plant communities (Rammig *et al.*, 2010), but the more competitive interactions under warmer climates (Olsen *et al.*, 2016) also give a directional selective pressure for traits that are more competitive for light (Rammig *et al.*, 2010; Coble and Cavaleri, 2015). Hence, the increase in plant height and shift towards resource acquisitive traits in some of the warmer sites (**Paper I,** Figure 7) could be a response to an indirect effect of climate change, namely increased competition for light.

In **Paper I,** we test for changes in alpine plant communities to climate change using observational resurveys and the space-for-time method. In the observational study over ten years we find some changes in the community trait syndrome, but few of the community weighted means of individual traits change over time. The predictions we obtain from the space-for-time method does not necessarily match the actual changes we observe in the ten-year period, even if studies argue that space-for-time is well indicative of temporal changes (Blois *et al.*, 2013). In **Paper I** we argue that this lag in trait shifts could be caused by i) a complex relationship to several climatic factors leading to unexpected direction or lack of change to climate shifts in time, ii) a strong lag in the functional response to climate change making our ten-year study period a too short time series to detect trends, or iii) intraspecific trait variability, or plasticity, over time, which we did not record as we have traits for one year (see **Paper I** for details). The complex relationships could include responding to different drivers at the same time (as we investigate in **Paper I**), or the indirect effects of climate change (as we investigate in **Paper III**), or that different parts of the life history are affected in different ways, or vital rates respond in opposite ways (as we investigate in **Paper II** and **Paper III**). In the study of **Paper I,** we are not able to disentangle the direct and indirect effects. To further understand the changes in plant communities, I isolate separate mechanisms of change and disentangle the direct and indirect effects of climate change through controlled field and lab experiments.

THE DIRECT EFFECTS OF CLIMATE CHANGE: WARMING & DROUGHT

RQ2: To what extent are the direct effects of climate change driving changes in alpine plant individuals, populations, and communities?

To investigate the direct effects of climate change alone, we experimentally removed sources of potential indirect effects. Specifically, I isolated the direct effect of warming on plant populations in a field experiment by removing all surrounding neighbors (**Paper III**), and I studied the direct effect of drought on germination in a controlled lab environment (**Paper II**). Further, I investigate how the different life stages are affected by the direct effects of climate change, specifically the full population dynamics of two alpine species in **paper III** and zooming in on the early life stages of the same two species in **paper II**.

Many studies on warming are done using either experimental methods in the field (e.g., Hudson *et al.* (2011) and Fazlioglu and Wan (2021)) or by observing the changes in systems that have been warmed over time (e.g., Steinbauer *et al.* (2022)). Because these studies do not control for changes in plant-plant interactions it is not possible to disentangle the direct effect of warming from the indirect effect which arise due to changes in species interactions, as discussed in for example Töpper *et al.* (2018). In **paper III** we are able to do just that, as we investigate the direct warming effect *alone* by removing all vegetation except the two alpine focal species, *i.e.*, warming them without neighbors present. Here, we find that warming increases the population growth rate (λ) for the snowbed specialist *S. procumbens* in all sites*,* and in the driest population for the alpine generalist *V. alpina* (Figure 9)*.* In the wetter populations of *V. alpina*, warming decreases λ, yet still all λs were positive (Figure 9) (differences along the precipitation gradient will be discussed in the "Climate change in high precipitation systems" section)*.* Our findings support the general expectation that warming alone, when excluding plant-plant interactions often affects alpine plants positively (Elmendorf *et al.*, 2012; Fu *et al.*, 2015; Fazlioglu and Wan, 2021).

The processes and vital rates underlying the positive effect of warming are important to predict changes in alpine plant populations in the future. Different combinations of vital rate responses can lead to the same λ response, but still make crucial differences for the population dynamics via size distribution, recruitment patterns, dispersal, population genetics etc. (Villellas *et al.*, 2015). Generally, warming has been found to increase plant growth (Nomoto and Alexander, 2021), as we also found for *S. procumbens,* and I most cases for *V. alpina*. As vital rates in plants often show a positive relationship with biomass or size, which is the case for my study species (Appendix 2 in **Paper III**), an increase in growth will subsequentially likely lead to increased survival and fecundity. However, if survival is directly negatively affected by warming, as for *V. alpina* in some populations (Figure 9) any positive effect on growth might be cancelled out if the positive effect operating via increased growth is less important for the overall λ than the negative effect via high mortality (Nomoto and Alexander, 2021).

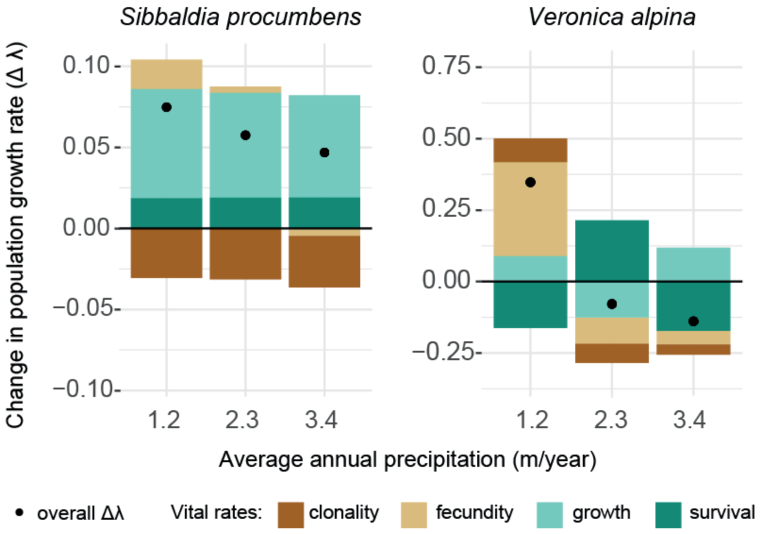


Figure 9: Contribution of vital rates (clonality, fecundity, growth and survival) to changes in population growth rates (λ) when *Sibbaldia procumbens* (left) and *Veronica alpina* (right) are warmed without surrounding neighbors. The contributions of vital rates are based on one-way life table response experiments (LTRE's). The black dot marks the overal change in population growth rate between the removal treatment with and without warming. Each treatment comparison is done across three precipitation levels; first column: 1200 mm/year, second: 2300 mm/year and third: 3400 mm/year. Note the difference in scale between the two species. Figure adapted from **Paper III**.

