Predicting and assessing climate-change impacts on the population dynamics of alpine and lowland forbs

Joachim Paul Töpper

SOGN OG FJORDANE
UNIVERSITY COLLEGE

Dissertation for the degree philosophiae doctor (PhD)
at the University of Bergen

2015

Dissertation date: 29.05.2015

Predicting and assessing climate-change impacts on the population dynamics of alpine and lowland forbs

Dissertation for the degree of Philosophiae Doctor (PhD)

Joachim Paul Töpper

Department of Biology
Faculty of Mathematics and Natural Sciences
University of Bergen, Norway
2015

Advisors:
Prof. Vigdis Vandvik, University of Bergen
Prof. Knut Rydgren, Sogn og Fjordane University College, Sogndal
Senior Researcher Olav Skarpaas, Norwegian Institute for Nature Research, Oslo

Acknowledgements

As far as I can think back into my childhood, I have always wanted to be a ‘nature researcher’. I feel grateful, honoured and privileged to have had the opportunity to actually become one.

First of all, I would like to thank my PhD-advisors for their support and guidance through the last years. Vigdis, ever since I first walked into your office, you have played a significant role for my life here in Norway. You hired me for small jobs, introduced me to the heathlands, made me a part of SeedClim, supported me on the way to getting this PhD position, and finally became my principal advisor. As an advisor and co-author you are simply priceless. But more than that you are also a beautiful person, showing respect for family and private life, accepting a ‘no’ from your PhD-students, and knitting Hugin & Munin mittens to my children. Thanks for being the scientist, advisor and person you are. Knut, thanks for always being there for me, with advice on science, writing and do-ability of plans, but also with a room when I needed a place to sleep. I really appreciate the Sogndal-Bergen flexibility, that I was granted, which made life so much easier for me and my family. Thank you also for having me teach the stats course at the college, you have no idea how much you made me learn by that! Olav, thanks a lot for introducing me to IPMs, and for reading and commenting manuscripts at both high-speed and high-quality. Your impressive analytical skills and critical thinking have contributed a lot to my personal scientific progression during the last years.

The SeedClim team (plus seasonal extensions) has been sort of a surrogate family for me during some long field seasons, each and every one of which I hold as dear memories. Kari, Siri, Pascale, Christine, Marianne, Tessa, Astrid, Serge and John, thanks for the good times in the field, in both sunshine and rain, bathing temperatures and snow. Eric, I could not

have had a better PhD-colleague than you. Those summers with the two of us roaming the SeedClim grid, doing vegetation analysis with flora's in languages we hardly read, and discussing our projects, food, goats, the world, and more…well, they were kind of epic. Thanks for these times, but also for being a critical co-author and friend. I thank my colleagues, both in Sogndal and Bergen, who fill the days at work with life. Marte, thank you for having been a fantastic partner in the stats course!

All the data that this PhD is based on would not have been possible to collect without the many field-assistants who I had the honour to work with during the last years: Annick, Antonia, Alistair, Bernarda, Ellen, Fanny, Izzie, Keno, Monika, Nina, Simon, thanks a lot!

My family has always been a support for me during this PhD. A special thanks goes to Heike and Joachim, my parents in law, who flew in from Germany whenever we needed their help in juggling two kids, two workings places and two PhDs. Another special thanks goes to my mother: Mum, you have always supported me, no matter which decisions I made and where they led me. You have taught me, that I can accomplish anything, if I really want it. This has helped med a lot during this PhD by giving me confidence as well as the will to make an effort.

A big thanks goes to Ilias and Jannis, my sons, who make me let go and forget about work every afternoon and weekend, make my life complete, and allow me to see the world a little bit with these wondering eyes of a child again.

Birte, thanks a lot for your support and not least for taking me with you to Norway. You were and are the reason for this journey, that has brought us a really long way…I am looking forward to our next destinations!

List of papers

This thesis is based on the following four papers which will be referred to by their roman numerals hereafter.

Paper I: Töpper, J.P., Meineri, E., Olsen, S.L., Rydgren, K., Vandvik, V., Skarpaas, O.

Demography in space and time: temperature and precipitation impacts on alpine and lowland forb populations. *Manuscript*

Paper II: Töpper, J. P., Meineri, E., Olsen, S.L., Rydgren, K., Vandvik, V., Skarpaas, O.

Digging climate change? The fate of alpine and lowland forbs transplanted to future temperature and precipitation. *Manuscript*

Paper III: Olsen, S.L., Töpper, J. P., Skarpaas, O, Vandvik, V., Klanderud, K.

From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in semi-natural grasslands.
re-submitted to *Global Change Biology*

Paper IV: Meineri, E., Spindelböck*, J., Vandvik, V. 2013. Seedling emergence responds to both seed source and recruitment site climates: a climate hange experiment combining transplant and gradient approaches. *Plant Ecology*, **214**: 607-619.

Paper IV is re-printed with the permission of the publisher

* Töpper J. P. held the family name ”Spindelböck” until autumn 2013

Authorship contributions

Paper I: Töpper J. P., Meineri E., Olsen S. L., Rydgren K., Vandvik V., Skarpaas O.

Demography in space and time: temperature and precipitation impacts on alpine and lowland forb populations. *Manuscript*

Töpper J. P: Study design, data collection, data processing, analytical design, statistical analyses, writing

Meineri E: Study design, data collection, editing

Olsen S. L: Data collection, inputs on analytical design, editing

Rydgren K: Inputs on data collection, inputs on analytical design, editing

Vandvik V: Project design, study design, editing

Skarpaas O: Study design, data collection, inputs on analytical design, editing

Paper II: Töpper J. P., Meineri E., Olsen S. L., Rydgren K., Vandvik V., Skarpaas O.

Digging climate change? The fate of alpine and lowland forbs transplanted to future temperature and precipitation. *Manuscript*

Töpper J. P: Experimental design, data collection, data processing, analytical design, statistical analyses, writing

Meineri E: Experimental design, data collection, editing

Olsen S. L: Data collection, inputs on analytical design, editing

Rydgren K: Inputs on data collection, inputs on analytical design, editing

Vandvik V: Project design, experimental design, data collection, editing

Skarpaas O: Experimental design, data collection, inputs on analytical design, editing

Paper III: Olsen S. L., Töpper J. P., Skarpaas O., Vandvik V., Klanderud K.

From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in semi-natural grasslands. Re-submitted to *Global Change Biology*

Olsen S. L: Experimental design, data collection, data processing, analytical design, statistical analyses, writing

Töpper J. P: Data collection, data processing, analytical design, statistical analyses, writing

Skarpaas O: Data collection, inputs on analytical design, editing

Vandvik V: Project design, data collection, editing

Klanderud K: Experimental design, data collection, editing

Paper IV: Meineri, E., Spindelböck*, J., Vandvik, V. 2013.
Seedling emergence responds to both seed source and recruitment site climates: a climate change experiment combining transplant and gradient approaches. *Plant Ecology*, **214**: 607-619.
Meineri, E: Experimental design, data collection, data processing, analytical design, statistical analyses, writing

Spindelböck, J. P: Experimental design, data collection, inputs on analytical design, editing

Vandvik, V: Project design, experimental design, inputs on analytical design, editing

* Töpper J. P. held the family name ”Spindelböck” until autumn 2013

Contents

Abstract

Background and aims:

Global climate change is already affecting plant species worldwide. The global rise in temperatures and regional changes in precipitation are predicted to continue throughout the century. Therefore, studying how climate affects species performance is crucial for understanding the implications that future changes may hold for plants. Recently, there have been several calls for studies addressing the complexities of climate change impacts, by for instance combining and integrating spatial gradient approaches, time-series data, and experiments. Another important challenge is to incorporate precipitation change and its interaction with temperature increase, since the nature of these interactions (positive, negative, additive, non-additive) determines the net effect of the combined change. Moreover, climate change affects plants not only directly, through physiological constraints, but also indirectly, through changes in biotic interactions. Disentangling these biotic interactions is crucial for understanding and predicting climate change impacts. Finally, a need for investigating plant population dynamics is needed to gain a better understanding of how and why plants respond to climatic changes on the population, species and community level.

In this thesis I examine the combined effects of changes in temperature and precipitation on the population dynamics of sub-dominant forb species. I investigate climate control on the study species both along climatic gradients in space and time, and in turf- and seed-transplant experiments along climatic gradients. To assess the effect of biotic interactions along spatial climatic gradients, I use a removal experiment.

Study area and species:

The studies presented in this thesis were performed in the fjord-and-mountain landscape of Western Norway. The steep climatic gradients in this area enable the establishment of a 'climatic grid' comprising of 12 sites in three levels of temperature and four levels of

precipitation. The study species were two alpine / lowland species pairs, *Veronica alpina / officinalis* and *Viola biflora / palustris*, which were relatively common and representative for the forb communities at the study sites. The study area includes the rear altitudinal range edge of the two alpine species and the leading altitudinal range edge of the two lowland species.

Main findings:

All species were under strong climate control. Warmer temperatures had mainly negative effects on both population growth rates (λ) and seedling establishment, while precipitation increase had more varying effects with some positive impacts on the *Viola* species and mainly negative effects on the *Veronica* species. Seedling establishment increased with increasing precipitation. The effects of temperature and precipitation change were generally not additive in the combined treatment, they either cancelled each other out, or stayed at the level of one of the single-factor effects. The biotic interaction experiment revealed a shift from facilitation to competition as temperature increases, but no overall pattern for precipitation. This suggests that the negative impacts of a warmer and a warmer+wetter climate found in the other studies may be related to changes in biotic interactions, whereas the responses to precipitation may reflect more direct effects. The results were independent of the species' alpine or lowland habitat affinities, suggesting that also lowland species will and already do face challenges under climate change. In fact, the studies in this thesis, when taken together, indicate that *Veronica officinalis* already may be on the move upwards, potentially being pushed out of its historic range by increased competition under climatic warming. In conclusion, this thesis highlights the benefits of including higher complexity in ecological climate change research through 'integrated studies' that allow for (1) detecting climate control on species where single approaches fail, and (2) revealing underlying mechanisms and time scales for the found effects

Sammendrag

Bakgrunn og mål:
Jordens klima er i endring, og dette påvirker allerede plantearter på hele kloden. Den globale økningen i temperatur og regionale endringer i nedbør vil fortsette gjennom dette århundret, Derfor er det viktig å studere samspillet mellom klima og planter, slik at vi øker kunnskapen om hva et fremtidig klima vil bety for planteartene. Gjennom de siste årene har mer komplekse tilnærminger i klimaeffekt-forskningen blitt etterlyst. Dette kan være gjennom kombinasjon og integrering av ulike tilnærminger som romlige gradienter, tidsserier og eksperimenter. Klimaendring er ikke oppvarming alene, og det å inkorporere nedbørendringer og deres interaksjon med temperaturøkning er viktig, for å forstå samspillet mellom disse to. Videre påvirker klimaendringene plantene både direkte og gjennom endringer i samspillet mellom artene, og disse indirekte effektene kan ha stor betydning for utfallet. Endringer på plantesamfunnsnivå drives av effekter på ankeltarter, populasjoner og individer, og for å forstå hvorfor planter reagerer på klimaendringene er det derfor også viktig å undersøke de underliggende populasjonsprosessene.

