

# The neighborhood matters: warming and novel competitors alter flower production of alpine plants



Susanne Berthelsen

Master of Science in Biology – Biodiversity, Evolution and Ecology



Department of Biological Sciences  
University of Bergen

Spring 2022

© Susanne Berthelsen 2022

UiB Master's Thesis in Biology.

Submitted as a thesis in the course: 'BIO399 Master's Thesis in Biology', spring 2022, under the supervision of  
Joachim Paul Töpper | Norwegian Institute for Nature Research (NINA) | Department of Biological Sciences,  
University of Bergen  
Ragnhild Gya | Department of Biological Sciences & Bjerknes Centre for Climate Research, University of Bergen.

All rights reserved. No part of this thesis may be copied without the permission of the author.

Cover photo by Susanne Berthelsen  
Flowering plants at Gudmedalen, Flåm

## Acknowledgements

Firstly, I would like to extend an enormous thank you to my dedicated and talented supervisors, Joachim Paul Töpper and Ragnhild Gya. Thank you for all your valuable guidance and input throughout this year, from teaching me to identify my first grasses during fieldwork to showing me the ropes of Bayesian statistics, ordination analysis and population modelling – none of which I had done before. Thank you for sharing your knowledge with me. I am most grateful for all your support!

Thank you to the Between the Fjords research group for warmly welcoming me into your crew. I truly appreciated all your feedback on my project and my thesis, as well as all the educational scientific discussions. I would also like to thank the NINA Bergen team for your kind hospitality and for generously providing me with a permanent workspace this last year. This MSc project was funded by the NFR project INCLINE (RCN FriMedBio # 274712). A huge thanks to all the researchers, technicians, students and interns who have participated in the INCLINE fieldwork and data collection over the years. A special thanks to the landowners of the 'Vestland Climate Grid' sites for granting us permission to do research and collect data on their land.

## Abstract

Sexual reproduction, and the genetic variation it entails, could prove vital for plants' ability to persist under a changing climate. Climate warming is causing species to shift their ranges to higher elevations and latitudes. The assembly of novel species combinations after asynchronous migrations with climate may have implications for the flower production of alpine plants. Studying how novel competitors affect flowering performance under climate warming is important to understand potential impacts of climate change on alpine plant population persistence and range dynamics. To investigate this, I used an established field experiment along a natural precipitation gradient in the mountains of western Norway, where both temperature and competitive conditions in alpine vegetation were manipulated through open-top chambers and transplant experiments. Data on flower production of graminoids and forbs in alpine plant communities and demographic data on two focal alpine species, *Veronica alpina* and *Sibbaldia procumbens*, were collected in four alpine semi-natural grasslands. In this study, experimental warming and the presence of novel competitors triggered higher flower production for graminoids and forbs, respectively. Additionally, the graminoid flowering community shifted towards more flowering in Cyperaceae- and Juncaceae species and less in Poaceae species under warming. Furthermore, fecundity clearly contributed to changes in population growth rates ( $\Delta\lambda$ ) of both *V. alpina* and *S. procumbens* with warming and novel competitors. The population models revealed trade-offs in resource allocation between fecundity and vegetative growth and compensatory increases in fecundity with reduced survival. Thus, fecundity is strategically used in the ontogeny of alpine plant individuals. These findings suggest that genetic variation in alpine species will be preserved and that alpine plants may persist in alpine regions when influenced by the projected climate warming and range-expansion of lowland competitors, but also that the character of alpine grasslands may change towards more graminoid-dominant.

# Table of Contents

<b>1</b>	<b>Introduction</b> .....	1
<b>2</b>	<b>Methods</b> .....	6
2.1	Study sites.....	6
2.2	Study design .....	8
2.2.1	Selecting species for the transplant experiment.....	10
2.3	Data collection.....	11
2.4	Community data on flower production.....	11
2.5	Demography data on two target species .....	12
2.6	Data management.....	13
2.7	Data- and statistical analysis .....	14
<b>3</b>	<b>Results</b> .....	17
3.1	Flower production in alpine plant communities .....	17
3.1.1	Ordination-analysis of the alpine plant community.....	19
3.2	Population dynamics of two alpine species .....	20
<b>4</b>	<b>Discussion</b> .....	26
4.1	Effects of warming and novel competitors on flower production in alpine plant communities.....	26
4.2	Fecundity's role in the population dynamics of two focal alpine forbs .....	29
4.3	Context dependency related to precipitation regimes .....	31
4.4	Conclusions.....	33
<b>5</b>	<b>References</b> .....	34
<b>6</b>	<b>Appendix</b> .....	42

# 1 Introduction

A long-standing question in ecology, with ever-increasing relevance in the face of climate change, is how climate affects sexual reproduction and the dynamics of natural populations (Evers et al., 2021; Petry et al., 2016; Sutherland et al., 2013). The evolution and persistence of a plant population may be affected by whether the individuals reproduce sexually or asexually (Aerts et al., 2004; Callaghan & Jonasson, 1995). The genetic reorganization occurring through sexual reproduction enables species to adapt to new environments, which provides them with a survival advantage (Booy et al., 2000). Therefore, flowering is a key event for plant population persistence, dispersal and species range dynamics (Meineri et al., 2014). Flowering performance begets seed availability, which in turn begets seedling recruitment (Giménez-Benavides et al., 2008), enabling plants to spread to, and populate, new ground. Hence, sexual reproduction and the genetic variation it introduces into a population, may be vital for the plants' ability to persist under a changing climate.

Climate change has particularly pronounced impacts on plants, and their sexual reproduction, in environments vulnerable to warming, such as alpine zones (Dorji et al., 2020; Fazlioglu & Wan, 2021; Inouye et al., 2003; S. H. Schneider & Thomsson, 1981; Stephen H Schneider, 1975). Climate warming not only increases temperature, but also reduces soil moisture through evapotranspiration, which is a key factor affecting reproduction of plants (Crimmins et al., 2011; Körner, 2021; Wolkovich et al., 2012). Furthermore, warming is expected to alter the character of plant-plant interactions in alpine vegetation, where facilitative interactions between plants often dominate (Anthelme et al., 2014; Bertness & Callaway, 1994). Growing close to each other provides protection against low temperatures and loss of moisture, which exceeds the disadvantages of competition for light and nutrients, especially in alpine ecosystems (Körner, 2021; Larcher, 2003). Such biotic interactions can outweigh the direct effects of the abiotic environment, as facilitation can make plants persist in suboptimal habitats, whereas competition may prevent species from benefiting from seemingly favorable abiotic conditions (Choler et al., 2001). Climate warming is expected to release temperature stress and thereby shift the balance between competition and facilitation towards increased competition in alpine regions (Brooker, 2006; Fridley et al., 2016). Accordingly, several studies have reported increased competitiveness with increasing temperatures, both along climate gradients (Anthelme et al., 2014; Callaway

et al., 2002; Kikvidze et al., 2005; Olsen et al., 2016) and with experimental warming (Dunnett & Grime, 1999; Klanderud, 2005; Olsen & Klanderud, 2014). Elevated temperatures, and the increased competitiveness it entails, could have profound consequences for flower production of alpine species. Flower production has shown mixed responses to elevated temperatures, where some studies show increased flowering (Aerts et al., 2004; Arft et al., 1999; De Valpine & Harte, 2001) whereas others report a decrease in flower production with warming (De Valpine & Harte, 2001; Saavedra et al., 2003). Whether or not an alpine species' fecundity can benefit from warming may depend on its ability to compete with its neighbors (Alexander et al., 2015), which in turn may be linked to its functional plant life strategy (Funk & Wolf, 2016).