As for fecundity, warming has been found to increase flowering at the community level in Arctic and alpine plant communities (Hollister *et al.*, 2005; Walker *et al.*, 2006; Elmendorf *et al.*, 2012), which we also found in our specific field sites, especially for graminoids (Berthelsen, 2022). However, at the population level for our two focal species we found that fecundity was affected negatively by warming in the wetter end of the precipitation gradient (Figure 9). Kudo and Hirao (2006) also found negative effects of warming on fecundity of alpine species. Reduced fecundity is important for the level of genetic recombination in a population and thus for its ability to adapt to stressors from climate change (Steltzer *et al.*, 2008).

In addition to warming, climate change is causing an increase variability in precipitation which will most likely lead to plants being exposed to more frequent drought events in our study region (Hanssen-Bauer *et al.*, 2017). Drought as a direct effects of climate change is often related to negative responses in alpine plants (Walck *et al.*, 2011; Magaña Ugarte *et al.*, 2019; Dolezal *et al.*, 2020). The timing of these drought events matters for what effects they might have. Drought events that occur in the early spring, during alpine plants' regular germination time, might pose many challenges for the recruitment stage in alpine plants (Walck *et al.*, 2011). In **Paper II** we found a negative impact of drought on germination in both *S. procumbens* and *V. alpina*. Drought led to a decrease in germination percentage (Figure 10), and a delay in germination onset (**Paper II**), in line with findings from global meta-analysis of other alpine species (Vázquez-Ramírez and Venn, 2021). Once germinated, the seedling stage is also susceptible to drought. In drier regions of the world, allocating resources more to roots than to shoots has been shown as an effective strategy for seedlings to cope with dry conditions (Harrison and LaForgia, 2019; Larson *et al.*, 2020). Interestingly, I find the same pattern in our study based on wetter habitats in one of our study species: in *V. alpina* the root:shoot ratio of in biomass was higher under drought condidions (**Paper II**). Skarpaas *et al.* (2016) found a similar pattern for adult individuals in the same field sites, where the plants invested more in roots, and less in leaves as precipitation decreased along the climate gradient. This indicates that drought has a negative effect on germination success and timing, but also influences the seedling traits in species from generally high precipitation habitats (**Paper II**).

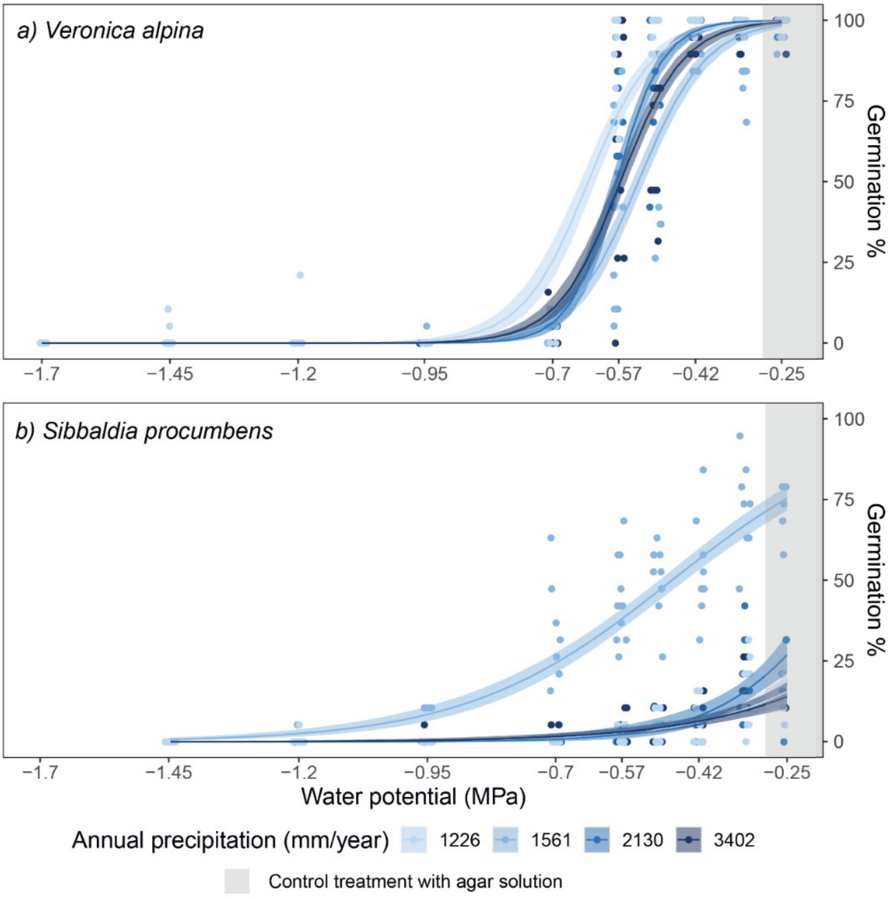


Figure 10: Germination % (number of seeds germinated/viable seeds in the petri dish) for a) *Veronica alpina*, and b) *Sibbaldia procumbens* across different water potentials (MPa). -0.25 MPa represents pure agar medium with no drought treatment. The decreasing water potentials yield increasing levels of drought. The colors are based on the precipitation level of the populations the seeds were sampled from, going from light blue in the driest to dark blue in the wettest population. Seeds were sampled at alpine sites in western Norway. The lines represent predicted means with 95% credible interval envelopes. Figure from **paper II.**

The key question is: are these species able to adapt to these novel climatic conditions and reduce the negative effect of drought or will more drought lead to an overall negative effect on alpine plants early life stages? I found that the population of *V. alpina* from the driest site germinates at higher proportions and at a faster rate under drought conditions compared to the populations from wetter conditions (Figure 10), which could indicate local adaptation (Radersma *et al.*, 2020). The seedlings from the driest populations also invest more biomass in roots when exposed to drought (**Paper II**), a strategy that is found to be more effective in drier conditions (Harrison and LaForgia, 2019; Larson *et al.*, 2020). Local adaptation to drought in dry habitats has repeatedly been documented for germination in arid parts of the world (Cochrane *et al.*, 2014; Everingham *et al.*, 2021) but it has never before been shown in high precipitation areas like our study system (**Paper II**). This evidence for local adaptation was only found in *V. alpina* and we did not find any indication of this in *S. procumbens* (**Paper II**; Figure 10). This does not necessarily mean that *S. procumbens* does not respond to drought. For example, in the demographic study we found that the probability of flowering for *S.* procumbens was higher in the driest populations (Appendix 2 in **Paper III**). Since the number of seeds per reproductive unit did not change along the precipitation gradient (Appendix 1 in **Paper III**), the total number of seeds was therefore higher in drier populations. Although **Paper III** did not test drought specifically, this response could make the driest population better able to maintain recruitment rate needed to ensure a positive population growth rate even in cases when drought events would decrease germination success and/or seedling survival (**Paper II**). Additionally, we found that for *S. procumbens* high seed mass increased germination success under drought conditions (**Paper II**), as is also true for other species in other environments (Leishman and Westoby, 1994). However, seed mass did not correlate with the precipitation of the site for neither species (**Paper II**), even if dry soil are often associated with production of heavier seeds (Westoby *et al.*, 2002). Despite the lack of correlation between seed mass and precipitation, seed mass could be an element for adaptive selection to act upon. Other factors can also lead to an increase in seed mass, such as increased shading and soil nutrients (Westoby *et al.*, 2002). This indicates that even if *S. procumbens* might not have any physiological local adaptations to drought (**Paper II**), an increase in seed mass, or the increased flower production