I dette arbeidet undersøker jeg effektene av endringer i temperatur og nedbør, både hver for seg og kombinert, på plantepopulasjoner av fire sub-dominante urtearter. Dette ble gjort både langs gradienter i rom og tid, i to eksperimenter der frø, og til og med hele plantesamfunn ble transplantert til lokaliteter med ulikt klima og i et eksperiment der en dominant plantegruppe ble fjernet for å studere effekter av samspillet mellom arter. Alle disse eksperimentene ble gjentatt langs klimagradienter i temperatur og nedbør.

Studieregion og plantearter:
Studiene i detter arbeidet ble hovedsakelig gjennomført i fjord-og-fjell landskapet på Vestlandet. Her ble det etablert et klimatisk nettverk som består av 12 lokaliteter fordelt på tre temperaturnivåer og fire nedbørsnivåer. Artene som ble undersøkt var to par av alpine /

lavlandsarter, fjellveronika / legeveronika og fjellfiol / myrfiol, som er representative for plantesamfunnet i lokalitetene våre. Hele studieregionen omfatter den nedre utbredelsesgrensen til de to alpine artene og den øvre utbredelsesgrensen til lavlandsartene.

Hovedfunn:

Alle fire artene var klart begrenset av klima. Populasjonsvekstrater og frøetablering ble negativt påvirket av varmere temperaturer i alle artene, mens høyere nedbør hadde noen positive effekter på fiolene og negative på veronikaene. Frøetableringen økte under våtere klima. Den kombinerte effekten av endring i både temperatur og nedbør var ofte på nivå med enkelteffektene eller disse effektene nøytraliserte hverandre. Samspillseksperimentet viste en overgang fra fasilitering til konkurranse med økende temperatur, men ingen mønstre for nedbør. Dette indikerer at de negative effektene som ble funnet under et varmere og varmere+våtere klima kan være relatert til endringer i samspillet mellom artene, mens nedbøreffektene kan være mer direkte fysiologiske responser. Stort sett var mønstrene som ble funnet i de ulike studiene ikke relatert til artenes affinitet til fjell aller lavland. Dette antyder at også lavlandsarter vil påvirkes negativt av klimaendringene. For en art, legeveronika, peker resultatene fra studiene i dette arbeidet i retning av at arten allerede er på vei oppover, antakelig fordi den blir fortrengt fra sin historiske utbredelse på grunn av økt konkurranse. Avslutningsvis kan det sies at dette arbeidet tar et skritt i retning av å forstå kompleksiteten i økologiske responser på klimaendringer, for det gjør det mulig å forstå komplekse årsakssammenhenger og forhold mellom direkte og indirekte effekter på forskjellige stadier i plantenes livssyklus.

Synopsis

Introduction

The global climate is changing. Temperatures have been rising rapidly over the last decades and will continue to do so in the decades to come, precipitation patterns are changing, and anthropogenic forcing is needed to explain these current climatic trends (IPCC, 2014). Temperature and precipitation are key environmental parameters for plants, determining the fates of single individuals and populations, as well as regional vegetation patterns (Bresinsky *et al.*, 2008, Gaston, 2000). Climate can affect plants directly through physiological responses or constraints or it can act indirectly through other abiotic and biotic factors (Körner, 2003, Larcher, 2003, Taiz & Zeiger, 2002). Given these well-established links between plants and the climates they live in, consequences of climatic change on plant species are expected. During the last two decades evidence that climate change is already affecting life on the planet has been accumulating (Grabherr *et al.*, 1994, Parmesan, 2006, Parmesan & Yohe, 2003, Pauli *et al.*, 2012), calling for the research community to contribute to improve our understanding of the consequences and implications of climate change for nature, ecosystems, and the services they provide for humankind.

Setting the stage: Climate-change research in ecology

Climate-change ecology is a big, and growing, research field. The Web of Science reports a total of 79,508 studies with the keywords “climate change” and “ecology”, with 9,143 hits for 2013 alone (but as all things, this should be seen in perspective: human cancer research, for instance, scores 160,429 articles in 2013). There are three main sources of climate variability available for empirical studies on climate-change impacts: space, time and experimental manipulation. Based on these, three main research approaches have been established for studying climate-driven variation in ecological performance: first, studies of temporal climate variability; second, studies along spatial gradients in climatic parameters; and third, climate-change experiments (Elmendorf *et al.*, 2015). Temporal studies document changes in biological performance across a period of climatic change and then try to extrapolate the observed patterns into the future. Their time frames and resolutions cover everything from a few years with seasonal climate signals in screening studies (Crone *et al.*, 2013) to decades with long-term comparisons in re-sampling studies (Grabherr *et al.*, 1994, Kapfer *et al.*, 2012). Spatial gradient studies use spatial differences in climate, such as elevational temperature gradients along mountain sides (Körner, 2007), latitudinal temperature gradients from South to North (De Frenne *et al.*, 2013) or precipitation gradients from areas with continental climate to areas with oceanic climate (Meineri *et al.*, 2014). Climate-change experiments test hypotheses by applying a controlled change in one or more climatic variables and then comparing the outcome to an untreated control (Aerts *et al.*, 2004, Elmendorf *et al.*, 2012b, Grime *et al.*, 2008, Wu *et al.*, 2011). All three approaches have strengths and weaknesses. Temporal studies bear the potential of identifying real-time responses (including plastic responses) to changes in climate parameters and allow for detection of the temporal response pattern, including immediate and, if the time frame of the study is sufficiently long, lagged responses. However, in temporal studies it is difficult to disentangle climate effects from other co-varying factors, as many studies have relatively low spatial replication, temporal studies also bear the risk that the patterns detected may simply reflect local phenomena (Rustad, 2008). Spatial gradient studies usually overcome the “local phenomenon” issue by including a number of geographically dispersed sites, they may cover a greater fraction of the climatic ranges that the study species tolerate, and may thus give valuable insights into what limits these ranges. However, the patterns found in space today, are a result of processes operating over longer or shorter time-spans in the past, and may or may not be in equilibrium with the current climate. This usually varies between, for instance, elevational vs. latitudinal gradients (Halbritter *et al.*, 2013), and it is hence not straightforward to translate differences found along geographical climatic gradients into climate-change responses (Dunne *et al.*, 2004, Rustad, 2008). Moreover, any investigated geographical gradient must be chosen with great care to avoid potential co-variation in important factors, as for instance temperature and precipitation on mountain slopes in various areas of the world (Körner, 2007). While such confounding factors probably represent the major challenge when setting up spatial gradient studies (cf. Meineri *et al.*, 2014) they are most often easier to avoid in climate-change experiments (cf. Aronson & McNulty, 2009). Testing climate-change impacts experimentally allows the researcher not only to choose the treatment intensities, but also the treatment complexity by, for instance, testing several factors separately and in concert in a multi-factorial experiment (Dunne *et al.*, 2004, Rustad, 2008, Wu *et al.*, 2011). Climate-change experiments can however fail to uncover time-lagged effects, unless the experiment is followed up for a longer time period (Dunne *et al.*, 2004, Rustad, 2008), or show initial responses that disappear in the longer run (Olsen & Klanderud, 2014). Overall it seems that the common, major factor for securing high-quality data and robust conclusions in all three approaches is careful study design: including at least some spatial replication in temporal studies, site selection in spatial gradient studies, experimental design, and 'enough' years to follow things up.

Scio me nihil scire?

What have we learned about climate-change impacts on plants so far from temporal studies, spatial gradients and experiments? We know of climate-warming-related range shifts of plant species from temporal resampling studies along elevatinal gradients (Felde *et al.*, 2012, Klanderud & Birks, 2003), and along latitudinal gradients (Boisvert-Marsh *et al.*, 2014), but also from temporal resampling of mountain summits (Gottfried *et al.*, 2012, Grabherr *et al.*, 1994, Pauli *et al.*, 2012). Warming experiments have shown that higher temperatures increase plant reproduction (Arft *et al.*, 1999), plant cover (Walker *et al.*, 2006), plant height and abundance of shrubs and forbs (Elmendorf *et al.*, 2012a, Elmendorf *et al.*, 2012b). A review of climate-change experiments by Wu *et al.* (2011) revealed stimulating effects of increased temperatures for net primary production. On the other hand, lichens, mosses and specialists among alpine vascular plants have demonstrated reductions in biomass and abundance (Cornelissen *et al.*, 2001, De Valpine & Harte, 2001, Elmendorf *et al.*, 2012a, Harte & Shaw, 1995). A Europe-wide pattern of a decline in more cold-adapted species and an increase in more warm-adapted species has been described as 'thermophilization' (Gottfried *et al.*, 2012). Moreover, this process has consistently been detected by both warming experiments, spatial gradient studies and temporal studies in tundra plant communities (Elmendorf *et al.*, 2015). For the impacts of precipitation changes, on the other hand, we know a great deal less. Experimental manipulations of available water revealed a general positive relationship between productivity and water supply (reviewed in Wu *et al.*, 2011), but the vast majority of the studies were performed in arid regions, and only a few in moderately humid locations. It remains largely unknown how changes in precipitation will affect plant species in relatively wet regions, which are mainly predicted to get more rainfall in the future (IPCC 4014). Moreover, Elmendorf *et al.* (2012a) have shown that warming effects vary between different moisture regimes and it seems intuitive that combined effects of temperature and precipitation change should be important (Luo *et al.*, 2008). The combined effect of changes in temperature and precipitation may be additive, i.e. the single effects of temperature and precipitation change may counteract each other or add up to even stronger effects, or it might show an effect size similar to the marginal treatments, indicating interactions between temperature and precipitation. These outcomes potentially hold very different consequences, both in quality and intensity, and hence it appears important to consider temperature and precipitation in concert. Nevertheless, the explicit parallel and interactive manipulation of temperature and precipitation is rarely investigated in climate-change experiments (Wu *et al.*, 2011) or gradient studies (but see Meineri *et al.*, 2014).

Zooming in: Climate-change impacts on plant populations

Climatic parameters are often reported to alter diversity, species richness, species composition and other broad-scale vegetation parameters. Behind all of this are the varying fates of different single species and populations. And likewise, behind changes in cover or abundance of single species are the fates of single individuals shaping the observed patterns. The fitness of every single individual can be affected in various ways, by altering a set of vital rates, for instance survival, individual and clonal growth, reproductive success, and seedling establishment. Studies illuminating the population-level responses of these vital rates to climate and climate change help us understand the mechanisms acting behind the community-scale patterns, and this process-level understanding may ultimately contribute to producing better climate-change impact predictions.

Population dynamics of plant species have been shown to be responsive to between-year variation in temperature (Adler & HilleRisLambers, 2008, Carlsson & Callaghan, 1994, Dalgleish *et al.*, 2011, Evju *et al.*, 2010, Nicolé *et al.*, 2011, Shryock *et al.*, 2014, Sletvold *et al.*, 2013, Souther & McGraw, 2011) and precipitation (Adler *et al.*, 2013, Buckley *et al.*, 2003, Dalgleish *et al.*, 2011, Marrero-Gomez *et al.*, 2007, Salguero-Gomez *et al.*, 2012, Shryock *et al.*, 2014, Sletvold *et al.*, 2013, Økland, 1997), but spatial gradient or experimental approaches have rarely been applied to investigate effects of predicted climate-change scenarios on population dynamics of plant species (Ehrlén & Morris, 2015). Negative effects of warming on population growth rates (λ), acting through reduced fecundity, were found by Williams *et al.* (2007) for forbs in steppe vegetation whereas Gornish (2014) reported positive effects of warming on λ, acting through increased fecundity, in an invasive grassland forb.