Disproportional increases of certain functional groups with climate warming are already evident in plant communities (Elmendorf et al., 2012; Hollister et al., 2005; Walker et al., 2006). In herbaceous plant communities, warmer or wetter conditions often lead to increased biomass or height (Huxman et al., 2004; Wang et al., 2019; Wu et al., 2011), resulting in increased competition for light, which in turn determines which species are able to persist in the community (Vandvik et al., 2020). Species within the same functional group (e.g., within forbs or graminoids) often exhibit similar traits or growth forms, and functional groups can be expected to respond differently to abiotic and biotic drivers (Arft et al., 1999). Graminoids are typically better competitors for light and nutrients than most forbs (Klanderud & Totland, 2005), and responses in flower production may differ between these functional groups. Graminoids have also been shown to strongly increase with warming (Elmendorf et al., 2012; Hollister et al., 2005; Walker et al., 2006), suggesting that climate warming may further increase graminoid dominance and thereby the intensity of competitive interactions experienced by co-occurring subordinate forbs. Not only can warming cause increased competition between already present plant species, but it may also cause species to expand their ranges (Steinbauer et al., 2018) – bringing novel competitors into alpine ecosystems.

In addition to changes in the autochthonous alpine community, climate warming is causing significant alterations in plant communities through range shifts to higher elevation and latitude (Gómez-Ruiz & Lacher Jr., 2019; He et al., 2019; Lesica & McCune, 2004). According to climate projections, western Norway will be experiencing higher temperatures and more

precipitation in the future (Walther et al., 2002), enabling species adapted to a warmer climate to extend their ranges to higher altitudes (Cahill et al., 2014; Grytnes et al., 2014; Klanderud & Birks, 2003; Lenoir & Svenning, 2015; Steinbauer et al., 2018). The assembly of novel species combinations after asynchronous migrations with climate could bring about dramatic impacts of community change (Blois et al., 2013; Urban et al., 2012; J. W. Williams et al., 2013), particularly if they introduce novel, resource-acquisitive features into their newly attained neighborhood (Alexander et al., 2015). Such range expansions entail novel interactions between species that have not previously co-occurred (Alexander et al., 2015). Novel competitors have been found to reduce survival and growth of certain alpine species, whereas their effect on flowering varies (Alexander et al., 2015). As flowering-responses may be species-specific, more knowledge on flower production for an extended number of species or for the alpine plant community as a whole is needed. Studying how novel competitors affect flowering performance under climate warming is important to understand potential impacts of climate change on plant population persistence and range dynamics.

Changes in the contribution of fecundity in regard to the population dynamics of alpine plants can have implications for population size, gene pool size, selection processes and spatial dynamics (Ehrlén & Morris, 2015; Pearson et al., 2014). By studying the role of fecundity in relation to other vital rates, demographic studies can provide insights on how well alpine plant populations safeguard genetic variation long-term (Forbis, 2003; Töpper et al., 2018). Recent studies show that plant population dynamics can be quite sensitive to natural climate fluctuations (Dalglish et al., 2011; Jongejans et al., 2010; Nicolè et al., 2011; Sletvold et al., 2013) and experimental warming (A. L. Williams et al., 2007). Vital rates can change in opposite directions in response to the same environmental condition across populations, a phenomenon known as 'demographic compensation' (Villellas et al., 2015). A comparison of fecundity-responses to other vital rates in a changing climate may reveal if potential increases in flowering were caused by a form of demographic compensation or as a result of positive effects on the population as a whole. Compensatory increases in sexual reproduction have been reported for trailing-edge populations (Sheth & Angert, 2018), suggesting that species may alter their responses to climate change. Nonetheless, reproductive responses of alpine plants to a changing climate may be context dependent.

Responses of plant communities or populations to climate change often depend on climatic context (Vandvik et al., 2020). Such context dependency makes it difficult to predict the consequences of a changing climate (Bertrand et al., 2016; Dickinson et al., 2014; Urban et al., 2016). Community or population dynamic responses to warming for instance, may be dependent on local precipitation levels (Vandvik et al., 2020). Accounting for precipitation regime may therefore be essential to predict species' responses to climate change accurately. Several studies have investigated floral traits in dry environments experiencing drought stress (Galen et al., 1999; Lambrecht & Dawson, 2007; Xie et al., 2016), yet the impact of high levels of precipitation on plant reproduction has received less attention thus far.

In this study, I will look into the influence of warming and novel competitors on flower production in alpine plant communities, as well as their effects on fecundity's contribution to the population dynamics of two selected alpine forb species. To quantify the effects of warming and novel competitors on flowering in alpine plants, I used an established field experiment along a natural precipitation gradient in the mountains of western Norway. In this climate change field experiment both temperature and competitive conditions in alpine vegetation were manipulated by using open-top chambers and transplant experiments. To simulate novel species colonizing alpine plant communities, lowland species with functional traits that are novel to the alpine vegetation were transplanted into alpine semi-natural grasslands. This creates interactions between species that have not co-occurred previously, and allows me to investigate the climate-driven colonization effects on sexual reproduction of the alpine plants. The study sites' varying precipitation regimes enable me to study context-dependency of the plants' responses to climate change. In addition, I examine potential differences in responses between the dominant functional plant groups of the alpine grasslands I surveyed; forbs and graminoids. In this study, I will investigate the following questions:

**Q1.** How does warming and novel competitors, alone and in concert, affect flower production in alpine species?

**Q2.** Are responses in flower production to warming and novel competitors different between functional plant groups?

**Q3.** How important is fecundity compared to other vital rates in the population dynamics of selected alpine forb species?

**Q4.** Do community- and population level reproductive responses to warming and novel competitors vary systematically with precipitation context?

## 2 Methods

### 2.1 Study sites

To study how sexual reproduction of alpine plants will be affected by global warming and increasing pressures from competitive lowland species under various precipitation regimes, a field experiment in the existing ‘Vestland Climate Grid’ located in western Norway was established (Between the Fjords, 2022; Klanderud et al., 2015). The experiment takes place in the climate grid’s four alpine sites, namely Ulvehaugen, Låvisdalen, Gudmedalen and Skjellingahaugen (Table 1). These four alpine locations have a mean growing season temperature of about 7 °C (mean of the four warmest months). As the sites are situated from the continental east to the oceanic west in the fjord landscape of western Norway, their geographical distribution creates a natural precipitation gradient where precipitation levels increase from east to west (Klanderud et al., 2015). The precipitation gradient has four levels, with mean annual precipitation of 1226, 1561, 2130 and 3402 mm for Ulvehaugen, Låvisdalen, Gudmedalen and Skjellingahaugen, respectively (Figure 1).

*Table 1: Overview of information about each of the four alpine study sites in the 'Vestland Climate Grid', including longitude, latitude, altitude (meters above sea level), mean annual precipitation and mean temperature of the four warmest months for each site.*

<b>Site</b>	<b>Longitude</b>	<b>Latitude</b>	<b>Altitude (m a.s.l.)</b>	<b>Precipitation (mm/year)</b>	<b>Temperature (°C)</b>
<b>Uelvehaugen</b>	61.0243	8.12343	1208	1226	6.93
<b>Låvisdalen</b>	60.8231	7.27596	1097	1561	7.15
<b>Gudmedalen</b>	60.8328	7.17561	1213	2130	6.53
<b>Skjellingahaugen</b>	60.9335	6.41504	1088	3402	7.21