(**Paper III**) could maintain germination success during drought events. Hence, I document for the first time, that some species from the wettest end of the precipitation range of the alpine regions globally, might still be able to cope with a future climate that includes more frequent and severe droughts.

Warming seems to have a generally positive effect on alpine plants (**Paper III**), while drought has a negative effect (**Paper II**). This might be the reason why De Boeck *et al.* (2016) found that heat waves did not affect alpine plants negatively unless it was coinciding with a drought. This is why studying several climate change components at the same time is important. In this thesis, I study both the effect of warming (**Paper III**), and drought (**Paper II**), but not in the same study. Although I study single climatic factors, in **Paper III**, we did so across a large precipitation gradient to test for climatic context dependencies in the effect of warming (as further discussed in the “Climate change in high precipitation systems” section below). As the variation in precipitation and the average temperature keeps increasing, Norwegian alpine systems will experience more droughts (Hanssen-Bauer *et al.*, 2017) and local adaptation to dry conditions could become more important. Species that do not have any morphological or physiological adaptations to handle drought might therefore be more sensitive to future direct effects of climate change (as further discussed in the “Snowbed specialist vs. alpine generalist” section below).

THE INDIRECT EFFECTS OF CLIMATE CHANGE: SPECIES INTERACTIONS

RQ3. How are alpine plants affected by the indirect effects of climate change, due to changes in species’ interactions?

To be able to investigate the indirect effects of climate change, for instance in relation to warming, we need to disentangle the effect of altered species interactions with the direct effect of temperature increase. The INCLINE experiment was designed to disentangle the direct and indirect effects in a field experiment by combining warming, removal, and transplant treatments (**Paper III**; **Paper IV**). To understand how the interactions between species in alpine communities change with warming I compared the effects of removing neighboring vegetation in the ambient and warmed climates (**Paper III;** Figure 11). I also investigate the effect of novel interactions from species that are predicted to shift from lower elevations into the alpine habitats in the near future (hereafter: sub-alpine species) in ambient and warmed climates treatments (**Paper III**). Finally, I ask if the functional identity of the sub-alpine species matters for their effects on alpine plants (**Paper III**).

As climate is warming, many studies predict that plant-plant interactions in the alpine will shift from facilitative towards increasingly competitive (Maestre *et al.*, 2009; Anthelme *et al.*, 2014). We do not find any evidence suggesting facilitative interactions between alpine species in the current alpine climate, rather neutral interactions for *S. procumbens*, or competitive ones for *V. alpina* (Figure 11; **Paper III**). A previous study in our study system did find facilitative interactions between specific alpine species, including *V. alpina,* and their surrounding alpine neighbors (data until 2013) (Olsen *et al.*, 2016). This could be consistent with a shift in species interactions from facilitative towards more competitive over time due to the warming that has already happened in our region (Figure 1; Figure 2). Further in our study, removing neighbors in the warm treatment was positive for both species (i.e., competitive release) (Figure 11), confirming the literature that predicts increasing competitive interactions in the warmer future alpine (Anthelme *et al.*, 2014; Olsen *et al.*, 2016). For *S. procumbens* the interactions with surrounding alpine neighbors changed from neutral in the ambient alpine climate to competitive in the warmed climate (Figure 11). For *V. alpina* the competitive release with warming decreased with precipitation, indicating less competitive interactions in the wetter habitats (Figure 11), which could be because of more stressful environments in the wettest end of the precipitation gradient. This is in line with the stress-gradient hypothesis which suggests that as environments becomes more stressful interactions within plant communities will become more facilitative (Maestre *et al.*, 2009). The precipitation gradient results will be further discussed in the “Climate change in high precipitation systems” section further down.

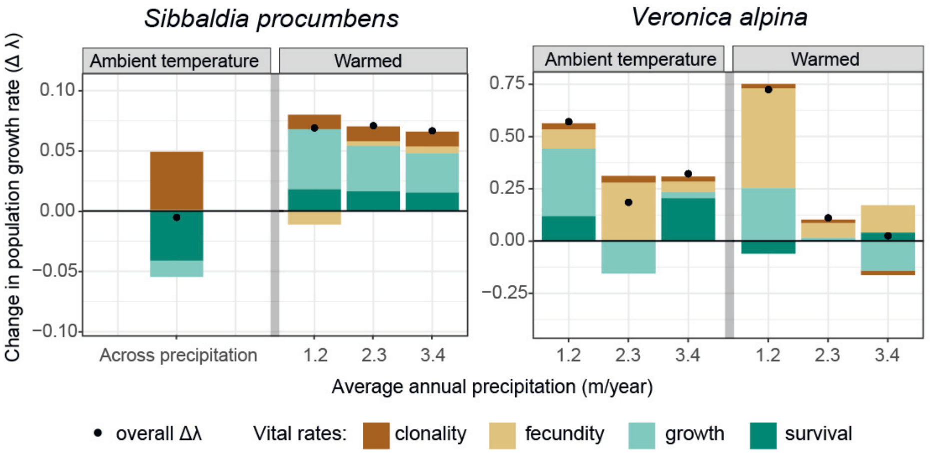


Figure 11: Contribution of vital rates (clonality, fecundity, growth and survival) to changes in population growth rates (λ) between experimental treatments of removal of neighboring vegetation in the ambient and warmed climate. The contributions of vital rates are based on one-way life table response experiments (LTRE’s). Each treatment comparison is done across three precipitation levels; first column: 1200 mm/year, second: 2300 mm/year and third: 3400 mm/year. Except for *Sibbaldia procumbens* in the ambient temperature where there were no difference between precipitation levels, so the IPM was built across precipitation levels. Note the difference in scale between the two species, *Sibbaldia procumbens* on the left and *Veronica alpina* on the right. Figure adapted from **Paper III**.