Both studies were performed in disturbed vegetation habitats, where reproduction from seed naturally plays an important role (Bullock, 2000, Grime *et al.*, 1981, Vandvik, 2004). In closed vegetation, λ relies more on clonal growth and survival, and hence climate-change induced changes in these vital rates could be expected to be of higher importance in such habitats. Here, fecundity contributes to expansion or shifts in the distribution of populations via colonization of new patches through seedling establishment in occasional gaps. Since the vulnerability of seedlings to higher temperatures is well documented (Classen *et al.*, 2010, Gimenez-Benavides *et al.*, 2008, Graae *et al.*, 2009, Shevtsova *et al.*, 2009), a future warmer climate may penalize the contributions of fecundity to both λ and colonization.

For water addition mainly negative effects on λ have been found by Adler *et al.* (2013), which is in contrast to the documented general trend of beneficial effects in water addition experiments (Wu *et al.*, 2011). Reproduction from seed is closely related to moisture availability (Baskin & Baskin, 1998) and can hence be expected to contribute positively to population growth and expansion under wetter future conditions, and *vice versa* in regions with predicted precipitation reductions. The effects of combined changes in temperature and precipitation on population dynamics have, to my knowledge, not yet been investigated for any species (but see Pfeifer-Meister *et al.*, 2013 for an example of such a study on single demographic parameters).

Apart from direct impacts through physiological constraints, climate also affects plant populations through biotic interactions; the stress gradient hypothesis predicts stronger competition/weaker facilitation under warmer temperatures and weaker competition/stronger facilitation under colder temperatures (Bertness & Callaway, 1994, He *et al.*, 2013). Under climate warming this balance could shift towards more competition/less facilitation (Callaway *et al.*, 2002, Dunnett & Grime, 1999, Kardol *et al.*, 2010, Klanderud, 2005, Michalet *et al.*, 2014, Soliveres & Maestre, 2014). However, studies that assess the effects of species interactions on population dynamics in different climatic contexts are lacking in the scientific literature. Non-climate related dominance shifts in plant communities have been shown to alter population dynamics of component species of various plant communities (Hamre *et al.*, 2010, van der Meer *et al.*, 2014, Williams & Crone, 2006), highlighting the importance of considering species interactions in climate-change related population studies as well.

Getting to the point: Aims of this PhD thesis

This PhD thesis comprises population studies exploring the effects of climate, climatic change, and species interactions on the population dynamics of two alpine/lowland species pairs, the forbs *Veronica alpina / Veronica officinalis* and *Viola biflora / Viola palustris*. The use of alpine specialist species with narrow ecological niches vs. lowland species with wider ecological niches allows for assessing contrasts in climate-change responses. This thesis and its papers assess climate and climatic-change effects on variation and change in both temperature and precipitation, following up the call for studies combining these two major climatic parameters (Luo *et al.*, 2008, Wu *et al.*, 2011). Since the population studies presented in this thesis were all performed in closed grassland vegetation, changes in fecundity can be expected to play a minor role for population growth under differences in climate (see above). Therefore climate control on reproduction from seed is assessed in a separate study, specifically performed in vegetation gaps. The specific topics investigated in the thesis are:

1. Climatic control and climate-change impacts on population dynamics
2. The effects of climate on the outcome of biotic interactions
3. The role of reproduction from seed in a changing climate

I present four papers in this thesis to cover these topics. Aim #1 is explored along natural spatial and temporal gradients in a population study comparing sites and years with differences in temperature and precipitation (Paper I), and experimentally in a population study performed within a transplant experiment, where populations of the study species were transplanted to warmer, wetter and warmer+wetter climates (Paper II). Aim #2 was investigated in a spatially replicated field experiment testing for species interactions by removing a dominant plant group and comparing species interaction patterns across spatial gradients in temperature and precipitation (Paper III). Aim #3 was investigated in a spatially replicated seed-sowing experiment where seeds were sown in gaps in sites warmer, wetter and warmer+wetter than the sites of their origin. (Paper IV).

Material and Methods summary

The SEEDCLIM climate grid

This PhD thesis was carried out within the SEEDCLIM project, funded by the Norwegian Research Council through the NORKLIMA programme. In SEEDCLIM the unique Norwegian landscape with its many sources of climatic variation was used to set up a climatic grid (hereafter called the SEEDCLIM grid) of four precipitation and three temperature levels (Fig. 1). The variation in temperature relies on different elevations and the variation in precipitation on an East-West gradient with precipitation increasing from the semi-continental East towards the oceanic West. To break the elevational correlation between temperature and precipitation the three different elevations within each of the four precipitation regimes were selected to lie in different areas (with the exception of two sites which lie on the same mountainside). In practice, the selection of the 12 SEEDCLIM sites was based on overlaying maps of mean summer temperature (defined as the mean of the four warmest months) and annual precipitation, and was specifically targeting grazed intermediate-rich meadows (Potentillo-Festucetum ovinae; G8 sensu, Fremstad, 1997) on nutrient-rich phyllitic or calcareous bedrock. All sites are situated on south-facing, shallow slopes and were fenced to avoid animal disturbance. To mimic past grazing regimes the meadows were mowed in peak season every year.

All climate data in this PhD thesis were provided by the Norwegian Meteorological Institute (met.no). The SEEDCLIM grid is based on interpolated temperature and precipitation data from the normal period 1961-1990 with a resolution of 100m (see Tveito *et al.*, 2000, Tveito *et al.*, 2001, Tveito *et al.*, 2005 for method description) where temperature is represented by summer temperature, i.e. the mean of the four warmest months June-September, and precipitation is represented by annual precipitation. The analyses in Paper I are based on daily interpolated data on temperature and precipitation for every site and year during the project period with a resolution of 1000m. A comparison of the normal values and the annual values for summer temperatures and annual precipitation during the study period is given in Fig. 2.

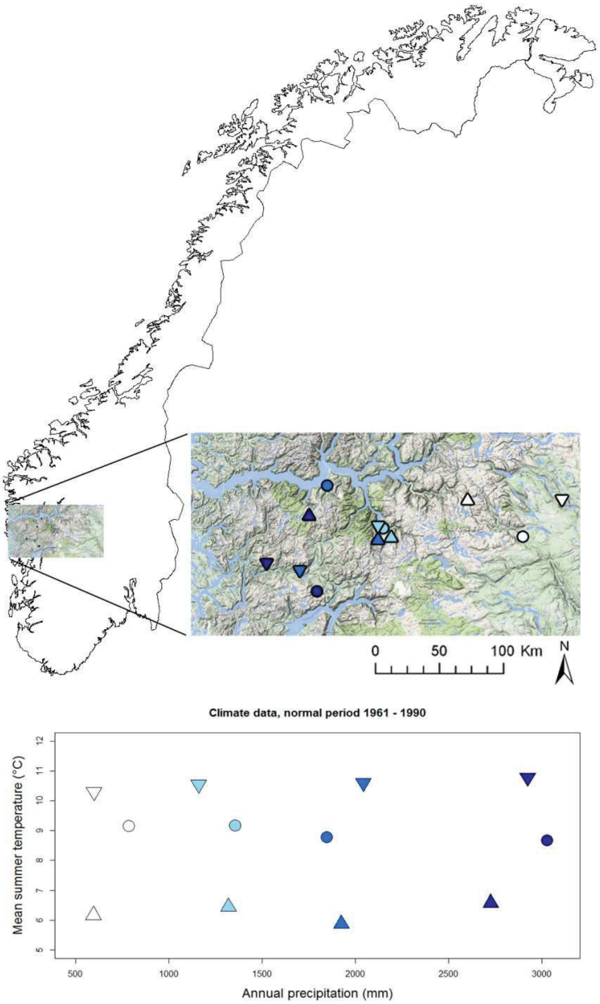

Fig. 1. Geographical location of the study area and the study sites in south-western Norway (top). The climatic context of the SEEDCLIM climate grid (bottom). Symbol coding: ▲ = alpine sites, ● = sub-alpine sites, ▼ = boreal sites. Increasing blue-intensities from white to dark blue indicate increasing precipitation.

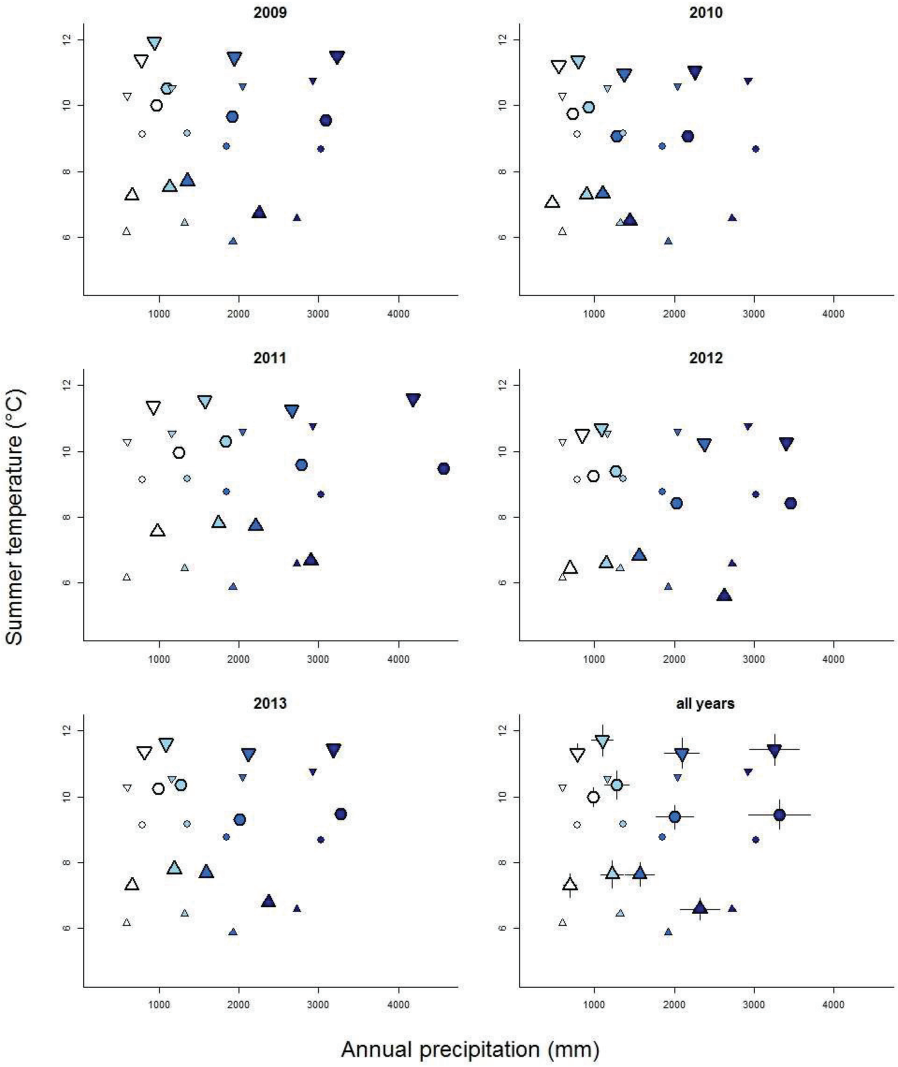

Fig. 2. Long-term average climate data from the normal period 1961-90 (small symbols, same in all panels) and annual data from the study period 2009-13 (large symbols). Symbol coding: ▲ = alpine sites, ● = sub-alpine sites, ▼ = boreal sites. Increasing blue-intensities from white to dark blue indicate increasing precipitation. Horizontal and vertical lines in panel "all years" indicate two standard errors for temperatures and one standard error for precioitation.