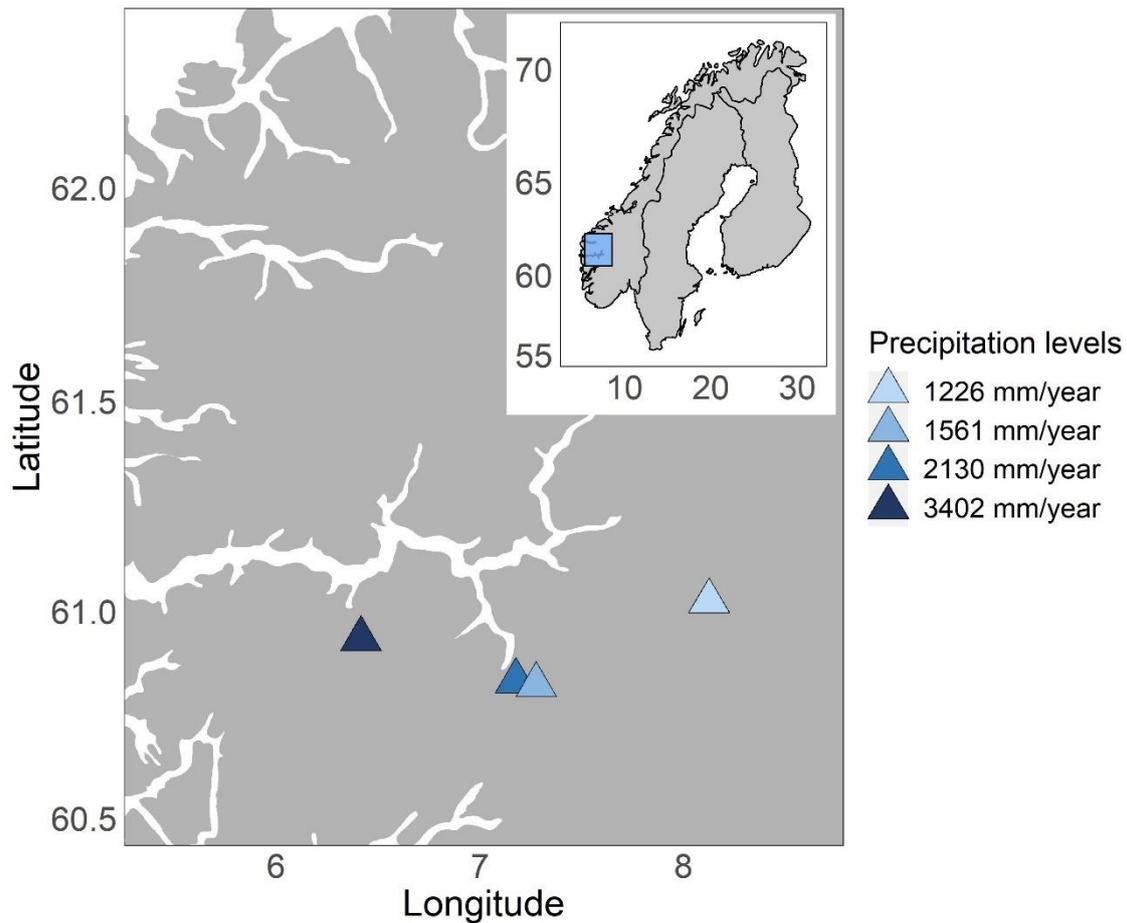


Figure 1: Map of the study area in western Norway, showing the geographical location of the four alpine sites along a natural precipitation gradient. The more blue-saturation the site-triangles have, the more annual precipitation the site receives. The four alpine sites are, from east to west: Ulvehaugen (1226 mm/year), Låvisdalen (1561 mm/year), Gudmedalen (2130 mm/year) and Skjellingahaugen (3402 mm/year).

To facilitate comparisons between sites, the sites were selected to be as similar as possible with respect to all factors other than precipitation. All the sites are moderately grazed grasslands associated with calcareous bedrock, with south-west exposed slopes of circa twenty degrees inclination (Klanderud et al., 2015). The plant communities are within the sociological association *Potentillo-Festucetum ovinae*, but tends towards *Potentillo-Polygonium vivipari* (Fremstad, 1997; Klanderud et al., 2015). In terms of ecosystem typology after the NiN-system (Halvorsen & medarbeidere og samarbeidspartnere, 2016), the sites are semi-natural grasslands with a tendency towards alpine grasslands of snowbed and leeside type (Gya, 2017). Additionally, all sites are fenced in during the summer to prevent animal disturbance.

## 2.2 Study design

In the field experiment, we manipulate both temperature and competitive conditions in alpine vegetation, by using open-top chambers (OTCs) and lowland colonizer transplants. Inside the OTCs we are able to increase the temperature by approximately 2 °C on average. The OTCs were designed according to the hexagon standard shape with an inner diameter of 1.5 meters, described in the ITEX protocol (Marion, 1996). Annually, the OTCs were installed 1-3 weeks after snowmelt (around mid-June) and were taken down after the growing season and before first autumn snowfall (October) to avoid damage in the winter months. To simulate novel species colonizing upland plant communities, lowland species, namely *Succisa pratensis*, *Carex pallescens* and *Hypericum maculatum*, were transplanted into the four alpine sites (see separate section on “Selecting species for the transplant experiment”). Transplanting lowland species into the experimental plots creates interactions between species that have not co-occurred previously. In the control plots without lowland colonizers, we transplanted alpine species that already exist in the alpine vegetation to keep plot manipulation itself equal between treatments.

In essence, the individuals within the experimental plots either have to manage with the alpine sites' extant temperature or they receive warming within the OTCs (Figure 2). Within both of these climates (extant and warmer) there are colonization-treatments and controls. In the colonization treatments, species from lower altitudes had been transplanted into the alpine vegetation in 2018. These lowland species exhibit traits that are different from, or novel to, the alpine species' traits. Thus, we end up with four different treatments: 1) a control treatment, with extant temperature and the existing alpine vegetation (CC), 2) extant temperature and transplanted lowland species with novel traits (CN), 3) warming and the existing alpine vegetation (WC), and 4) warming and transplanted lowland species with novel traits (WN).

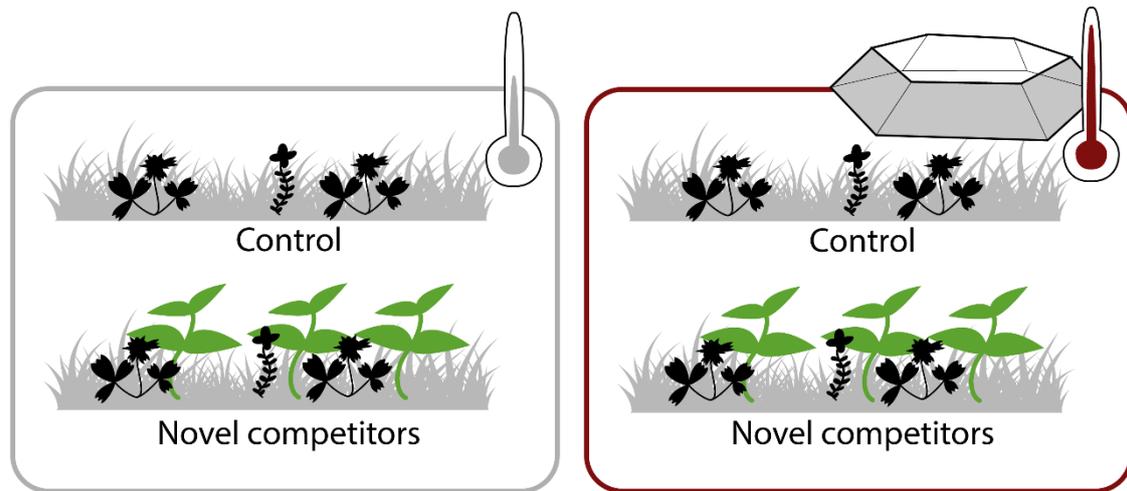


Figure 2: Schematic illustration of the experimental design of this study. To simulate novel competitors colonizing alpine plant communities, sub-alpine species were transplanted into the alpine vegetation. The transplant treatment was replicated with (red square) and without (grey square) experimental warming using open-top chambers.

The lowland transplants originate from the sub-alpine sites of the Vestland Climate Grid (Gya et al., in prep; Klanderud et al., 2015), with the exception of *Succisa pratensis* which was collected from Bolstadøyri – a location outside of the climate grid (Gya et al., in prep; Sjøgaard, 2020). Individuals from sub-alpine elevation are most likely to migrate into the alpine regions in the near future due to their geographical proximity, and sub-alpine individuals were therefore chosen for the transplant experiment. Thus, the transplants (except *S. pratensis*) were moved from sites with a mean growing season temperature of 9.5 °C to the alpine sites with a mean temperature of about 7 °C. Preferably, individuals from the corresponding precipitation level were chosen as transplants. If this was not possible, individuals from the closest precipitation level were used to avoid transplanting individuals into a very different precipitation regime than they were adapted to. The transplanting took place at the end of the growing season in 2018, from late August to mid-September. Thus, the transplanted individuals were already in the senescing stage of their annual life cycle, and would first experience the new environment the next growing season. At the end of the field season in 2019, 90% of the transplanted individuals had survived the winter, whereas the 10% that had died from the transplanting were replaced with new ones. In accordance with the method of Alexander et al. (2015), the individuals that died after this point were not replaced.