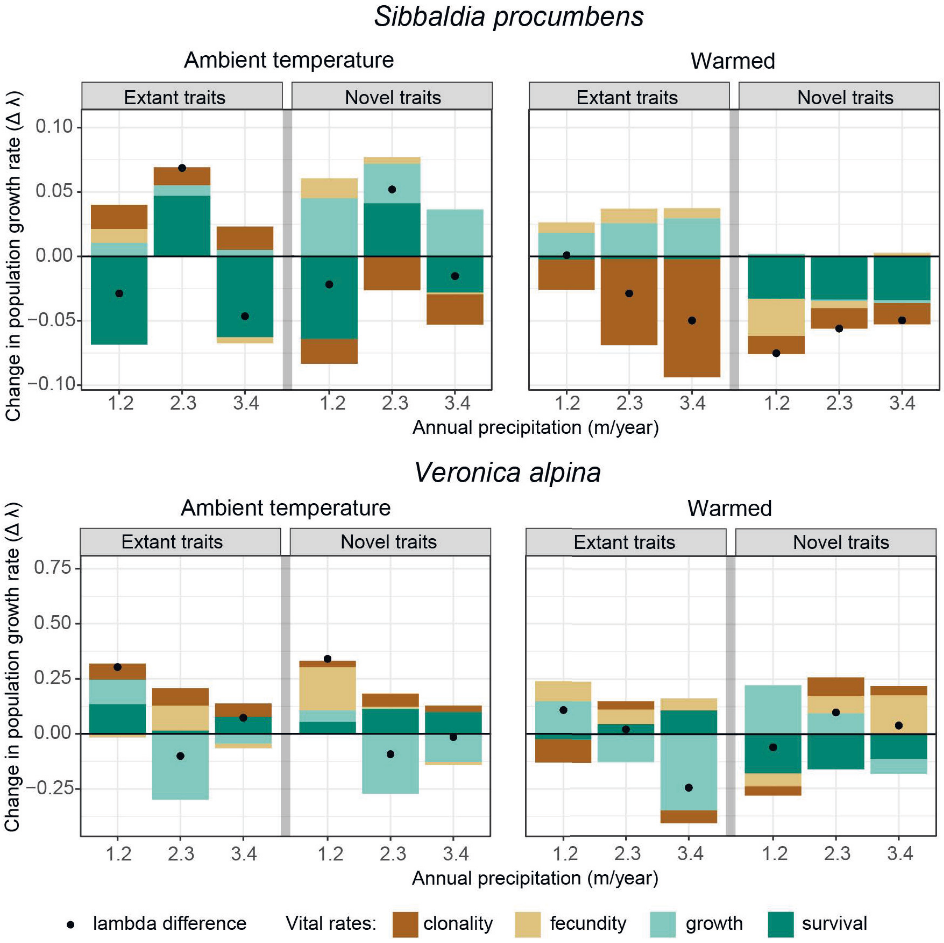


Figure 12: Contribution of vital rates (clonality, fecundity, growth and survival) to changes in population growth rates (λ) between experimental treatments of transplant treatments with extant and novel traits, in the ambien and warmed climate. Contributions of vital rates are based on one-way life table response experiments (LTRE's). Each treatment comparison is done across three precipitation levels; first column: 1200 mm/year, second: 2300 mm/year and third: 3400 mm/year. Note the difference in scale between the two species, *Sibbaldia procumbens* in the top row and *Veronica alpina* on the bottom. Figure adapted from **Paper III**.

In addition to changes in interactions within the current plant community, climate change might also introduce new species into these communities. As sub-alpine species shift their ranges upslope and start to interact with the alpine plants, they create novel interactions between species who have never co-occurred (Alexander *et al.*, 2015). I expected the sub-alpine species to increase the competitiveness in the alpine plant community, giving a negative effect on the population growth rate of our study species (cf. Alexander *et al.* (2015) and Nomoto and Alexander (2021)). Our results mostly confirmed this, but there were some variations between species, vital rates, and across the precipitation gradient (**Paper III**; Figure 12). For *V. alpina* the most negative effects of the novel interactions were usually in the intermediate and wettest end of the precipitation gradient (Figure 12). The sub-alpine species generally had a negative effect on λ for *S. procumbens,* especially when the sub-alpine species were combined with a warmer climate (Figure 12). However, these interactions might also change in the future. It has been documented that range-expanding sub-alpine species, i.e. the thermophilous species, will benefit more from warming than the alpine species (Stuble *et al.*, 2021). Additionally, we found that these sub-alpine species are already capable of flowering and establishing from seed in the current climate in the alpine environment if they are moved there (**Paper IV**; Dahle *et al.*, 2022), and we know that the rate at which species move up in elevation is accelerating (Steinbauer *et al.*, 2018). Hence, it is likely that more sub-alpine species will colonize the mountains, and that the negative effect of novel competitors on alpine species will increase as climate is warming.

As far as I know, **Paper III** is the first study that investigated if range-expanding sub-alpine species with different traits have different effects on alpine plants. By categorizing sub-alpine species into species with similar traits to the alpine plant community (extant traits), and species with more competitive strategies than the alpine plant community (novel traits), we might be able to generalize our results beyond the species used in the study. We found that the species with novel traits did have a larger negative effect on λ, especially in warmer climates for *S. procumbens* (Figure 12). Although we did not see the same clear pattern for λ for *V. alpina*, there is a switch to a negative effect on survival when we combined sub-alpine novel traits species and warming (Figure 12). If the chance of survival decreases, it is hard for the population to compensate by increasing in growth or clonality, although an increase in fecundity could keep the population going for a while (Villellas *et al.*, 2015). Nomoto and Alexander (2021) did indeed find that when survival was excessively reduced the other vital rates could not compensate, which leads to a population decline. Hence, both species show signs of being extra sensitive to sub-alpine species with novel, i.e., more competitive traits. Our findings coincide with theory from invasive species, which proposes that species with more competitive strategies, such as taller plants with larger leaves of high photosynthetic capacity, making them better equipped to compete for light, have a higher success of invading and outcompeting native plant species (Van Kleunen *et al.*, 2010; Liao *et al.*, 2021). Our findings combined with the invasive species literature suggests that the species that might create the most negative effect on alpine species are the sub-alpine species with more competitive traits.