Study species

Two pairs of forb species were selected as the focal species in the SEEDCLIM project. Each pair consists of one lowland species with a wide ecological niche and one alpine specialist species with a narrow ecological niche of the same genus: *Viola palustris* L. - *Viola biflora* L. and *Veronica officinalis* L. - *Veronica alpina* L (Fig. 3). These species were chosen so that the climate grid would cover the lower-elevation (rear) edge of the two alpine species and the upper-elevation (leading) edge of the two lowland species (Meineri *et al.*, 2012). These four species were also chosen because they were common across the 12 sites and were judged as good representatives of the forbs in the target communities of the SEEDCLIM sites. All study species are perennial, clonal and produce long lateral rhizomes, each with multiple flowering ramets, on the same genet. Working with species pairs with similar branching structures was chosen to allow for easier comparison between alpine and lowland species. *Viola biflora* is common in moist and relatively nutrient rich mountain habitats and is found in snowbeds and leesides, grazed upland pastures, stream banks, and birch forests. *Viola palustris* grows on moist soils and is common in moist pastures, meadows, and forests, mires, and stream banks. *Veronica alpina* is found in a wide range of upland habitats and is common in snowbeds, upland forests, grasslands, and stream banks. *Veronica officinalis* is often found on shallow well-drained soils within pastures and meadows, along road verges, and in grazed forests and uplands (Lid & Lid, 2005, Mossberg & Stenberg, 2007).

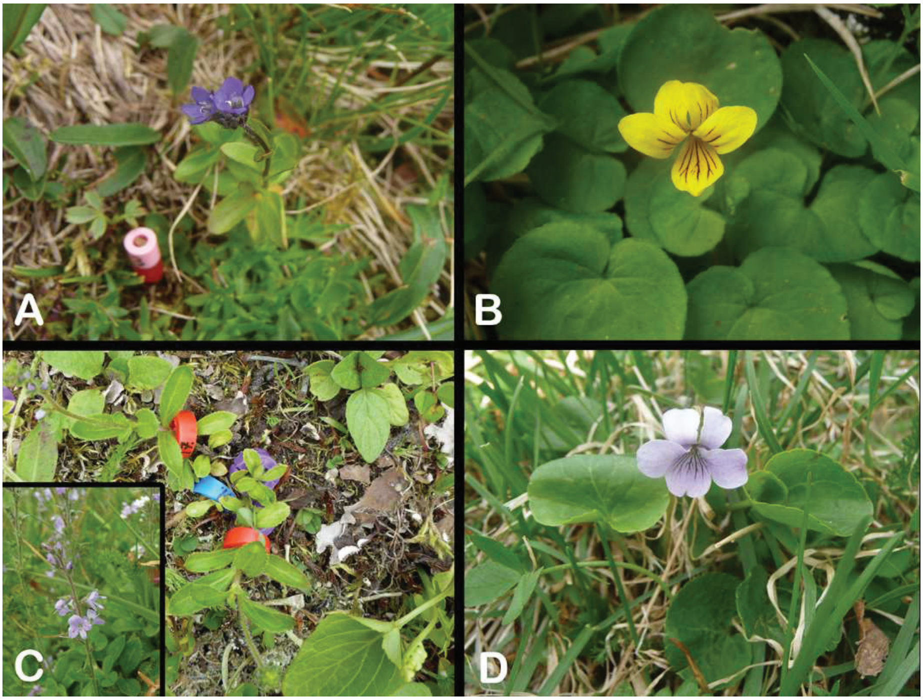

Fig. 3. The four study species, *Veronica alpina* (A), *Viola biflora* (B), *Veronica officinalis* (C, with flower inset), and *Viola palustris*. Photos: Siri Lie Olsen.

Experimental and analytical approaches

Paper I

This paper assesses whether or not the focal species' population dynamics are under climatic control and if any observed patterns arise from climatic variations in either space or time, i.e. between sites or years. We applied size structured integral projection models (IPMs) (Easterling *et al.*, 2000, Merow *et al.*, 2014, Metcalf *et al.*, 2013) to five annual transitions of demographic data. The underlying vital rates regressions of the IPMs were performed with generalized linear mixed effects models with a random effects structure of site-within-transition, which allowed us to build IPMs for every site in every transition. We analysed the resulting population growth rates (λ) in two sets of linear mixed effects models using different random effects structures for testing whether or not λ was related to climatic differences in space or time, respectively. The random structure of a mixed effects model is useful for describing the structure of the data and the right contrast for the regression. A random effect of site was hence used to estimate the relationship between λ and transition climate as well as a random effect of transition to estimate the relationship between λ and site climate. Finally, we performed two-way life table response experiments (LTREs) (Caswell, 2001) on the population models to uncover the contributions of the underlying vital rates to climate-driven changes in λ.

Paper II

This study investigates the impacts of predicted changes in temperature and precipitation on the study species in a transplant experiment. We transplanted whole turfs of vegetation (29 × 29 cm) to sites one step warmer, one step wetter and one step warmer+wetter, as well as at home (control) within the SEEDCLIM grid (Fig. 4). We constructed size structured integral projection models (IPMs) (Easterling *et al.*, 2000, Merow *et al.*, 2014, Metcalf *et al.*, 2013) on demographic data for three annual transitions. The underlying vital rates regressions of the IPMs were performed with generalized linear mixed effects models with a random effects structure accounting for differences between transitions and sites separately. We then built IPMs for the overall treatments across all sites and for every site separately. By non-parametric bootstrapping of the original demographic data sets we created a set of 2000 IPMs and their respective λ values for every treatment and every site per species to be able to statistically compare both controls with treatments, and also transplant effects across the sites of the SEEDCLIM grid. One-way life table response experiments (LTREs) (Caswell, 2001) on the population models were performed to uncover the contributions of the underlying vital rates to climate transplant-driven changes in λ.

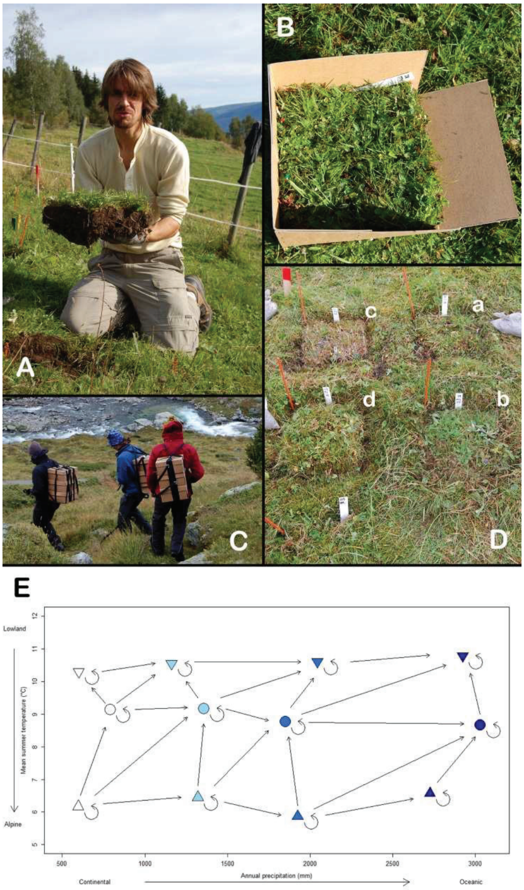

Fig. 4. The transplant experiment. Transplants were cut out of the soil ca. 10cm deep (A, featuring Olav Skarpaas), stored in herbarium boxes (B), carried to the car (C), and planted into excavation holes at the target sites. Panel 'D' shows a block in the site SUB2, with four transplant plots (a-d) and one untreated plot (bottom left). SUB2 received all three climate transplants, i.e. from sites colder (a), drier (b), and colder+drier (c) and a locally transplanted control plot (d). The untreated plot was used in Paper I. Panel 'E' shows the transplanting directions within the SEEDCLIM climate grid. Symbol coding: ▲ = alpine sites, ● = sub-alpine sites, ▼ = boreal sites. Increasing blue-intensities from white to dark blue indicate increasing precipitation. Photos by Kari Klanderud.

Paper III

This paper describes species-interactions within the SEEDCLIM grid. We compared performance of the focal species in plots, where all above-ground plant biomass of graminoid species, the dominant group in the 12 sites, was removed (Fig. 5A), to untreated plots. We constructed size structured integral projection models (IPMs) (Easterling *et al.*, 2000, Merow *et al.*, 2014, Metcalf *et al.*, 2013) to two annual transitions of demographic data. The underlying vital rates regressions of the IPMs were performed with generalized linear mixed effects models with a random effects structure accounting for differences between transitions and sites separately. We then built IPMs for the overall treatments across all sites and for every site separately. One-way life table response experiments (LTREs) (Caswell, 2001) on the population models were performed to uncover the contributions of the underlying vital rates to climate transplant driven changes in λ. Finally both differences in λ between graminoid removal plots and control plots, as well as the LTRE contributions were regressed with temperature and precipitation in generalized linear mixed models across all species to examine whether the overall effect of dominant graminoid removal varied with climate within the SEEDCLIM grid. Hereafter I express climate effects that increase competition effects and reduce facilitation effects as negative effects on species interactions, and climate effects that reduce competition effects and increase facilitation effects as positive effects on species interactions.

Paper IV

This paper investigates how seedling emergence is affected by the climate conditions occurring at the sowing sites and experienced by the seed-source populations. We transplanted mature seeds from each site within the SEEDCLIM grid to sites one step warmer, one step wetter and one step warmer+wetter, as well as at home. The original experiment was carried out in both closed vegetation and gaps. In Papers I, II and III the results from the closed vegetation plots are used for population models of the undisturbed vegetation, whereas Paper IV is based on the data from the gaps (Fig. 5B). The analysis of the emergence data includes both an experimental (the transplanted vs. the control seeds) and a gradient (the transplanted seeds along the gradients) approach. In the experimental approach, we used log-linear mixed models where we adapted the random structure to the hypothesis tested. The random structure of a mixed model is normally used to describe the structure of the data and so the contrast between control and treatment groups. Hence, we used models nested on source site to compare the emergence of seeds sown at home versus the emergence of seeds sown away, and in contrast, models nested on sowing site to compare the emergence of foreign seeds versus the emergence of seeds of the local populations. In the gradient approach, log-linear mixed effects models were used to analyse how seedling emergence responds along the extended temperature and precipitation gradients of the SEEDCLIM grid. The effect of the sowing-site climate and the effect of the seed-source climate could be studied separately by excluding the emergence scores of the seeds in the control group which experienced similar sowing-site and seed-source climate. Using both experimental and gradient approaches allowed us to not only compare local responses to gradient-wide patterns but also to identify signs of adaptive seedling emergence (local adaptation or pre-conditioning maternal environmental effect). In the experimental approach, adaptive seedling emergence was indicated by higher seedling emergence for the seeds sown at home compared to seeds sown away (home vs. away criterion in Kawecki & Ebert, 2004) and higher emergence for the local seeds of a sowing site compared to the foreign seeds (local vs. foreign criterion in Kawecki & Ebert, 2004). However, the gradient approach was necessary to confirm that this effect was not caused by potential negative effects of the sowing-site climate since the transplants were only made in a single direction. NB: in this study the three different elevations within the SEEDCLIM grid are called alpine, intermediate and lowland. For Papers I, II and III, we decided on an ecologically more descriptive nomenclature and the levels are hence called alpine, sub-alpine and boreal.