Six lowland colonizers were transplanted into each experimental plot – two of each of the transplant species, *Succisa pratensis*, *Carex pallescens* and *Hypericum maculatum*, per plot. To enable an even distribution of the transplants within the experimental plots, the plots were divided into 35 5x5 subplots (Figure 3). Hence, the whole experimental plot measures 35x25 cm.



Figure 3: Permanently marked experimental plot at Skjellingahaugen. The plots are 35 x 25 cm, and are divided into 35 equally sized subplots of 5 x 5 cm. The subplots marked in red are the subplots where transplanting takes place. In these subplots we either transplant already present alpine species for control plots or transplant novel lowland competitors into the plots receiving transplant treatment. This plot has received novel transplants: from the left we have *Succisa pratensis*, *Carex pallescens* and *Hypericum maculatum*. Photo: Ragnhild Gya.

### 2.2.1 Selecting species for the transplant experiment

The selection of species was based on several vegetative traits, providing information about various aspects of plant strategies (Hulme & Bernard-Verdier, 2018; Kraft et al., 2015).

Functional traits such as vegetative height, specific leaf area (SLA) and leaf area are indicators of light interception or growth rate, which are considered important for competitive ability of species (Van Kleunen et al., 2010). The lowland species selected for the

transplant experiment differed from the alpine communities' trait range on at least two of the three traits (Table 2).

Table 2: A comparison of the range of trait values for the alpine plant species and the trait values of the selected lowland species. These lowland species have traits that are different from, or novel to, the alpine plant community.

	Species	Vegetative height (mm)	SLA (cm <sup>2</sup> /g)	Leaf area (cm <sup>2</sup> )
Alpine	Alpine species range (mean + SD)	73.3 +/- 37.5	242.0 +/- 94.3	2.22 +/- 1.35
	<i>Sibbaldia procumbens</i>	47.5	191.1	2.55
	<i>Veronica alpina</i>	101.9	228.3	0.76
Novel	<i>Succisa pratensis</i>	166.0	192.0	14.5
	<i>Carex pallescens</i>	249.0	288.0	4.63
	<i>Hypericum maculatum</i>	260.0	285.5	2.81

### 2.3 Data collection

Vegetation sampling was conducted in 35 x 25 cm plots randomly positioned within five blocks at each of the four alpine sites (Figure 3). All blocks are situated in the selected grassland where they cover a total area of ca. 75-200 m<sup>2</sup> (Klanderud et al., 2015). Each experimental plot is divided into 35 equally sized subplots of 5 x 5 cm. To enable yearly monitoring of the vegetation at the exact same spots, the plots are permanently marked.

Both community- and demography data was collected during the peak growing season, between 26<sup>th</sup> of July and 20<sup>th</sup> of August 2021. Moreover, demography data has been collected for a period of four years by the INCLINE research team. Thus, we have additional demography data from 2018, 2019 and 2020 as well (Gya et al., in prep).

### 2.4 Community data on flower production

In the field, I collected data on flower production in the whole alpine plant community, to investigate whether flower production changes when exposed to warming and novel competitors. I registered the flower abundance for all flowering individuals of alpine species in the plant community within the experimental plots. Per site, data were collected in three replicate plots from each of the four treatments – 12 plots in total per site.

Flower production was measured differently for the various species (Appendix), depending on inflorescence type. For most species I simply counted (a) number of flowers, buds, and

capsules, whereas I used the measures (b) number of flower heads for species in the Asteraceae family, (c) percent cover of the inflorescences for species belonging to the genus *Alchemilla*, (d) number of flowering individuals for *Euphrasia sp.*, (e) length of the inflorescence for Poaceae- and Polygonaceae-family members, and (f) number of reproductive inflorescence units, or spikelets, for species in the genus *Carex* and *Luzula*. When measuring length of the inflorescence for grasses and similar species, the inflorescence was stretched before using a ruler to measure its length in millimeters. Counts and measurements were collected for all flowering species per subplot.

## 2.5 Demography data on two target species

To examine the role of reproduction versus other vital rates in the population dynamics of alpine plant species, I used demographic data for two selected alpine species, namely *Sibbaldia procumbens* and *Veronica alpina*, collected annually by the INCLINE project in the period 2018-2020 and in 2021 including myself. Both target species are perennial, clonal and produce lateral rhizomes on the same genet. Each rhizome can have multiple flowering shoots or ramets. As determining the complete branching structure of a genet was not possible without destructive sampling of the plants, we used ramets as our working unit. All ramets of the two target species within each plot were tagged.

All the targeted ramets in the experimental plots were monitored once a year in the peak growing season, where we registered survival, reproduction, clonality and biomass-related measures for each ramet. To monitor growth and quantify fecundity we measured a selected set of vegetative traits needed for nondestructive biomass estimation, and counted the number of floral buds, flowers and capsules. To quantify survival, growth and fecundity we subsequently continued with these measurements in the following years, by recording survival of old ramets, tagging new ramets and seedlings, and measuring vegetative traits on all live ramets, juveniles and seedlings. For *S. procumbens* the measured vegetative traits were leaf stalk length of longest leaf, number of leaves and length of biggest leaf. We also counted the number of flower stems for this species. For *V. alpina* we measured shoot height, number of leaves, as well as length and width of the biggest leaf.

For the two alpine target species it is not possible to determine how ramets are connected without digging them out. Therefore, we visually assessed potential above- or belowground connections to determine whether ramets belonged to the same genet. If we were unable to sense the genets branching structure, we assigned new clones to the closest potential parent ramet. Furthermore, both species exhibit prolonged vegetative dormancy. Although ramets can resprout after being dormant (Spindelböck & Olsen, 2013), we regarded all newly emerged ramets as new clonal offspring and disappearing ramets as dead. This simplification of the life cycle may underestimate survival and overestimate clonal reproduction (Olsen et al., 2016), but it was not possible to separate ramets returning from dormancy and newly produced clonal offspring, or ramets going dormant and dead ramets, within the timeframe of this study.

## 2.6 Data management

The original community flowering data were used directly and untransformed in the regression analysis assessing the abundance of flowers per subplot (see separate section on “Data- and statistical analysis”). For ordination analysis and for visual representations, however, the different flower-measurements needed to be standardized to facilitate comparisons between experimental treatments and precipitation levels. By species-wise subtracting the total mean of all flower measurements (across treatments and sites for the respective species) from each of the species’ individual measurement-values and dividing by the same total mean, I thus generated a unit-less ‘flower production index’. Thus, all the flower measurements are on the same scale. However, differences in total abundance of flowers between species can no longer be compared, but the standardization enables comparisons of flower abundance between experimental treatments or precipitation regimes.

Furthermore, each registered species was assigned to a functional group – forbs, graminoids, dwarf shrubs, lycophytes or ferns. Due to data deficiency in some groups, only the most abundant, flower-producing groups were selected for analysis; forbs and graminoids. In total, I made 1384 flower-registrations for 49 species of forbs and graminoids.