SNOWBED SPECIALIST VS. ALPINE GENERALIST

RQ4-1. Are there context dependencies in the responses to climate change between species with different niches and between places with different climates?

In this thesis, two of the papers focus specifically on *S. procumbens* and *V. alpina* (**Paper II** and **Paper III**), giving me the opportunity to contrast different habitat strategies. Although they were both chosen because they are typical alpine species, and they both occur in the grassland plots in the INCLINE experiment, their optimum habitats in the alpine are different. *S. procumbens* mostly grows in snowbeds, but it can also be found in grasslands where the competition is low and there is enough moisture (Lid and Lid, 2007; Mossberg and Stenberg, 2012; Sperduto *et al.*, 2018). In contrast, *V. alpina* is more of a generalist species growing across habitats like grasslands, heath, and some dry snowbeds (Lid and Lid, 2007; Mossberg and Stenberg, 2012). Although I fully acknowledge the limitation of comparing just two species, I do find differences between them in a way we would expect based of their niches and ecology that I find worthy of discussing in this thesis.

Alpine generalist species (such as *V. alpina*) are adapted to handle a variety of conditions, while specialists such as snowbed species (*S. procumbens*) are adapted to the conditions of their specific habitat. The snowbed habitat possesses extra challenges like shorter growing seasons, but are sheltered from other stressors due to the cover of snow in winter (avoiding freezing events) and high moisture due to the snowmelt (avoiding drought events) (Körner, 2003). A lack of selection pressure towards drought tolerant traits in snowbed species could explain why we did not find strategies for dealing with drought during germination or the seedling stage for *S. procumbens* (**Paper II**). On the other hand, *V. alpina* did possess strategies to deal with drought events, and even showed evidence of local adaptation to drought in drier environments (**Paper II**). These results are in line with previous literature that has shown that snowbed species are more sensitive to drought than generalist species as in response to drought they produce fewer seeds (Kudo and Hirao, 2006; Tonin *et al.*, 2019) and adult individuals have higher mortality (Oberbauer and Billings, 1981). When the generalist species are better at dealing with drought as snowbeds are becoming drier due to changes in precipitation patterns, snowbed species are being outcompeted by the generalist grassland and shrubland species (Matteodo *et al.*, 2016).

Additionally, I find that *S. procumbens* is more sensitive to competition than *V. alpina* (**Paper III**). *S. procumbens* seems to mostly have neutral interactions with its neighbors in the ambient alpine climate (Figure 11). The species is sensitive to competition (Sperduto *et al.*, 2018), and **paper III** clearly shows that warming, both in the current alpine plant community and in combination with range-expanding sub-alpine species, generates adverse competitive condition for *S. procumbens* (Figure 11; Figure 12). Other specialist species that are restricted to certain habitats in the alpine have also been identified as inferior competitors compared to alpine generalists (Kudo and Hirao, 2006; Björk and Molau, 2007; Matteodo *et al.*, 2016; Steinbauer *et al.*, 2020). The alpine generalist, *V. alpina*, on the other hand did not suffer under warmer conditions, and it seemed able to compete with the current alpine community, and the new sub-alpine species to a certain degree (**Paper III**). Based on what I find in this thesis and the literature we might expect snowbed species to be more sensitive than alpine generalists to climate change, at least when it comes to increased warming, more drought events, and increased intensity of competitive interactions from co-occurring species as well as range-expanding species.

CLIMATE CHANGE IN HIGH PRECIPITATION SYSTEMS

RQ4-2. Are there context dependencies in the responses to climate change between species with different niches and between places with different climates?

In the study system of this thesis, I cover a large range of mean annual precipitation from 800-4400 mm/year (in **Paper II**, **Paper III**, and **Paper IV**, we mostly use the alpine sites, which span a precipitation range of 1200-3400 mm/year). These averages are the mean annual precipitation based of the 2009-2019 period, which has increased since the 1960-1990 “normal period” (Figure 1). Additionally, I find that the largest increase has happened in the wettest end of the precipitation gradient, which also has the highest variation in precipitation between years (Figure 1; Figure 2). High precipitation can lead to several different abiotic conditions that are important for plants, beyond the mere increase in precipitation. Generally, soil moisture increases with precipitation, but there is not a direct link between the amount of precipitation and soil moisture, as soil moisture also depends on temperature, soil texture, soil depth, vegetation etc. (Daly and Porporato, 2005). Our precipitation gradient results in a soil moisture gradient but seem to taper off at the highest precipitation levels likely due to water saturation of soils (**Paper II**). In alpine areas a lot of the precipitation comes as snow, impacting important ecological processes linked to phenology and growth by altering growing season length, snow depth, and snow melt-out. High precipitation can also lead to less nutrients in the soil when water drains the soil for nutrient through run-off and percolation, and slower decomposition rates, which again impacts plant growth and survival (Althuizen *et al.*, 2018; Lambers and Oliveira, 2019; Martinez-Almoyna *et al.*, 2020). Further, in areas with very high precipitation light availability can also be low due to the increase in cloud cover which could influence alpine plant recruitment and growth (Pagès *et al.*, 2003). Vandvik *et al.* (2020a) have suggested a biotic rescaling of how we think of climate gradients. Specifically in our sites graminoid and bryophyte cover increases towards wetter habitats, while plant community biomass is highest in the intermediate precipitation levels of the boreal and sub-alpine sites, and highest in the driest precipitation level in the alpine sites (Klanderud *et al.*, 2015). The low biomass in the wettest alpine sites is most likely due to the shorter growing season that comes with additional snow. Bryophytes have a strong insulating effects on both extreme warm and cold temperatures (Jaroszynska, 2019), and as the bryophyte layer becomes thicker in the wettest habitats (Jaroszynska, 2019; Vandvik *et al.*, 2020a), we can expect these climate extremes to be dampened for the individuals that are able to stay in the thick bryophyte covers. Bryophyte layers also limit colonization by new species and could thus slow down the range-expansion of species from lower elevations (Vandvik *et al.*, 2020a). Along this large precipitation gradient with all that entails, I find that i) the functional composition of the plant communities are different across the precipitation gradient (**Paper I**), ii) how community functional composition changes with time depends on the current precipitation average (**Paper I**), iii) the current and future interactions within plant communities vary with precipitation (**Paper III**), and iv) the adaptability of alpine plants to future conditions might vary along the precipitation gradient (**Paper II**; **Paper III**). Before I go deeper into the potential changes with climate change, I will start by highlighting the current differences across the precipitation gradient in terms of functional traits and nature of interactions.