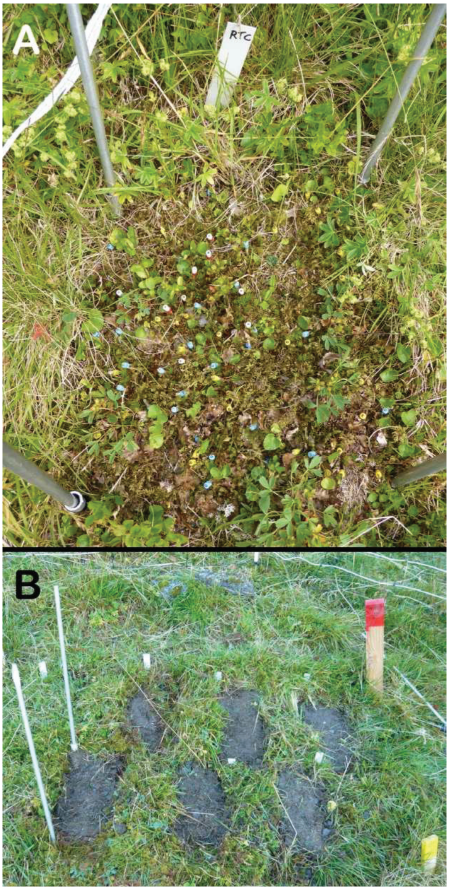

Fig. 5. Panel 'A' shows a 'clipped' plot from Paper III where all above-ground graminoid biomass was removed. Panel 'B' shows a seed sowing block with disturbed vegetation (Paper IV) and intact vegetation (used for seedling establishment constants in Papers I, II & III). Photos by Siri Lie Olsen (A) and Kari Klanderud (B).

Results and Discussion

All species investigated in this thesis were affected by climate, both from spatial and/or temporal climatic variation, in the climate-change experiments, and through changes in biotic interactions. Overall, temperature increases showed consistent negative effects on all species, whereas increased precipitation showed varying effects, both between species and between experiments within species (Box 1 and Table 1). In the following chapters, I first compare the patterns of climate control from Paper I and the climate-change impacts revealed in Paper II separately for every species, then draw the lines to the biotic interaction patterns shown in Paper III, and subsequently discuss the effects of climate change on reproduction from seed in disturbed vegetation.

Climatic control and climate-change impacts on population dynamics

The patterns of climatic control along the climate gradients (Paper I) and in the transplant experiment (Paper II) were mainly in agreement, although not all effects were reflected in both studies (Table 1). In one case - the response of *Viola palustris* to higher precipitation - the two studies yielded contradictory results. However, in general, warmer temperatures had a negative effect on λ both in the alpine species and the lowland species, whereas higher precipitation largely affected λ in the *Veronicas* negatively and in the *Violas* positively.

In *Veronica alpina* the lower λ in sites with warmer springs (Paper I) was reflected by a decrease in λ under warmer temperatures in the transplant experiment (Paper II). Such a pattern can be expected in a sub-dominant alpine forb species (De Valpine & Harte, 2001, Harte & Shaw, 1995, Klanderud & Birks, 2003). This pattern could be attributed to increased competition in Paper II since overall vegetation height increased in the warmer transplants. However, in Paper I this appears unlikely since *Veronica alpina* has been shown

BOX 1. Main results from Papers I-IV

Warmer temperatures had negative effects on λ in ***Veronica alpina*** along the spatial climatic gradient (Paper I) and in the warmer transplants (Paper II).

Increased precipitation reduced λ in the wetter transplants, though less than in the warmer transplants. The combined increase of temperature and precipitation also reduced λ, and reflected the effect magnitude from the wetter transplants, which indicates that the two negative single effects were not additive (Paper II). Temperature had a positive effect on species interactions by increasing facilitation in the sub-alpine sites as compared to the alpine sites and also increased precipitation had a tendency of increasing facilitation (Paper III). Seedling establishment decreased with higher sowing site temperature and increased with higher sowing site precipitation (Paper IV).

In ***Veronica officinalis*** λ was lower in sites with warmer summer temperatures and sites with higher precipitation (Paper I). Increased temperature in the warmer transplants had no effect on λ but increased precipitation reduced λ in the wetter transplants. This reduction, including the effect size, was also reflected in the warmer+wetter transplants (Paper II). Competitive interactions were stronger in the warmer boreal sites than in the sub-alpine sites but also had a tendency to be lower where precipitation was higher in the boreal sites (Paper III).

Seedling establishment was affected positively by a warmer maternal environment and an adaptive seedling emergence was indicated for this species (Paper IV).

In ***Viola biflora*** temporal episodes of high precipitation (Paper I) and increased precipitation in the wetter transplants (Paper II) affected λ positively.

Warmer temperatures decreased λ in the transplant experiment and these two single effects canceled each other out in the combined treatment (Paper II). Increased temperatures affected species interactions negatively by leading to a switch from facilitation in alpine sites to competition in sub-alpine sites and facilitation was highest in the driest site (Paper III). Seedling establishment decreased with higher sowing site temperatures and increased with higher sowing site precipitation (Paper IV).

Viola palustris showed negative effects of higher temperatures on λ in warmer years while increased precipitation had positive effects on λ both with spatial and temporal variation in precipitation (Paper I).

In the transplant experiment λ was reduced in all treatments, but the reduction was strongest in the warm transplants, whereas the warmer+wetter transplants reflected the effect magnitude from the wetter transplants, which indicates that the two negative single effects were not additive (Paper II). Increasing temperatures led to a shift from facilitation to competition and there was a tendency of stronger facilitation and weaker competition with increasing precipitation in the alpine and boreal sites (Paper III). Seedling establishment decreased with higher sowing site temperatures and increased with higher sowing site precipitation (Paper IV).

to be facilitated by neighbours both elsewhere and in our sites in particular (Schoeb *et al.*, 2010, Paper III). While neither spatial nor temporal variation in precipitation affected λ systematically (Paper I), transplantation to both a wetter and a warmer+wetter climate led to lower population growth (Paper II). This disparity indicates a) that the *Veronica alpina* populations might be adapted to the precipitation regime at their home sites, and b) that annual fluctuations in seasonal precipitation may not be sufficient to trigger a response, whereas a more consistent change in precipitation, as in the transplant experiment, is. Together these results forecast negative prospects for *Veronica alpina* under a warmer and wetter future climate.

In *Viola biflora* neither spatial nor temporal variation in temperature had any effect on λ. Within the SEEDCLIM grid this species is present in three alpine and only one sub-alpine site, which limits natural temperature variability and hence the detectability of any temperature effect on λ along the gradients (Paper I). In another study performed in Southern Norway, population growth of *Viola biflora* populations was shown to be negatively related to warmer temperatures (Evju *et al.*, 2010), and so we would expect a negative temperature effect on this sub-dominant alpine forb. This expectation was confirmed in the transplant experiment where λ was reduced under a warmer climate. Temporal variation in precipitation affected λ in *Viola biflora* via increased re-sprouting after vegetative dormancy (Paper I), a process that has been linked to remobilization of stored resources (Gremer *et al.*, 2010). Since the effect was only present in the two driest sites of *Viola biflora's* occurrence in the SEEDCLIM grid, it appears that dormancy patterns might be linked to precipitation in this species and that a high precipitation pulse may be necessary for re-sprouting in drier sites. Also in the wetter transplants *Viola biflora* showed an increase in λ, but here the pattern was related to increased survival and did not vary systematically between the sites (Paper II). This indicates that the positive precipitation effects on λ in *Viola biflora* found in papers I and II

Table 1. Effects of increasing temperature and precipitation on population growth rate (λ) in population models and on seedling emergence according to the papers in this thesis. Positive effects are indicated by black color, negative effects by red color. For the population models, the vital rate contributing most to changes in λ is indicated. For seedling emergence, effects of source and sowing site is indicated. Significance level: $p < 0.05$. Parentheses indicate $p < 0.1$.

	Veronica alpina	***Veronica officinalis***	***Viola biflora***	***Viola palustris***
Population models				
Temperature increase				
Spatial gradient effect	**clonality**	**survival**		
Temporal gradient effect				**(survival)**
Climate transplant effect	**survival**		**clonality**	**survival**
Species interaction effect		**survival**	**clonality**	**survival**
Precipitation increase				
Spatial gradient effect		**clonality**		**survival**
Temporal gradient effect			**clonality**	**survival**
Climate transplant effect	**clonality**	**survival**	**survival**	**clonality**
Species interaction effect				
Temperature & precipitation increase				
Climate transplant effect	**clonality**	**survival**		**clonality**
Seedling emergence				
Temperature increase				
Transplant effect	**Sowing**	**Source/Sowing**	**Sowing**	**Sowing**
Gradient effect	**Sowing**	**Source**	**Sowing**	**Sowing**
Precipitation increase				
Transplant effect	**(Sowing)**	**Source/Sowing**	**Sowing**	**Sowing**
Gradient effect			**Sowing**	**Sowing**

are caused by two different underlying mechanisms. Still, a general positive response to higher precipitation may be expected in this species based on its affinity to moist environments (see S1 in Lenoir *et al.*, 2010). Since the effect of the two marginal transplant treatments cancelled each other out in the combined warmer+wetter transplants, the prospects for *Viola biflora* under a future warmer and wetter climate do not appear negative. Especially in microsites characterized by high moisture this species will likely have a high chance of persisting. However, apart from the response to temporal precipitation variation, *Viola biflora* also showed a substantial variation in λ in Paper I, which could not be attributed to the climate parameters. This indicates that, in the climatic context of this study, some other unknown factor has influence, which adds uncertainty to future predictions about the species' performance. Moreover, high variability in λ itself increases the risk of local extinction (Morris & Doak, 2002).