## 2.7 Data- and statistical analysis

To assess how flower production in alpine plant communities changes under the influence of warming and range-expanding species, and if any such effects vary with precipitation and functional group, I used regression models based on 'Integrated Nested Laplace Approximation' (INLA), a deterministic Bayesian method (Gómez-Rubio, 2020). The fixed effects part of the model was specified with flower abundance as response, and with warming, lowland transplants, functional group and precipitation regime as explanatory variables. Flowering abundance includes four different count data, as well as length- and percent cover measurements (Table 3). Hence, the data follow different distributions, where the four count variables are Poisson distributed, and length- and percent data are gamma- and beta-distributed, respectively. INLA allows variables from several different distributions to be combined in a multivariate response, modeling each with a different likelihood and link function (Table 3). To account for the study's nested design, 'Block ID' was specified as a random intercept effect. Although the flowering variable 'percent cover' principally is beta-distributed, I used a gamma distribution as an approximation in the model to allow specifying log-link as a common link function for all response variables (beta does not support log-link). As the highest registered value for percent cover was 0.25, and thus far below 1, a gamma distribution with log-link is highly unlikely to yield any noteworthy probabilities for values close to or even above 1, and thus represents a valid approximation for this variable. Overdispersion in the INLA-model was accounted for by extending an error structure with an observation-level random effect (Maindonald & Braun, 2010). Furthermore, Bayesian models, such as the INLA-model used in this study, do not operate with a significance level, and do not provide any p-values. Instead, the model output may be interpreted through the assigned probabilities estimated for each parameter in the model.

*Table 3: Overview of all the flower production measurement types used in the analysis of the community data. The measurement types' corresponding distributions and link-functions are listed, as well as number of registrations per measurement type. See Appendix for information about which species belong to which measurement type. \*The percent cover measurements are principally beta-distributed, yet I used gamma distribution as an approximation for this measurement type (see section "Data analysis and statistical analysis" for explanation).*

Measurement type	Distribution	Link-function	Registrations
Number of reproductive organs (flowers, buds, capsules)	Poisson	log-link	412
Number of flower heads	Poisson	log-link	100

Number of flowering individuals	Poisson	log-link	244
Number of reproductive inflorescence units (spikelets)	Poisson	log-link	151
Length of inflorescence	Gamma	log-link	448
Percent cover of the inflorescence	Gamma*	logit-link	29

Furthermore, to investigate whether the flowering community composition varied between experimental treatments, as well as various precipitation regimes, I performed an ordination analysis using non-metric multidimensional scaling (NMDS), applying a stress-value requirement  $<0.2$  to find the sufficient number of dimensions. The NMDS-ordination was based on occurrence of flowering species and the standardized abundance of flowers for each species. Potential grouping patterns in flowering species and their flower abundance with regard to treatment may reveal which species respond more strongly to warming or the presence of novel competitors.

The demography data collected for *S. procumbens* and *V. alpina* were used to build Integral Projection Models (IPMs), a population modelling method (Merow et al., 2014). The population models were built in collaboration with Ragnhild Gya, who was in charge of data curation and formal analysis of the demography data, whereas I assisted in both the aforementioned processes. The IPMs were used to uncover the role of sexual reproduction in the population dynamics of the two focal species under warming and in the presence of novel lowland colonizers. IPMs are based on vital rate regressions (growth, survival, fecundity and clonality as a function of plant size) and allow a mechanistic analysis of the impacts of warming, transplants, and precipitation context on populations of the two alpine target species (Merow et al., 2014). For detailed methodology regarding the vital rate regressions and population matrices used in this study, see Gya... Berthelsen... et al. (in prep)<sup>1</sup>. Fecundity in the IPMs involves multiple processes; production of flowers and seeds, number of seeds entering the seedbank, number of germinating seeds, germination success and size of seedlings. We built IPMs for each species and treatment. From these IPMs, we calculated (i) population growth rates ( $\lambda$ ), as well as (ii) vital rate contributions to the differences in  $\lambda$  between the experimental treatments (warming and transplants) and their

<sup>1</sup> This article is an unpublished draft which will be forwarded to the sensors.

respective controls through separate one-way life table response experiments (LTRE) for each treatment.

All analyzes were conducted in R version 4.1.3 (R Core Team, 2022) and RStudio version 2022.2.1.461 (RStudio Team, 2022), using the packages INLA for flower production analysis (Lindgren & Rue, 2015), vegan for ordinations (Oksanen et al., 2020) and IPMPack for population models (Metcalf et al., 2013).

### 3 Results

#### 3.1 Flower production in alpine plant communities

Warming and the presence of novel colonizers led to a change in flower production in the alpine plant community. Forbs and graminoids showed opposing responses to elevated temperatures and novel competitors. Warming had a positive effect on flower production of graminoids, whereas novel competitors led to increased flowering for forbs. Hence, responses in flower production to warming and novel competitors were different between functional plant groups, but I found no systematic patterns for flower production under different precipitation regimes. Here I present flower abundance results as number of flowers, based on the INLA regression models' standardization.

For forbs, I found a slight negative effect of warming and a clear positive effect of novel competitors, with probabilities of 80% and 98%, respectively (Table 4). The positive effect of the presence of novel competitors on flower production resulted in the highest mean number of flowers per treatment for forbs in this study, with 2.9 flowers per subplot (Table 5) – an increase of 1.1 flowers compared to the extant climate control. There was no interaction between warming and novel competitors for forbs (62% probability), indicating that the positive effect of novel competitors on flower production also applies under warming. Accordingly, alpine forbs that receive warming produced 1.1 more flowers per subplot when interacting with novel competitors rather than the existing alpine vegetation.

Graminoids produced more flowers than forbs (100% probability), and this difference became even greater under warming. Warming of the alpine vegetation had a clear positive effect on flower production in graminoids (98% probability), and resulted in this study's highest mean number of flowers produced in a treatment (4.4 flowers per subplot). The interaction between novel competitors and graminoids was negative (95% probability), but had the same effect size as the positive effect of novel competitors for forbs. Thus, there was no net effect of novel competitors on graminoids. Further, the interaction between warming and novel competitors for graminoids was weak with a mere probability of 76%. Thus, the positive warming effect remains for graminoids when exposed to both warming and novel competitors.

Table 4: Estimated means and standard deviations for the parameters from the INLA-model, and the parameters' respective probabilities. Additional information regarding each of the proxies is also included. INLA allows variables from several different distributions to be combined in a multivariate response, modeling each with a different likelihood and link function. The measurement types used to estimate flower production were number of flowers, number of flower heads, number of flowering individuals, number of reproductive inflorescence units (spikelets), length of inflorescence and percent cover of inflorescence. In this table, the treatment parameters reflect number of flowers, whereas the scaling parameters are the model estimates for converting treatment parameters to make predictions for the other measurement types.

<b>Treatment parameters (for number of flowers)</b>	<b>Mean</b>	<b>Standard deviation</b>	<b>Probability</b>
(Intercept)	0.959	0.083	100%
Warming	-0.028	0.090	80%
Novel	0.115	0.081	98%
Warming:Novel	-0.009	0.119	62%
Graminoids	0.350	0.097	100%
Warming:Graminoids	0.194	0.133	98%
Novel:Graminoids	-0.116	0.120	95%
Warming:Novel:Graminoids	-0.042	0.182	76%
<b>Scaling parameters for flower abundance proxies</b>			
Proxy: Flower heads	-0.460	0.110	-
Proxy: Flowering individuals	-0.245	0.077	-
Proxy: Spikelets	-0.204	0.105	-
Proxy: Inflorescence length	2.647	0.067	-
Proxy: Percent cover	-3.275	0.137	-

Table 5: Estimated flower abundance per subplot for forbs and graminoids in the experimental treatments, based on the INLA-model output. Flower abundances were calculated for each measurement type; number of flowers, number of flower heads, number of flowering individuals, number of reproductive inflorescence units (spikelets), length of inflorescence and percent cover of inflorescence. Differences between treatments cannot be calculated directly, as these flower abundance values were calculated on log-scale and back-transformed.