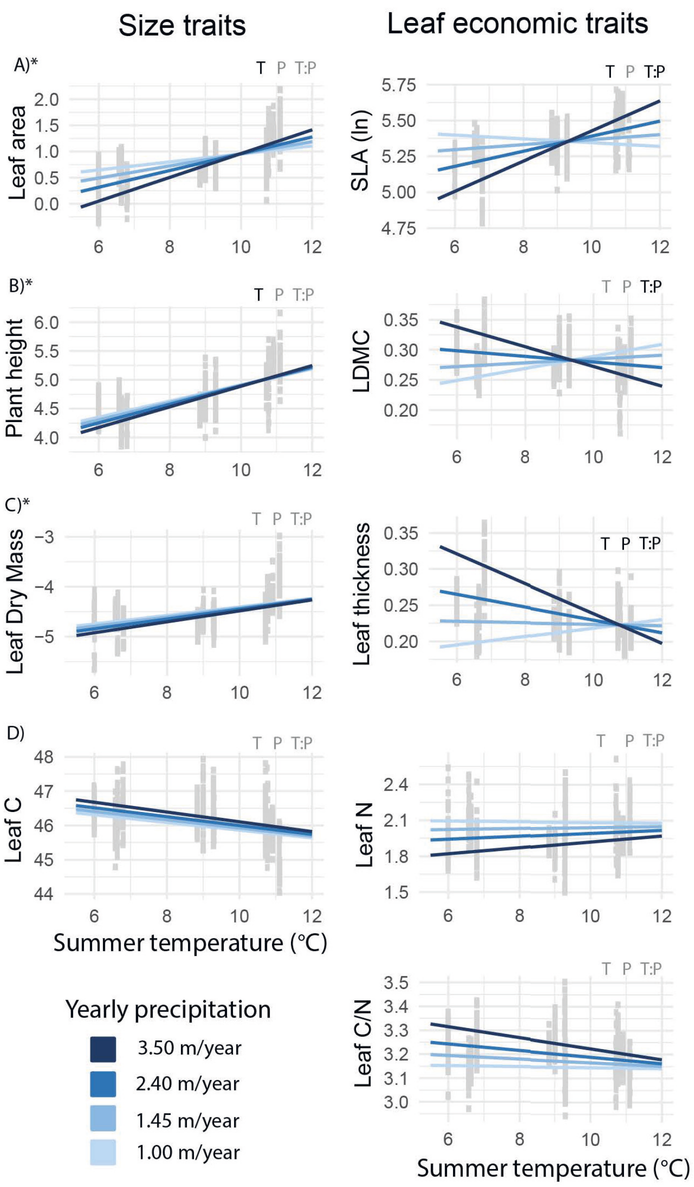


Figure 13: Community weighted means of functional traits along summer temperature and annual precipitation spatial gradients from 2009 - 2019. Size traits are in the left column, and the leaf economic traits are in the right column. Grey points are the observed community weighted means. The lines are predicted values from a mixed effect model, predicted from four different levels of mean annual precipitation corresponding to the four precipitation levels of the climate grid. For each trait, if the temperature (T), precipitation (P) or the interaction (T:P) is significant the letters are black (p-value < 0.05), and grey if they are not significant (p-value > 0.05). Units are cm^2/g for Specific Leaf Area (SLA), % for Leaf N and Leaf C, %/% for Leaf C/N, g/g for Leaf Dry Matter Content (LDMC), mm for Leaf Thickness, cm^2 for Leaf Area, mm for Plant Height, and gram for Leaf Dry Mass. * indicates that the trait was log transformed (ln). Figure from **paper I.**

In this thesis I find less competitive, or neutral interactions in the wetter end of the precipitation gradient (**Paper III**). I also find that the alpine plant communities have more conservative leaf economic traits than communities of sub-alpine and boreal sites (Figure 13; **Paper I**), which indicates that the conditions in the high precipitation sites are stressful (Grime, 1974; Pierce *et al.*, 2013). Additionally, LDMC increases in wetter years in the drier climates (Figure 8), indicating that also in the drier climates an increase in precipitation is stressful (**Paper I**). This is in contrast to many other studies that identifies precipitation as a resource, and find less conservative traits (Forrestel *et al.*, 2017) and more intense competitive interactions (Levine *et al.*, 2010; Moustakas *et al.*, 2013) in higher precipitation sites. However, few studies have investigated as wet a precipitation gradient as ours. Although some high precipitation studies have found plateauing at the wettest end of their gradients in the relationship between precipitation and productivity (biomass and resource acquisitive leaves) (Knapp *et al.*, 2017). We find that in our extremely wet sites plant communities go beyond a plateau and show evidence of a shift back towards stressful conditions as seen in a shift to resource conservative traits) (**Paper I**; Figure 13). These stressful conditions also lead to less competitive interactions within plant communities (**Paper III**; 11). However, the functional trait composition or less competitive interactions does not tell us what causes this stress. Over time we see a shift towards more resource acquisitive traits in the cold and wet alpine sites in the multivariate trait space, indicate a need for growth and high photosynthetic capacity (**Paper I**). The increased snow cover and shorter growing season length this entails, in addition to thicker cloud covers which all limits light, could explain this shift (Choler, 2005; Happonen *et al.*, 2019). Additionally, excess precipitation could lead to nutrient limitation as water drains the soils for nutrients through percolation and run-off – and nutrient-poor soils have been linked to more conservative traits (Eskelinen and Harrison, 2015). The limiting nutrients in the soil could also be the reason that Skarpaas *et al.* (2016) find higher root biomass in wetter conditions, both in the alpine, sub-alpine and boreal sites of our study sites. As there are generally very few studies on such high precipitation sites as ours, this thesis uniquely identifies that high levels of precipitation can be stressful for plant communities, as evidenced by the conservative strategies (**Paper I**) and less competitive nature of interactions (**Paper III**).