Veronica officinalis was negatively affected by spatial variation in both temperature and precipitation but not by temporal climatic variation (Paper I). In the transplant experiment however, there was no effect of warmer temperatures (Paper II). This disparity may be attributed to the different time scales operating behind these two effects, since differences between sites reflect long-term effects and differences between treatments constitute short-term effects (Elmendorf *et al.*, 2015, Rustad, 2008). A negative effect of temperature is generally unexpected for *Veronica officinalis*, a typical lowland generalist. The occurrences of this species in our sub-alpine sites approximately represent its local upper elevational distribution border in Norway (Meineri *et al.*, 2012), and better population performance could hence have been expected in the warmer boreal sites than in the colder sub-alpine ones. The fact that the sub-alpine populations instead perform better could indicate that *Veronica officinalis* is not in equilibrium with present-day climate and might be moving upwards (Paper I). This is not unrealistic given the climatic change the study region has already undergone during the last decades (Fig. 2). In the transplant study, a comparison of control plots from sub-alpine and boreal sites and warmer transplants to boreal sites reveals lower population growth in the warmer boreal controls (J. Töpper et al., unpublished data) whereas the plots transplanted to the warmer boreal sites were not affected (Paper II). Together with the lack of negative effects of temporal temperature variations (Paper I) this indicates that short-term changes in temperature are not sufficient to trigger a response corresponding to the observed site differences. *Veronica officinalis* showed reduced λ in sites with higher precipitation (Paper I) and in plots transplanted to a wetter and warmer+wetter climate (Paper II), which is in line with the species' low Ellenberg values for moisture affinity (Hill *et al.*, 1999). The fact that these effects appear both between sites (long term) and in the transplants (a consistent short-term climatic change) indicates a plastic response. The lack of a short-term effect of temporal precipitation variability suggests that a change in moisture has to be more consistent than a seasonal pulse in order to affect the species. Moreover, the λ reductions in the wetter and warmer+wetter transplants were mediated through reduced survival, and the effect sizes were large: in both treatments λ was reduced by ~0.4 in comparison to the controls (Paper II), which together indicate that *Veronica officinalis* is physiologically constrained by high moisture.

In *Viola palustris* negative effects of temperature on λ were found both in the warmer transplants (Paper II) and with temporal variation, but not with spatial variation, in temperature (Paper I). This indicates that *Viola palustris* is susceptible to short-term changes in temperature, potentially due to higher competition for light (Jensen & Meyer, 2001) from taller neighbour species (Paper II). Long-term establishment of *Viola palustris* in microsites with a suitable environment, both with respect to climate (the species is a temperature generalist but a wet site indicator, see Hill *et al.*, 1999) and species interactions (Jensen & Meyer, 2001), might obscure any related temperature effects along spatial temperature variation (Paper I). Regarding precipitation, Papers I and II do not agree on a common pattern, since there were positive effects on λ with both spatial and temporal variation in precipitation (Paper I) while transplanting to a wetter climate had negative effects (Paper II). This was unexpected, and especially the result in Paper II was counter-intuitive, given the species' high affinity to moisture (Hill *et al.*, 1999). In the course of transplanting great care was given to the selection of target microsites so that wetter transplants would actually end up in wetter microsites. While it cannot be excluded that some wetter transplants might have ended up in drier microsites (due to local variations in soil moisture) it appears unlikely that this would have happened consistently. Also in the warmer+wetter transplants, λ of *Viola palustris* was affected negatively, but less than expected from an additive model of the two marginal treatments. These contradictive results for precipitation make predictions for population performance under a predicted warmer and wetter future climate in the study region difficult. Yet, for warming alone, negative prospects can be predicted, for instance through drying of currently suitable microsites and changes in the neighbouring plant community and its productivity.

Experiments on the effects of combined changes in temperature and precipitation are still rather seldom (Wu *et al.*, 2011) even though they are important, since they inform on the actual net effect of climatic change. Herein lies the particular strength of the transplant experiment in Paper II, which assesses the effects of changes in temperature and precipitation both separately and in concert. *Viola biflora* and *Veronica officinalis* showed additive effects of the marginal treatments, with two opposing marginal effects cancelling each other out in *Viola biflora*, and a single significant marginal effect being reflected in the combined treatment in *Veronica officinalis*. In *Veronica alpina* and *Viola palustris* the combined treatment had a lower effect size than expected from the two marginal treatments, indicating a negative interaction between temperature and precipitation. Hence no positive enforcing additive effects were found in any of the species. This corroborates the findings of the few previous climate-change experiments that have addressed combined changes in temperature and precipitation; they have generally found responses to combined changes in temperature and precipitation to be smaller than expected from an addition of the single-factor responses (Wu *et al.*, 2011). In *Veronica alpina* and *Viola palustris*, but also in *Veronica officinalis*, the net outcome of this combined change response appears to be largely modified by precipitation change, which is in accordance with previous modelling assessments of interactive effects of temperature and precipitation (Luo *et al.*, 2008).

Survival and clonality were the most important vital rates contributing to changes in λ (Table 1). The lowland species, *Veronica officinalis* and *Viola palustris*, were mainly affected through changes in survival, whereas the alpine species, *Veronica alpina* and *Viola biflora*, were mainly affected through changes in clonality. Population size in all four study species depends on the balance between the rates of survival and clonality. Changes in these vital rates directly affect population size and by that also local population persistence, since population size is linked to the risk of stochastic local extinction (Morris & Doak, 2002). Growth contributed positively to changes in λ of *Veronica officinalis* in the warmer and warmer+wetter transplants, which could be expected for a lowland generalist (Wu *et al.*, 2011). However, these positive contributions were outweighed by the negative contributions of survival, leading to no net effect in the warmer transplants and to a strong λ decline in the warmer+wetter transplants. Fecundity did not contribute to changes in λ at all.

Biotic interactions and climate change

Differences and changes in climatic parameters may affect plant species either directly through species-specific physiological constraints or indirectly by changing other environmental aspects, such as species interactions. Especially for sub-dominant forbs, as our study species, changes in species interactions may be of crucial importance under climate change. Accordingly, Paper III shows an overall shift from facilitation to competition as temperature increases in both alpine and lowland species. This is in line with the stress gradient hypothesis (Bertness & Callaway, 1994, He *et al.*, 2013) and has been documented both along climate gradients (Anthelme *et al.*, 2014, Callaway *et al.*, 2002, Kikvidze *et al.*, 2005) and in climate-change experiments (Alatalo & Totland, 1997, Dunnett & Grime, 1999, Klanderud, 2005, Olsen & Klanderud, 2014). These patterns also contribute to explaining our results along the gradients (Paper I) and in the transplant experiment (Paper II).

The negative effects of temperature on λ in *Viola palustris* (Papers I & II), *Viola biflora* (Paper II) and *Veronica officinalis* (Paper I) may well be attributed to increased competition, which is also supported by an overall increase in vegetation height in both the warmer and warmer+wetter transplants (Paper II). For *Veronica officinalis* the stronger negative competition effect in the boreal sites (Paper III) supports our interpretation that the species is 'on the move' (Paper I). However, the lack of an overall temperature effect in the warmer transplants in Paper II indicates that this species is able to cope with increased competition in the short term. *Veronica alpina* showed a contrasting pattern with a trend of higher facilitation in the warmer sub-alpine sites as compared to the alpine sites (see also Schoeb *et al.*, 2010). The negative effect of warmer temperatures on λ in the warmer transplants (Paper II) may still be related to increased competition, since four of the six populations have been transplanted to 'new' sites with different communities where *Veronica alpina* does not naturally occur. However, the negative effect of temperature along the spatial gradient indicated in Paper I appears less likely to be caused by competitive interactions in the light of higher facilitation in the sub-alpine sites for this species.

Precipitation influenced the strength of the temperature effects on biotic interactions rather than directly affecting the outcome of biotic interactions. Increasing precipitation had a tendency to decrease high temperature-driven competition and increase low temperature-driven facilitation, although not all temperature levels or species followed that pattern (Paper III). In arid areas, competition was shown to increase with increasing precipitation (Armas *et al.*, 2011, Holzapfel *et al.*, 2006, Pugnaire & Luque, 2001) due to a release from water deficit and an increase in productivity. On the other hand, overly wet conditions, as can be experienced in the wetter half of the SEEDCLIM grid, may be detrimental to plants (Schuur, 2003). Such negative effects of high moisture on other species may benefit species with a high moisture affinity such as *Viola biflora* (Papers I & II) and *Viola palustris* (Paper I) through reduced competition. Accordingly, a species like *Veronica alpina* that seems to rely on facilitative neighbour effects (Paper III, see also Schoeb *et al.*, 2010), could be negatively affected by precipitation increase (see Paper II) due to reductions in neighbouring species.

Reproduction from seed in a changing climate

Fecundity did not contribute to differences or changes in λ in any of the studies on population dynamics in this thesis (Papers I, II and III). This is due to low elasticities of λ to changes in fecundity, which in turn is mainly due to low probabilities of seedling establishment (Papers I, II and III) and low survival probabilities of seedlings (i.e. the smallest sizes in the IPMs) beyond the first growing season in closed vegetation (see for instance APP 2 in Paper II). However, from a related study within the SEEDCLIM project we know that flowering and reproductive effort relate to climatic conditions (Meineri *et al.*, 2014), indicating that sexual reproduction might have another function than contributing to λ in our study populations. While clonal reproduction is a main contributor to λ and small-scale persistence in the study species, sexual reproduction may contribute to species persistence on a larger spatial scale. Successful germination and survival of seedlings depends to a large extent on the seeds' access to bare ground and the seedlings' access to light, and hence disturbance is crucial for seedling establishment (Bullock, 2000, Grime *et al.*, 1981, Vandvik, 2004). By germinating and establishing in disturbed patches where and when they arise, seeds may quickly colonize new areas since they travel faster than stolons. All study species maintain a seedbank (Vandvik et. al, unpublished data), thus the seeds may already be there, waiting and ready for when a spot is disturbed. Paper IV addresses the effects of climatic change on seedling establishment in disturbed vegetation and reveals generally negative sowing-site effects of warmer temperatures on seedling emergence in all four species (Table 1). Negative effects of temperature on seedling emergence is a well-documented pattern (Classen *et al.*, 2010, Gimenez-Benavides *et al.*, 2008, Graae *et al.*, 2009, Shevtsova *et al.*, 2009) and has been related to soil-drying (Classen *et al.*, 2010, Gimenez-Benavides *et al.*, 2007, Gimenez-Benavides *et al.*, 2008, Walck *et al.*, 2011). *Veronica officinalis* was the only species to show a positive effect of temperature; more precisely a positive relationship between seedling establishment and seed source temperature (Paper IV). Together with the absence of any effects along the recruitment site climate gradients, this indicates an adaptive seedling emergence pattern, which can be either due to pre-conditioning effects of the maternal environment (Blödner *et al.*, 2007, Galloway & Etterson, 2007, Johnsen *et al.*, 2005a, Johnsen *et al.*, 2005b) or local adaptation (Gimenez-Benavides *et al.*, 2007). Susceptibility of seedlings to low temperatures at a species' upper elevational limit, a bet-hedging strategy or local temperature-pH relations may be potential drivers for such an adaptive pattern (Paper IV). Higher precipitation showed positive sowing-site effects on seedling emergence in *Viola biflora* and *Viola palustris* (Table 1), which is in line with ecological theory that generally predicts positive effects on seedling establishment (Baskin & Baskin, 1998). In *Veronica officinalis* both a warmer and a wetter recruitment site climate reduced seedling establishment, but also here the response to a combined change in temperature and precipitation was weaker than expected from adding the two single factor responses (*cf.* Paper

II and Wu *et al.*, 2011). The net outcome of the responses to a combined change in temperature and precipitation was negative for all species, indicating that even in disturbed vegetation, reproduction from seed will contribute less to population growth and persistence under future climatic conditions than under present-day climate.

Zooming out: finding a place in the bigger picture

Climate-change impacts are complex. A growing number of records on patterns of plant performance along climatic gradients, climatic changes over time, and effects of experimentally imposed climate change have not just increased our knowledge on how climate and plants interact but also our understanding of how the different approaches vary in the underlying mechanisms shaping the species responses. Consequently, 'integrated approaches', as for instance climate-change experiments along gradients, have been called for during the last decade (Dunne *et al.*, 2004, Ehrlén & Morris, 2015, Rustad, 2008) rather than further single approach studies, in order to overcome "the current situation where we resemble the proverbial blind men examining different parts of an elephant" (Ehrlén & Morris, 2015, see appendix).