<b>Treatment</b>	<b>Functional group</b>	<b>Flower count</b>	<b>Flower head count</b>	<b>Flowering individuals</b>	<b>Reproductive spikelets</b>	<b>Length of inflorescence (mm)</b>	<b>Percent cover</b>
CC	Forbs	2.6	1.7	2.0	2.1	37	10%
WC	Forbs	2.5	1.6	2.0	2.1	36	10%
CN	Forbs	2.9	1.9	2.3	2.4	41	11%
WN	Forbs	2.8	1.8	2.2	2.3	40	11%
CC	Graminoids	3.7	2.3	2.9	3.0	52	14%
WC	Graminoids	4.4	2.8	3.4	3.6	62	17%
CN	Graminoids	3.7	2.3	2.9	3.0	52	14%
WN	Graminoids	4.2	2.6	3.3	3.4	59	16%

### 3.1.1 Ordination-analysis of the alpine plant community

The NMDS ordination required three dimensions to achieve an acceptable stress value of 0.186. Composition of the alpine flowering community varied across sites and treatments. The flowering community composition differed mainly between sites along the first NMDS-dimension (Figure 4a), but not in a systematic way along the precipitation gradient. Yet flowering community composition did differentiate the two wettest sites and the two driest sites to some degree. A larger proportion of the variation along the second NDMS-dimension was related to flowering community composition of Skjellingahaugen (3402 mm/year) than other sites. The difference in flowering for plots at Skjellingahaugen could be attributed to close association with snowbed species such as *Gentiana nivalis*, *Thalictrum alpinum* and *Juncus trifidus* amongst others. Låvisdalen (1561 mm/year) however, was more closely associated with grasses like *Agrostis mertensii*, *Avenella flexuosa* and *Phleum alpinum*.

Within sites, the flowering community composition also varied between treatments in three of the four sites (Figure 4b-d). The ordination-plots of community composition at Ulvehaugen, Låvisdalen and Gudmedalen reveal a shift in multivariate space in the flowering community from extant alpine climate plots to warmed plots (irrespective of novel competitors). Hence, the flowering community composition associated with warmed plots differed from that of the non-warmed plots for these three alpine sites. For Skjellingahaugen (Figure 4e), the flowering community was similar across experimental treatments.

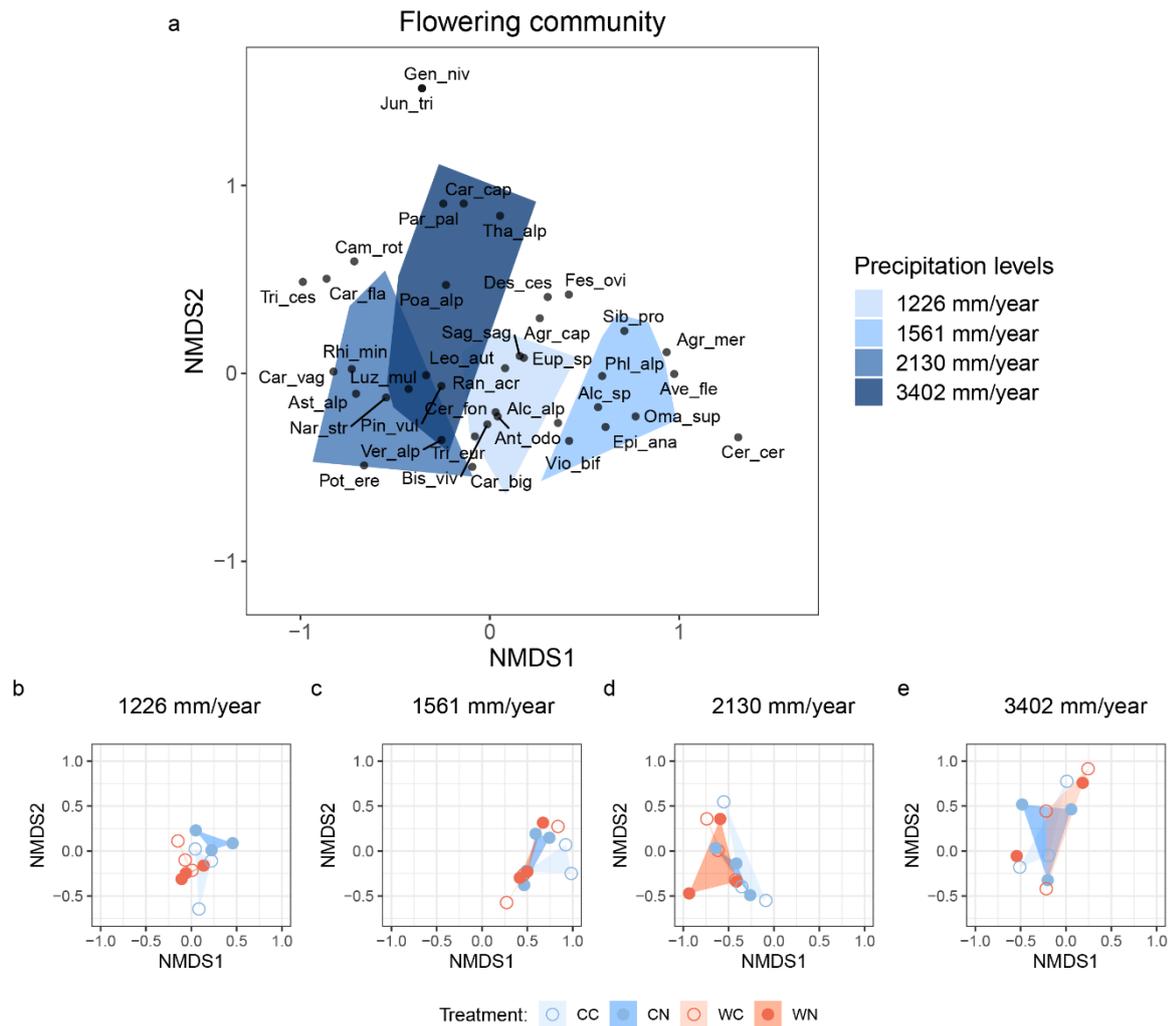


Figure 4: NMDS ordination of the flowering community composition for (a) the four alpine sites, and (b-e) the experimental treatments at each of the study sites, namely Ulvehaugen (1226 mm/year), Låvisdalen (1561 mm/year), Gudmedalen (2130 mm/year) and Skjellingahaugen (3402 mm/year). The ordination was based on abundance of flowers. These plots are two-dimensional projections of the three-dimensional NMDS ordination with a stress value of 0.186. In panel (e) the third WN-plot is hidden behind the lower WN-plot in the third dimension.

### 3.2 Population dynamics of two alpine species

Overall, the population growth rates ( $\lambda$ ) revealed that populations of *Veronica alpina* and *Sibbaldia procumbens* were generally stable or increasing across treatments and precipitation levels (Table 6 and 7). For *V. alpina*, mean  $\lambda$ -values increased for all treatments compared to the extant climate controls (Table 6). Populations of *S. procumbens* were stable when exposed to warming and novel competitors alone, as well as in the extant climate controls. However, we found slightly decreasing populations of *S. procumbens* when the individuals interacted with novel competitors under warming (Table 7).

Table 6: Population growth rates ( $\lambda$ ), and mean  $\lambda$ 's, for *Veronica alpina* in the experimental treatments across three precipitation levels. The lambdas are derived from the 'Integral Projection Models' which are based on size- and precipitation-dependent vital rates (survival, growth, clonality and fecundity).

Population growth rates ( $\lambda$ )				
	1.2 m/year	2.3 m/year	3.4 m/year	Mean
<b>Control (CC)</b>	1.03	1.12	1.01	1.05
<b>Novel (CN)</b>	1.37	1.02	1.00	1.13
<b>Warm control (WC)</b>	1.22	1.12	1.17	1.17
<b>Warm novel (WN)</b>	1.17	1.21	1.21	1.20

Table 7: Population growth rates ( $\lambda$ ), and mean  $\lambda$ 's, for *Sibbaldia procumbens* in the experimental treatments across three precipitation levels. The lambdas are derived from the 'Integral Projection Models' which are based on size- and precipitation-dependent vital rates (survival, growth, clonality and fecundity). Only one lambda-value is presented for models where the vital rates were not precipitation-dependent.