With conservative traits (**Paper I**; Figure 7; Figure 13), and less competitive interactions (**Paper III**; Figure 11), our findings suggest that alpine plant communities of high-precipitation regions might be more sensitive to both the direct and indirect effects of climate change. For the direct effects we find that warming has a negative effect, or a less positive effect, on populations from wetter habitats (**Paper III**; Figure 9). Additionally, we find evidence that the populations of *V. alpina* from wetter habitats are more sensitive to drought than populations from drier habitats (**Paper II**; Figure 10). Generally, previous studies have found a lower germination success in the wettest site in field experiments in our sites (Tingstad *et al.*, 2015; Dahle *et al.*, 2022). However, precipitation did not alter the community openness for seedling recruitment (Meineri *et al.*, 2019), indicating that the decreased germination success in Tingstad *et al.* (2015) and Dahle *et al.* (2022) is linked to abiotic conditions, or to biotic characteristics not studied in Meineri *et al.* (2019). In alpine systems such as ours, precipitation occurring as snow may play an important role in germination, where snow can be positive as an insulating cover, but negative if the growing season becomes too short (Briceño *et al.*, 2015). With warming and an increase in drought events (Hanssen-Bauer *et al.*, 2017) my results suggest that alpine plants from wetter habitats to have lower germination success (**Paper II**), and in combination with negative effects on other vital rates I expect this to lead to decreasing λ (**Paper III**).

Over the 2009-2019 period warming and wetting has led to a change in functional composition of the plant communities, but this change depends on the current climatic conditions (**Paper I**). This is illustrated by the change in community-weighted Leaf Dry Matter Content (LDMC) and how this change depends on the experienced long-term precipitation of the communities (Figure 8). Specifically, there is an increase in LDMC in wetter years, but only in the driest climates (Figure 8). A high LDMC indicates conservative strategies (Vile *et al.*, 2005), thus, an increase in LDMC indicates that higher precipitation years might be more stressful for plants in the drier end of the precipitation gradient, possibly as they are not adapted to high precipitation. Whereas the consistently high LDMC of the wettest alpine sites that does not change significantly in time, indicates a constant high stressor selecting for conservative species with high LDMC in wet and cold habitats (Figure 8). These results indicate that as the drier alpine sites are getting wetter, these plant communities are experiencing more stress.

As the plants in these wet alpine habitats have conservative strategies (**Paper I**) and the weak to non-existing competitive interactions (**Paper III**), the expected indirect effects of climate change, i.e., the increased intensity of competitive interactions, may have stronger negative effects for these plants (**Paper III**). We found that changes in current species interactions and interactions from range-expanding sub-alpine species as climate is warming for most focal species-treatment combinations the most negative effect was in the wettest population (**Paper III**; Figure 11; Figure 12). However, this negative effect from the range-expanding species could be hindered if the species were less able to establish in the wetter sites compared to the drier sites, as Vandvik *et al.* (2020a) found that bryophytes limited colonization by new species into local communities. But, when range-expanders were able to colonize, they also found that the cover of those colonists and bryophytes were the primary drivers of local extinctions of alpine plants. In other words, thicker bryophyte cover, combined with novel interactions from range-expanding species and warming, will likely lead to population decline for many alpine species (**Paper III;** Vandvik *et al.* (2020a)).

All in all, I find that the high precipitation alpine sites have the most stressful abiotic conditions, resulting in conservative functional composition (**Paper I**) and non-competitive interactions (**Paper III**), which makes these alpine plants more sensitive to increases in intensity of competitive plant-plant interactions in a warming climate (**Paper III**). Additionally, they are more sensitive to drought events in early life stages (**Paper II**) and respond with less positive changes in λ to warming (**Paper III**). Over time the increase in precipitation leads to higher LDMC in the drier alpine sites, indicating a shift towards more conservative strategies as the climate is getting wetter (**Paper I**) – a sign that these systems might be experiencing more of the harsh conditions linked to high precipitation alpine systems.

METHODOLOGICAL CONSIDERATIONS

By combining observations over time, space-for-time, field experiments and lab experiments, I am able to investigate the effects of climate change on alpine plants in many different ways, disentangling different mechanisms behind the observed changes in the field and laboratory conditions. Through the lab experiment I was able to identify the water potential limit for germination in the two alpine focal species were able to germinate (**Paper II**) – which we would not be able to obtain from field experiments. Water potentials obtained in the lab are poor representation of drought conditions in the field, but the ecophysiological responses uncovered in a lab experiment are still valuable to increase our knowledge about these systems and species. For example, by exposing the seeds to their minimum water potential we were able to identify that the seeds from the driest population of *V. alpina* germinated better compared to the other populations (Figure 10) – indicating that even species from not traditionally drought exposed habitats indicate evidence of local adaptation to drought.

To test for warming effects, I used OTCs as opposed to e.g., transplanting turfs to warmer habitats, which allowed me to avoid invasions of warmer-climate species from vegetation surrounding the transplants (Yang *et al.*, 2018), so that we could control the “invasion” that we wanted to test systematically with species of different traits (**Paper IV**). Turf transplants and

OTCs seem to have the same overall effect on plant phenology (Stuble *et al.*, 2021), indicating that the net warming effect of the two approaches might be similar. However, we know that OTCs have side effects, like hindering wind and therefore wind pollination (personal observation), but since none of the two species in the demography study (**Paper III**, **Paper IV**) are wind pollinated we think this has little impact on our results. A common criticism of OTCs is that along with the warming also follows a decrease in soil moisture (Dabros *et al.*, 2010). However, in this study there was no significant change in soil moisture with the OTCs (Appendix 3 in **paper III**).

To test the indirect effects of climate change I manipulated biotic interactions by completely removing all above-ground surrounding vegetation, and by transplanting in novel competitors. Removal experiments are an established approach for assessing the effect of biotic interactions (Díaz *et al.*, 2003). When we remove above ground biomass, we remove competition for resources and create openings in the vegetation giving more light to the remaining individuals. Belowground the roots might die off and create a fertilizing effect, or they might mobilize to grow and get resources to be able to grow back in the next growing season changing below ground interactions (Symstad and Tilman, 2001). Removing almost all above ground biomass will also cause changes in microclimate (Jaroszynska, 2019).

By transplanting adult individuals of the range-expanding sub-alpine species we are able to test the novel interactions as if they had already established and where a natural part of the plant community. Although we do not test the ability of these species to disperse and establish in the alpine (but see Dahle *et al.* (2022) for a study of establishment of these species), this was not the focus of our research questions. Through our experimental approach we investigate the early processes of range-expansion where with climate change a few species would move up and colonize the alpine habitat (Alexander *et al.*, 2016).

CONCLUSION: A NEW WORLD FOR ALPINE PLANTS

RQ5. What are the overall impacts of climate change on alpine plant communities in Norway?