This thesis is such an integrated study (though we are still far from getting near to seeing the entire elephant), assessing both effects of climatic variation in space and time and performing experiments along climate gradients. The presented results support the recent finding that the different approaches yield consistent results (Elmendorf *et al.*, 2015). For instance, four of the six spatial and/or temporal climate effects found in Paper I are confirmed in the climate-change experiment in Paper II. However, the study also demonstrated the strength of combining different approaches. Additional experiments on climate related processes relevant for plant performance, like the species interactions experiment in Paper III, add important information that helps understand the mechanisms behind any climate or climate-change related effect, as here in Papers I and II. Moreover, even the absence of effects contribute to understanding and predicting climate-change impacts, as highlighted in Paper I, and its comparison to Paper II (see above). Despite all these benefits of integrating various studies, increasing complexity in the study design is also to ‘ask for trouble’, since combining approaches also increases the chance of finding contradictory results (for example the precipitation effects on λ in *Viola palustris* in Papers I & II). While perhaps unsatisfying for the researcher in each individual case, detection of such inconsistent responses are important as they may yield information about strength and consistency of relationships as well as underlying processes. This thesis shows that the benefits clearly outweigh the costs. Combining different approaches enabled us to (1) detect climatic control on species where single approaches would have failed to do so (see also Dunne *et al.*, 2004, Rustad, 2008), (2) reveal underlying mechanisms and time scales for the found effects, and (3) detect indications of an ongoing elevational range shift in *Veronica officinalis*.

The focal species in the papers of this thesis, and generally in the SEEDCLIM project, shared some common characteristics such as life cycle and architecture within the species pairs, but were otherwise intentionally chosen to be different in their affinities to climate since the literature predicts alpine specialists to decrease (De Valpine & Harte, 2001, Harte & Shaw, 1995, Klanderud & Birks, 2003) in the course of climate warming and lowland generalists to increase (Klanderud & Birks, 2003, Walker *et al.*, 2006). In this thesis, all species were negatively affected by temperature, not just the alpine specialists (Papers I, II and IV). Increased competition appears to limit the two lowland species, and obviously ‘pushes’ one of them (*Veronica officinalis*) out of its current elevational distribution range (Papers I and II). The reduced population growth of *Veronica alpina* in the sub-alpine sites (Paper I) is, however, probably not related to competition, since Paper III shows increased facilitative benefit with higher temperatures. Again, these results highlight the importance of integrated studies which, despite the troubles they entail, permit the identification of complex patterns and increase the chance of finding unexpected results.

Further work and concluding remarks

The demography data behind the papers presented in this thesis allow for further questions to be addressed. While Paper II assesses the differences between transplants and controls at the source sites, further work will include the comparison of the transplanted populations to the populations at the target sites. This might give more insight on, for example, local adaptation patterns and range shifts. Another topic to investigate is the transplant effect *per se* and its dependence on climatic context, which can be assessed by comparing the transplant control plots from Paper II to the plots used in Paper I. The vastness of demographic data in general, appears to give rise to many topics to explore and hypotheses to test. One of them would be to modify the population models in order to include the seedling-establishment patterns with climate in gaps from Paper IV. For this, seedlings would need to get their own "survival in gaps" vital rate assigned so that some seedlings actually survive in the IPM. From such an approach I expect we could obtain better insights on fecundity dynamics in disturbed habitats under climate change (cf. Stokes *et al.*, 2004). As mentioned above, population studies in climate-change experiments as in Paper II are rare, and hence there is a need for more such studies on more species, both sub-dominant and dominant ones. Three of the four study species in this thesis show vegetative dormancy, which despite being an intriguing feature in plants in my opinion, has only been studied by a very limited number of researchers. The role and implications of vegetative dormancy in a future climate are not well understood and further research on that topic appears necessary.

This thesis and its papers show that temperature increase largely holds negative consequences for grassland forbs like our focal species, while responses to precipitation increase may be highly species specific and potentially counteract the temperature responses. Species interactions are suggested to be a main driving force behind the negative temperature effects, whereas increased precipitation appears to affect the species rather directly through physiological constraints. The fact that not just the alpine species were affected by climate-driven changes in species interactions but also the alleged temperature generalists stresses the importance of considering biotic interactions in climate-change studies.

Acknowledgments

I want to thank Vigdis Vandvik, Knut Rydgren and Olav Skarpaas for valuable comments on this synopsis, and Cathy Jenks for language corrections. This work was financially supported by the Norwegian Research Council (NORKLIMA grant #184912/230) and the Olav Grolle Olsens fund at the University of Bergen.

References

Adler PB, Byrne KM, Leiker J (2013) Can the past predict the future? Experimental tests of historically based population models. Global Change Biology, **19**, 1793-1803.

Adler PB, Hillerislambers J (2008) The influence of climate and species composition on the population dynamics of ten prairie forbs. Ecology, **89**, 3049-3060.

Aerts R, Cornelissen JHC, Dorrepaal E, Van Logtestijn RSP, Callaghan TV (2004) Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. Global Change Biology, **10**, 1599-1609.

Alatalo JM, Totland Ø (1997) Response to simulated climatic change in an alpine and subarctic pollen-risk strategist, *Silene acaulis*. Global Change Biology, **3**, 74-79.

Anthelme F, Cavieres LA, Dangles O (2014) Facilitation among plants in alpine environments in the face of climate change. Frontiers in plant science, **5**, 387-387.

Arft AM, Walker MD, Gurevitch J *et al.* (1999) Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. Ecological Monographs, **69**, 491-511.

Armas C, Rodriguez-Echeverria S, Pugnaire FI (2011) A field test of the stress-gradient hypothesis along an aridity gradient. Journal of Vegetation Science, **22**, 818-827.

Aronson EL, Mcnulty SG (2009) Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. Agricultural and Forest Meteorology, **149**, 1791-1799.

Baskin CC, Baskin JM (1998) *Seeds. Ecology, Biogeography, and Evolution of Dormancy and Germination,* London, Academic Press.

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends in Ecology & Evolution, **9**, 191-193.

Blödner C, Goebel C, Feussner I, Gatz C, Polle A (2007) Warm and cold parental reproductive environments affect seed properties, fitness, and cold responsiveness in *Arabidopsis thaliana* progenies. Plant Cell and Environment, **30**, 165-175.

Boisvert-Marsh L, Perie C, De Blois S (2014) Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere, **5**.

Bresinsky A, Körner C, Kadereit JW, Neuhaus G, Sonnewald U (2008) *Strasburger Lehrbuch der Botanik,* Berlin, Spektrum Akademischer Verlag.

Buckley YM, Briese DT, Rees M (2003) Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. Journal of Applied Ecology, **40**, 481-493.

Bullock JM (2000) Gaps and Seedling Colonization. In: *Seeds – The ecology of regeneration in plant communities.* (ed Fenner M) pp Page. Wallingford, Great Britain, CAB International.

Callaway RM, Brooker RW, Choler P *et al.* (2002) Positive interactions among alpine plants increase with stress. Nature, **417**, 844-848.

Carlsson BA, Callaghan TV (1994) Impact of climate-change factors on the clonal sedge *Carex bigelowii* - implications for population-growth and vegetative spread. Ecography, **17**, 321-330.

Caswell H (2001) *Matrix population models: construction, analysis, and interpretation.,* Sunderland, Massachusetts, Sinauer Associates, Inc. Publishers.

Classen AT, Norby RJ, Campany CE, Sides KE, Weltzin JF (2010) Climate Change Alters Seedling Emergence and Establishment in an Old-Field Ecosystem. Plos One, **5**.

Cornelissen JHC, Callaghan TV, Alatalo JM *et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? Journal of Ecology, **89**, 984-994.

Crone EE, Ellis MM, Morris WF *et al.* (2013) Ability of Matrix Models to Explain the Past and Predict the Future of Plant Populations. Conservation Biology, **27**, 968-978.

Dalgleish HJ, Koons DN, Hooten MB, Moffet CA, Adler PB (2011) Climate influences the demography of three dominant sagebrush steppe plants. Ecology, **92**, 75-85.

De Frenne P, Graae BJ, Rodriguez-Sanchez F *et al.* (2013) Latitudinal gradients as natural laboratories to infer species' responses to temperature. Journal of Ecology, **101**, 784-795.

De Valpine P, Harte J (2001) Plant responses to experimental warming in a montane meadow. Ecology, **82**, 637-648.

Dunne JA, Saleska SR, Fischer ML, Harte J (2004) Integrating experimental and gradient methods in ecological climate change research. Ecology, **85**, 904-916.

Dunnett NP, Grime JP (1999) Competition as an amplifier of short-term vegetation responses to climate: an experimental test. Functional Ecology, **13**, 388-395.

Easterling MR, Ellner SP, Dixon PM (2000) Size-specific sensitivity: Applying a new structured population model. Ecology, **81**, 694-708.

Ehrlén J, Morris WF (2015) Predicting changes in the distribution and abundance of species under environmental change. Ecology Letters, **18**, 303-314.

Elmendorf SC, Henry GH, Hollister RD *et al.* (2015) Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proceedings of the National Academy of Sciences of the United States of America, **112**, 448-452.

Elmendorf SC, Henry GHR, Hollister RD *et al.* (2012a) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters, **15**, 164-175.

Elmendorf SC, Henry GHR, Hollister RD *et al.* (2012b) Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change, **2**, 453-457.

Evju M, Halvorsen R, Rydgren K, Austrheim G, Mysterud A (2010) Interactions between local climate and grazing determine the population dynamics of the small herb *Viola biflora*. Oecologia, **163**, 921-933.

Felde VA, Kapfer J, Grytnes J-A (2012) Upward shift in elevational plant species ranges in Sikkilsdalen, central Norway. Ecography, **35**, 922-932.

Fremstad E (1997) Vegetasjontyper i Norge. NINA Temahefte, **12**, 1-279.

Galloway LF, Etterson JR (2007) Transgenerational plasticity is adaptive in the wild. Science, **318**, 1134-1136.

Gaston KJ (2000) Global patterns in biodiversity. Nature, **405**, 220-227.

Gimenez-Benavides L, Escudero A, Iriondo JM (2007) Local adaptation enhances seedling recruitment along an altitudinal gradient in a high mountain Mediterranean plant. Annals of Botany, **99**, 723-734.

Gimenez-Benavides L, Escudero A, Iriondo JM (2008) What shapes the altitudinal range of a high mountain Mediterranean plant? Recruitment probabilities from ovule to seedling stage. Ecography, **31**, 731-740.

Gornish ES (2014) Demographic effects of warming, elevated soil nitrogen and thinning on the colonization of a perennial plant. Population Ecology, **56**, 645-656.

Gottfried M, Pauli H, Futschik A *et al.* (2012) Continent-wide response of mountain vegetation to climate change. Nature Climate Change, **2**, 111-115.

Graae BJ, Verheyen K, Kolb A *et al.* (2009) Germination requirements and seed mass of slow- and fast-colonizing temperate forest herbs along a latitudinal gradient. Ecoscience*,* **16**, 248-257.

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. Nature*,* **369**, 448-448.