Population growth rates ( $\lambda$ )				
	1.2 m/year	2.3 m/year	3.4 m/year	Mean
<b>Control (CC)</b>		1.04		1.04
<b>Novel (CN)</b>	1.02	1.10	1.03	1.05
<b>Warm control (WC)</b>	1.04	1.03	1.02	1.03
<b>Warm novel (WN)</b>		0.97		0.97

Fecundity clearly contributed to changes in population growth rates ( $\Delta\lambda$ ) of both *V. alpina* and *S. procumbens*. The one-way life table response experiments (LTRE) revealed differences in the direction and proportion of fecundity's contribution to the differences in  $\lambda$  between the experimental treatments (warming and novel competitors) and their respective controls for both focal alpine species (Figure 5 and 6). Fecundity's contribution to  $\Delta\lambda$  between controls and treatments were greater in value for *V. alpina* than for *S. procumbens*.

For *Veronica alpina*, fecundity had a weak negative contribution to  $\Delta\lambda$  with warming (Figure 5a, WC – CC). Contrary to warming alone, fecundity contributed positively to  $\Delta\lambda$  in the presence of novel competitors (CN – CC), as well as for novel competitors under warming (both WN comparisons). Further, contributions of fecundity to  $\Delta\lambda$  in *V. alpina* also showed variation between precipitation levels, both in terms of the direction and extent (Figure 5b). Under warming fecundity contributions followed a unimodal pattern, influencing  $\Delta\lambda$

positively in the mid-precipitation level and negatively in the driest and wettest sites. When exposed to the novel competitors, fecundity of *V. alpina* largely contributed positively to changes in  $\lambda$  in the dry site, whereas towards the wetter sites this contribution shrank to a bare minimum and negatively affected population growth rates. However, for both the warmed transplant treatments (compared to warmed climate (WC) and extant climate (CC)) the pattern was switched. Here, fecundity negatively influenced  $\Delta\lambda$  in the dry site, but contributed positively to  $\Delta\lambda$  in the wetter sites. Fecundity and growth or survival frequently pulled  $\Delta\lambda$  in opposite directions (Figure 5). Negative influences of growth or survival on  $\Delta\lambda$  was often accompanied by a largely positive influence of fecundity.

## *Veronica alpina*

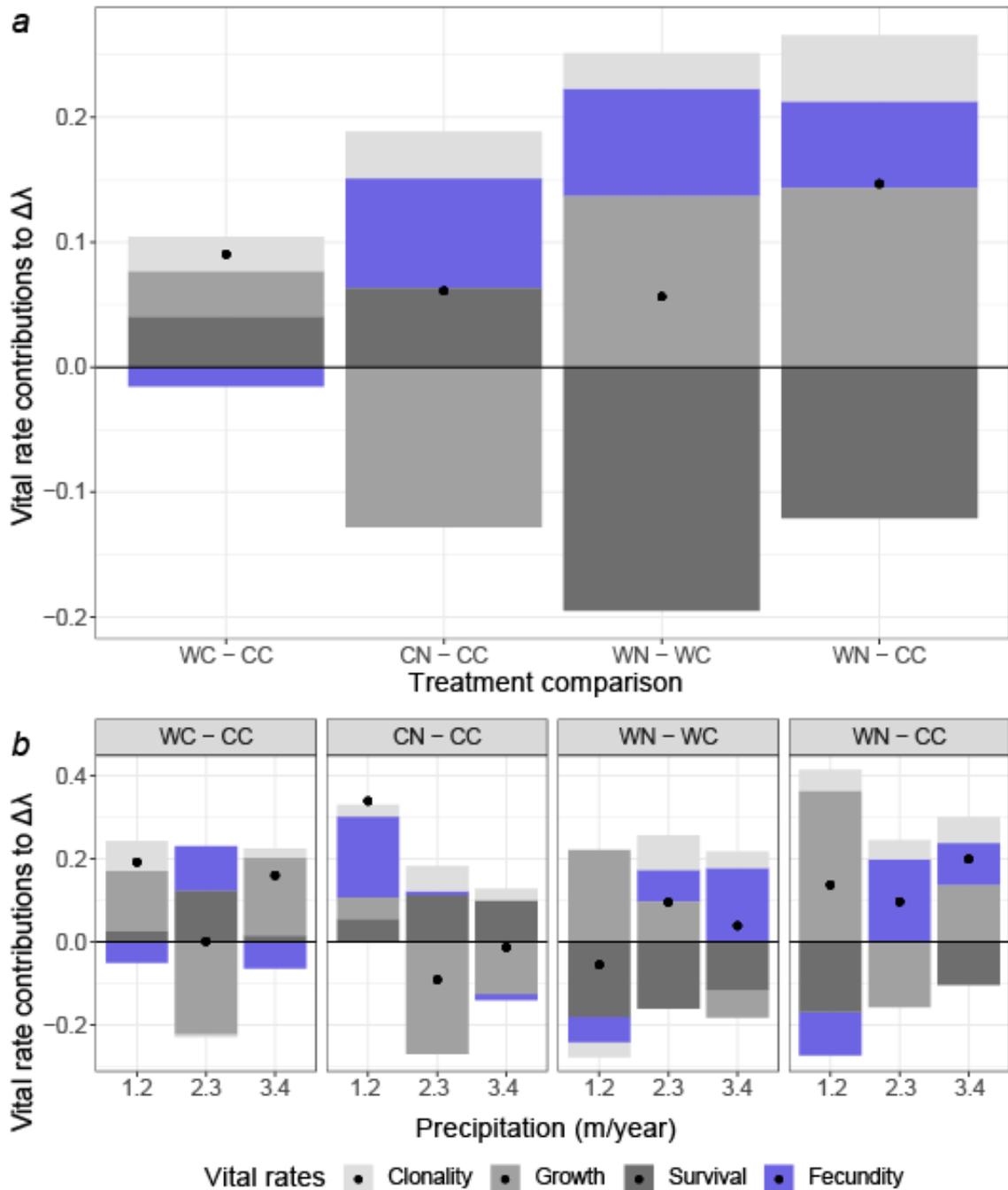


Figure 5: Vital rate contributions for *Veronica alpina* to the differences in  $\lambda$  between the experimental treatments (warming and novel colonizers) and their respective controls, calculated through separate one-way life table response experiments (LTRE) for each treatment. Shown are (a) mean vital rate contributions to  $\Delta\lambda$  across precipitation levels, for all treatments, and (b) vital rate contributions to  $\Delta\lambda$  between precipitation levels, for all treatments. The fecundity of *V. alpina* is highlighted in blue. The treatment-abbreviations translate to; CC = extant climate control, WC = warming control, CN = extant climate with novel colonizer transplant, and WN = warming with novel colonizer transplant.

For *Sibbaldia procumbens*, fecundity had a weak positive contribution to changes in  $\lambda$  with warming (Figure 6a, WC – CC) and in the presence of novel competitors (CN – CC). Contrary to warming and novel competitors alone, the presence of novel competitors under warming (both WN comparisons) made fecundity contribute negatively to  $\Delta\lambda$ . Additionally, contributions of fecundity to  $\Delta\lambda$  in *S. procumbens* also showed variation between precipitation levels for some treatment comparisons, in terms of both direction and extent (Figure 6b). Regardless of experimental treatment, the contribution of fecundity to  $\Delta\lambda$  was greatest in the dry site, and generally decreased in proportion as the local precipitation levels increased. However, there were no significant differences in precipitation effects between the warmed novel competitor treatment (WN) and the extant climate control (CC). Therefore, we only have one bar for this treatment comparison (Figure 6b). Fecundity of *S. procumbens* generally contributed positively to  $\Delta\lambda$  with warming and when interacting with novel competitors, whereas the two factors in concert generally made fecundity contribute negatively to  $\Delta\lambda$ . However, these general trends switched in direction at the wettest site for all the aforementioned treatments. Reduced survival appears to be the crucial factor determining the fate of *Sibbaldia procumbens* populations. When *S. procumbens* received warming or interacted with novel competitors, fecundity contributed positively – yet not enough to tip the lambda-difference to a highly positive value (Figure 6a).