As Norway becomes warmer and wetter, alpine plant communities will change, and my work illustrates how drivers pull vegetation changes in different directions. Due to the different methods, and different response variables I was able to understand the mechanisms behind these changes, which makes it possible to predict beyond the scope of these studies. One of the direct effects – warming – has generally positive effects on alpine plant growth, survival, and population growth rates (**Paper I, Paper III**). Drought, on the other hand, had negative effects on alpine plants' germination (**Paper II**). Additionally, the indirect effects also come into play. In a warmer climate, interactions with alpine plant communities become increasingly competitive (**Paper III**), which will have a negative impact on the population growth rate of many alpine species that have conservative strategies (**Paper I**) and therefore are less adapted to competition for resources (**Paper III**; Anthelme *et al.*, 2014). As more competitive species from lower elevations invade the alpine plant communities (Steinbauer *et al.*, 2018), they will increase the competitive nature of species interactions within the vegetation even more and thus further impact alpine species negatively (**Paper III**; Alexander *et al.*, 2015; Nomoto and Alexander, 2021). In this thesis, I find evidence that the indirect effects of climate change (through altered species interactions) could counteract the positive effects of climate warming (**Paper III**). Range-expanding species with more competitive traits seem to have a stronger negative effect on population growth rates, and survival (**Paper III**), and might be the strongest indirect effect at counteracting the positive direct effect. I also find evidence that species from wetter climates, and specialized alpine species, might be more sensitive to increased competitive effects, both within the current plant community and from novel competitors (**Paper III**), and drought events (**Paper II**).

Based on the results from this thesis I expect alpine plant communities to suffer from the combined direct and indirect effects of climate change. Eventually, I expect that the current alpine plant communities in southwestern Norway will change to grow taller due to warming (**Paper I**), and that the increase in precipitation will lead to more conservative leaf traits in the drier sites, and more resource acquisitive traits in the wetter sites (**Paper I**). Further, my results indicate that there will be a shift towards more competitive interactions both within the current plant community, and due to range-expanding species (**Paper III**). As more of the competitive range-expanding species establish in the alpine communities, the more negatively the alpine species will be affected by novel interactions (**Paper III**). Additionally, my results show that the specialized species will be the biggest losers (**Paper II**, **Paper III**), and the wettest habitats seem to be where the current plant community is most affected by the increased competition (**Paper III**). Based on the results from this thesis, and the current literature I suggest that more effort be put into investigating climate change impacts on specialized alpine species and high precipitation ecosystems to gain more knowledge on what seems to be the most sensitive species and system in Norwegian alpine environments.

MODERN ECOLOGY – INCLUSIVE AND OPEN

Finally, in the last section of this thesis I want to briefly reflect on my experience with doing science as part of a large and collaborative research group (Between the Fjords[2]). As a master student I was involved in the FunCaB project (Vandvik *et al.*, 2022), first as a field assistant, then later researching on my own during my master thesis. These data were further used by two PhD students as parts of their thesis work. Hence, my experience as a student was that I got to collect a dataset that would be further used in papers, and I was a member of a "proper" research team.

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[2] https://betweenthefjords.w.uib.no/home/

Later I started my PhD in the INCLINE project, and I got to coordinate the main field experiment in this project from the start. In my PhD, I also use data that other people have collected, as well as sharing my data with other researchers. This collaborative effort is also reflected in the pronouns in this thesis, where when I write about the thesis as a whole I use “I” or “me” (even though the different projects, experiments, and data collection was planned and conducted in collaboration by many people, the thesis as a whole is my work), whereas for the papers in this thesis I used the pronoun “we” to reflect that each paper is a collaborative effort between different groups of people.

I have co-supervised six master students, four bachelor students and fourteen interns. These students have contributed datasets and written theses and reports on the following research questions/topics relevant to the different research projects in our group: Floral traits and how they change with temperature and precipitation (Skjelstad, 2020). Resource allocation above and belowground along a precipitation gradient (Søgaard, 2020). How resilient is *Calluna vulgaris* to drought during germination and its seedling stage? (Birkeli *et al.*, 2021) Can sub-alpine species emerge and establish in the alpine? (Dahle *et al.*, 2022) Do reproduction in alpine communities change with warming and/or novel competitors? (Berthelsen, 2022). All relevant topics for our research, giving us the opportunity to dig further down into our hypothesis and research questions.

In our research group we collaborate on research, that means we help with data collection, we have collective writing groups and journal clubs, and we help each other with different projects. All “levels” are included, from bachelor students to master students, to PhD candidates, researchers, technicians, and PIs. We strive to be an inclusive research group on other areas than “research level” as well because diversity of backgrounds and worldview points in a group is good for creativity and productivity (Hunt *et al.*, 2015).

Sharing data and science also outside of the group is also important. Open Science is a global movement that aims to promote transparency, accessibility, integrity, and repeatability in scientific research (Fecher and Friesike Sascha, 2013; Hampton *et al.*, 2015). In this thesis I have used open science practices extensively to ensure reproducibility in my research. Specifically, I used the registered report (Chambers, 2019) for **paper II,** whereas **paper IV** is a draft of a manuscript for a data descriptor where we will share data and document the data management process thoroughly for others to use later (Mongeon *et al.*, 2017). The registered report is a relatively new publishing method in ecology, where the aim is to avoid publishing biases, and analysis problems such as p-hacking (Chambers, 2019). Authors submit their proposed research project for peer review prior to conducting the experiment. Peers will review the report on the basis of whether the research questions are relevant and interesting and if the methods are sufficient to answer said questions. The reviewers might come with input that will change the methods used, which can improve studies before it is too late to change the data collection process. After one round of revisions, we got **paper II** accepted as a registered report, and it has been openly available on the open science framework (OSF) since then. In addition to **paper II**, we used the registered report method with two of the master students I co-supervised during my PhD as well (Birkeli *et al.*, 2021; Dahle *et al.*, 2022). The data paper (**Paper IV**) documents the data collected in a thorough way, with open access to the raw data, code for cleaning it, and the finished cleaned data sets. The goal with data papers is to make scientific data more easily accessible and strive for better documentation of the data collection process (Mongeon *et al.*, 2017). In addition to **paper IV** in my thesis, data from **paper I** will be a part of a data paper from the Vestland Climate Grid (Vandvik et al. in prep), and I have contributed data to other data descriptors (Vandvik *et al.*, 2020b; Vandvik *et al.*, 2022). By using these methods, I hope to contribute my small part in making science more open and transparent.

This is modern ecology: collaborative, inclusive, open, and reproducible

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CHAPTER 1

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Graphic design: Communication Division, UIB / Print: Skipnes Kommunikasjon AS

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ISBN: 9788230859858 (print)
9788230848494 (PDF)