Gremer JR, Sala A, Crone EE (2010) Disappearing plants: why they hide and how they return. Ecology*,* **91**, 3407-3413.

Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR (2008) Long-term resistance to simulated climate change in an infertile grassland. Proceedings of the National Academy of Sciences of the United States of America*,* **105**, 10028-10032.

Grime JP, Mason G, Curtis AV *et al.* (1981) A comparative study of germination characteristics in a local flora. Journal of Ecology*,* **69**, 1017-1059.

Halbritter AH, Alexander JM, Edwards PJ, Billeter R (2013) How comparable are species distributions along elevational and latitudinal climate gradients? Global Ecology and Biogeography*,* **22**, 1228-1237.

Hamre LN, Rydgren K, Halvorsen R (2010) The effects of mulching and abandonment on the viability of the perennial grassland species *Plantago lanceolata*. Plant Ecology*,* **211**, 147-158.

Harte J, Shaw R (1995) Shifting dominance within a montane vegetation community - results of a climate-warming experiment. Science*,* **267**, 876-880.

He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. Ecology Letters*,* **16**, 695-706.

Hill MO, Mountford JO, Roy DB, Bunce RGH (1999) Ellenberg's Indicator Values for British Plants.

Holzapfel C, Tielborger K, Parag HA, Kigel J, Sternberg M (2006) Annual plant-shrub interactions along an aridity gradient. Basic and Applied Ecology*,* **7**, 268-279.

Intergovernmental Panel on Climate Change (2014) Climate Change 2014: Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Summary for Policymakers.

Jensen K, Meyer C (2001) Effects of light competition and litter on the performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow. Plant Ecology*,* **155**, 169-181.

Johnsen O, Daehlen OG, Ostreng G, Skroppa T (2005a) Daylength and temperature during seed production interactively affect adaptive performance of *Picea abies* progenies. New Phytologist*,* **168**, 589-596.

Johnsen O, Fossdal CG, Nagy N, Molmann J, Daehlen OG, Skroppa T (2005b) Climatic adaptation in *Picea abies* progenies is affected by the temperature during zygotic embryogenesis and seed maturation. Plant Cell and Environment*,* **28**, 1090-1102.

Kapfer J, Virtanen R, Grytnes J-A (2012) Changes in arctic vegetation on Jan Mayen Island over 19 and 80 years. Journal of Vegetation Science*,* **23**, 771-781.

Kardol P, Campany CE, Souza L, Norby RJ, Weltzin JF, Classen AT (2010) Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. Global Change Biology*,* **16**, 2676-2687.

Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. Ecology Letters*,* **7**, 1225-1241.

Kikvidze Z, Pugnaire FI, Brooker RW, Choler P, Lortie CJ, Michalet R, Callaway RM (2005) Linking patterns and processes in alpine plant communities: A global study. Ecology*,* **86**, 1395-1400.

Klanderud K (2005) Climate change effects on species interactions in an alpine plant community. Journal of Ecology*,* **93**, 127-137.

Klanderud K, Birks HJB (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. Holocene, **13**, 1-6.

Körner C (2003) *Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems. ,* Berlin, Springer-Verlag.

Körner C (2007) The use of 'altitude' in ecological research. Trends in Ecology & Evolution, **22**, 569-574.

Larcher W (2003) *Physiological plant ecology,* Berlin, Springer.

Lenoir J, Gegout J-C, Guisan A *et al.* (2010) Cross-Scale Analysis of the Region Effect on Vascular Plant Species Diversity in Southern and Northern European Mountain Ranges. Plos One, **5**.

Lid J, Lid DT (2005) *Norsk flora,* Oslo, Det norske samlaget.

Luo Y, Gerten D, Le Maire G *et al.* (2008) Modeled interactive effects of precipitation, temperature, and CO^2 on ecosystem carbon and water dynamics in different climatic zones. Global Change Biology, **14**, 1986-1999.

Marrero-Gomez MV, Oostermeijer JGB, Carque-Alamo E, Banares-Baudet A (2007) Population viability of the narrow endemic *Helianthemum juliae* (CISTACEAE) in relation to climate variability. Biological Conservation, **136**, 552-562.

Meineri E, Skarpaas O, Spindelböck J, Bargmann T, Vandvik V (2014) Direct and size-dependent effects of climate on flowering performance in alpine and lowland herbaceous species. Journal of Vegetation Science, **25**, 275-286.

Meineri E, Skarpaas O, Vandvik V (2012) Modeling alpine plant distributions at the landscape scale: Do biotic interactions matter? Ecological Modelling, **231**, 1-10.

Merow C, Dahlgren JP, Metcalf CJE *et al.* (2014) Advancing population ecology with integral projection models: a practical guide. Methods in Ecology and Evolution, **5**, 99-110.

Metcalf CJE, Mcmahon SM, Salguero-Gomez R, Jongejans E (2013) IPMpack: an R package for integral projection models. Methods in Ecology and Evolution, **4**, 195-200.

Michalet R, Schoeb C, Lortie CJ, Brooker RW, Callaway RM (2014) Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change. Functional Ecology, **28**, 75-86.

Morris WF, Doak DF (2002) *Quantitative Conservation biology*, Sinauer.

Mossberg B, Stenberg L (2007) *Gyldendals store nordiske flora,* Stockholm, Gyldendal.

Nicolé F, Dahlgren JP, Vivat A, Till-Bottraud I, Ehrlén J (2011) Interdependent effects of habitat quality and climate on population growth of an endangered plant. Journal of Ecology, **99**, 1211-1218.

Økland RH (1997) Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. III. Six-year demographic variation in two areas. Lindbergia, **22**, 49-68.

Olsen SL, Klanderud K (2014) Biotic interactions limit species richness in an alpine plant community, especially under experimental warming. Oikos, **123**, 71-78.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics, **37**, 637-669.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature, **421**, 37-42.

Pauli H, Gottfried M, Dullinger S *et al.* (2012) Recent Plant Diversity Changes on Europe's Mountain Summits. Science, **336**, 353-355.

Pfeifer-Meister L, Bridgham SD, Little CJ, Reynolds LL, Goklany ME, Johnson BR (2013) Pushing the limit: experimental evidence of climate effects on plant range distributions. Ecology, **94**, 2131-2137.

Pugnaire FI, Luque MT (2001) Changes in plant interactions along a gradient of environmental stress. Oikos, **93**, 42-49.

Rustad LE (2008) The response of terrestrial ecosystems to global climate change: Towards an integrated approach. Science of the Total Environment, **404**, 222-235.

Salguero-Gomez R, Siewert W, Casper BB, Tielboerger K (2012) A demographic approach to study effects of climate change in desert plants. Philosophical Transactions of the Royal Society B-Biological Sciences, **367**, 3100-3114.

Schoeb C, Kammer PM, Kikvidze Z, Choler P, Von Felten S, Veit H (2010) Counterbalancing effects of competition for resources and facilitation against grazing in alpine snowbed communities. Oikos, **119**, 1571-1580.

Schuur EaG (2003) Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. Ecology, **84**, 1165-1170.

Shevtsova A, Graae BJ, Jochum T, Milbau A, Kockelbergh F, Beyens L, Nijs I (2009) Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. Global Change Biology, **15**, 2662-2680.

Shryock DF, Esque TC, Hughes L (2014) Population viability of *Pediocactus bradyi* (Cactaceae) in a changing climate. American Journal of Botany, **101**, 1944-1953.

Sletvold N, Dahlgren JP, Øien D-I, Moen A, Ehrlén J (2013) Climate warming alters effects of management on population viability of threatened species: results from a 30-year experimental study on a rare orchid. Global Change Biology, **19**, 2729-2738.

Soliveres S, Maestre FT (2014) Plant-plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies. Perspectives in Plant Ecology Evolution and Systematics, **16**, 154-163.

Souther S, Mcgraw JB (2011) Evidence of Local Adaptation in the Demographic Response of American Ginseng to Interannual Temperature Variation. Conservation Biology, **25**, 922-931.

Stokes KE, Bullock JM, Watkinson AR (2004) Population dynamics across a parapatric range boundary: *Ulex gallii* and *Ulex minor*. Journal of Ecology, **92**, 142-155.

Taiz L, Zeiger E (2002) *Plant Physiology,* Sunderland, USA, Sinauer Assiciates, Inc.

Tveito OE, Bjordal I, Skjelvag AO, Aune B (2005) A GIS-based agro-ecological decision system based on gridded climatology. Meteorological Applications, **12**, 57-68.

Tveito OE, Førland EJ, Heino R *et al.* (2000) Nordic temperature maps. No. 09/00. DNMI-klima.

Tveito OE, Førland EJ, Heino R *et al.* (2001) Nordic temperature maps. No.06/01. DNMI-klima.

Van Der Meer S, Dahlgren JP, Milden M, Ehrlén J (2014) Differential effects of abandonment on the demography of the grassland perennial *Succisa pratensis*. Population Ecology, **56**, 151-160.

Vandvik V (2004) Gap dynamics in perennial subalpine grasslands: trends and processes change during secondary succession. Journal of Ecology, **92**, 86-96.

Walck JL, Hidayati SN, Dixon KW, Thompson K, Poschlod P (2011) Climate change and plant regeneration from seed. Global Change Biology, **17**, 2145-2161.

Walker MD, Wahren CH, Hollister RD *et al.* (2006) Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America, **103**, 1342-1346.

Williams AL, Wills KE, Janes JK, Schoor JKV, Newton PCD, Hovenden MJ (2007) Warming and free-air CO2 enrichment alter demographics in four co-occurring grassland species. New Phytologist, **176**, 365-374.

Williams JL, Crone EE (2006) The impact of invasive grasses on the population growth of Anemone patens, a long-lived native forb. Ecology, **87**, 3200-3208.

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology, **17**, 927-942.

Appendix

“The blind men and the elephant” (1872) by John Godfrey Saxe:

It was six men of Indostan
To learning much inclined,
Who went to see the Elephant
(Though all of them were blind),
That each by observation
Might satisfy his mind.

The *First* approached the Elephant,
And happening to fall
Against his broad and sturdy side,
At once began to bawl:
"God bless me!—but the Elephant
Is very like a wall!"

The *Second*, feeling of the tusk,
Cried: "Ho!—what have we here
So very round and smooth and sharp?
To me 't is mighty clear
This wonder of an Elephant
Is very like a spear!"

The *Third* approached the animal,
And happening to take
The squirming trunk within his hands,
Thus boldly up and spake:
"I see, "quoth he, "the Elephant
Is very like a snake!"

The *Fourth* reached out his eager hand,
And felt about the knee.
"What most this wondrous beast is like
Is mighty plain, "quoth he;
"'T is clear enough the Elephant
Is very like a tree!"

The *Fifth*, who chanced to touch the ear,
Said: "E'en the blindest man
Can tell what this resembles most;
Deny the fact who can,
This marvel of an Elephant
Is very like a fan!"

The *Sixth* no sooner had begun
About the beast to grope,
Than, seizing on the swinging tail
That fell within his scope,
"I see, "quoth he, "the Elephant
Is very like a rope!"

And so these men of Indostan
Disputed loud and long,
Each in his own opinion
Exceeding stiff and strong,
Though each was partly in the right,
And all were in the wrong!

So, oft in theologic wars
The disputants, I ween,
Rail on in utter ignorance
Of what each other mean,
And prate about an Elephant
Not one of them has seen!