## *Sibbaldia procumbens*

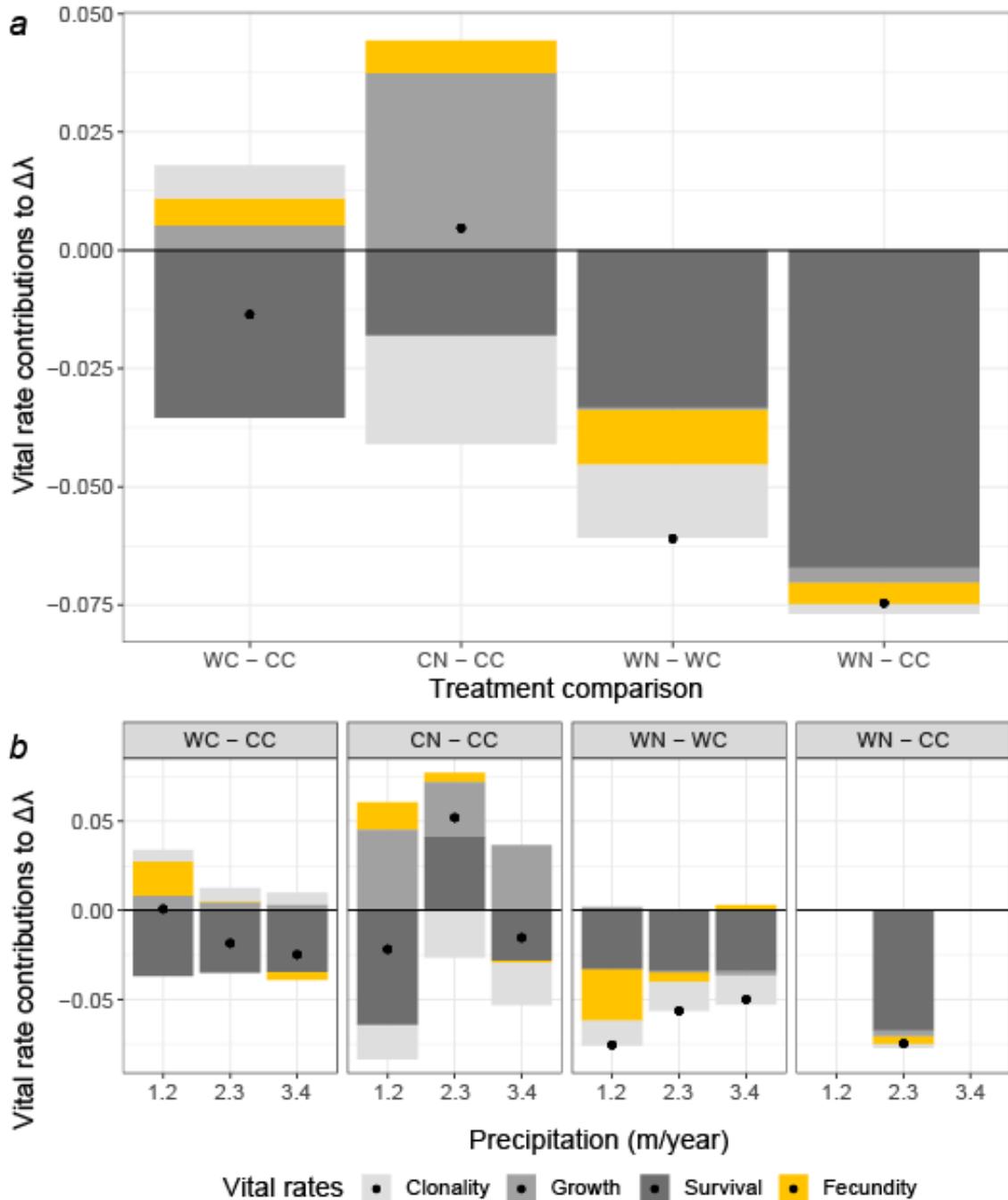


Figure 6: Vital rate contributions for *Sibbaldia procumbens* to the differences in  $\lambda$  between the experimental treatments (warming and novel colonizers) and their respective controls, calculated through separate one-way life table response experiments (LTRE) for each treatment. Shown are (a) mean vital rate contributions to  $\Delta\lambda$  across precipitation levels, for all treatments, and (b) vital rate contributions to  $\Delta\lambda$  between precipitation levels, for all treatments. The fecundity of *S. procumbens* is highlighted in yellow. The treatment-abbreviations translate to; CC = extant climate control, WC = warming control, CN = extant climate with novel colonizer transplant, and WN = warming with novel colonizer transplant.

## 4 Discussion

This study demonstrates that flower production of alpine species is likely to change in response to the projected climate change, and that fecundity's contribution to population growth depends on whether or not warming is accompanied by colonization. Warming had a clear positive effect on flower production in graminoids with both alpine- and novel neighbors, yet only a slight negative effect on forbs. Novel competitors positively affected flowering of forbs both with and without experimental warming, whereas these new neighbors showed no effect on graminoids. Although the community level flowering responses did not vary systematically with precipitation regimes, the vital rates (survival, growth, clonality and fecundity) affecting the population dynamics of *Veronica alpina* and *Sibbaldia procumbens* were dependent on precipitation level when exposed to warming and novel competitors. Furthermore, fecundity contributions to changes in population growth rates of *V. alpina* and *S. procumbens* differed between experimental treatments. The vital rates' responses were often opposite, indicating demographic compensation, where increased fecundity often was accompanied by reduced growth or survival. Hence, climate warming and the presence of novel competitors can be expected to affect the sexual reproduction of alpine plants both on the population- and community level.

### 4.1 Effects of warming and novel competitors on flower production in alpine plant communities

Flower production of alpine plants was altered by warming in this study, yet the direction and extent of the response varied between functional groups. Graminoids showed a clear positive response in flower abundance with warming (regardless of whether they interacted with alpine species or novel competitors), which is consistent with the fact that they a) are considered strong competitors for light and nutrients (Klanderud & Totland, 2005), and b) generally have been shown to benefit from elevated temperatures (Elmendorf et al., 2012; Hollister et al., 2005; Walker et al., 2006). Graminoids' benefit from elevated temperatures could in part be connected to their strong nutrient acquisitive abilities, as artificial warming has been found to increase nitrogen mineralization (De Valpine & Harte, 2001; Harte et al., 1995). Since graminoids are better competitors for nutrients than forbs, they might benefit from warming and produce more flowers. Forbs, however, might not attain enough

resources to flower due to increased competition (cf. Fridley et al., 2016; Olsen et al., 2016), and may even respond by reducing flower production (cf. slight but ambiguous reduction of flowering of forbs in this study). Higher flowering rates leading to reproductively successful graminoid populations could result in more genetic reorganization and an enhanced ability to disperse and colonize gaps (cf. Booy et al., 2000; Giménez-Benavides et al., 2008; Körner, 2021; Meineri et al., 2014). Thereby, the increased flower production with warming can enable graminoids to increase more in absolute abundance than forbs (Elmendorf et al., 2012; Hollister et al., 2005; Walker et al., 2006), resulting in increased graminoid-dominance at the expense of subordinate forb species. Graminoids' positive reproductive response to warming suggests that the increased genetic diversity that comes with sexual reproduction may make graminoids better equipped to face changing environmental conditions (Booy et al., 2000).

The functional groups' differing responses to warming is in line with the varying results of previous studies, where some studies report increased flowering with elevated temperatures (Aerts et al., 2004; Arft et al., 1999; De Valpine & Harte, 2001; Meineri et al., 2014; Schaubert et al., 2002), while others found decreased flower production under warming (De Valpine & Harte, 2001; Liu et al., 2012; Menzel & Simpson, 2015; Saavedra et al., 2003). A possible explanation for these opposing findings could be linked to species' variation in phenological sensitivity (Cleland et al., 2012). Generally, species that rely on temperature cues to regulate flowering may be better able to respond to warming (Cleland et al., 2012; Willis et al., 2008). Such responses could perhaps be associated with a transcription factor that activates flowering at higher temperatures (Kumar et al., 2012). Another plausible explanation could be species' varying ability to 'pre-fabricate' flowers (Körner, 2021). Flower preformation is employed by many alpine species in order to make maximum use of the short growing season in alpine regions (Körner, 2021), allowing flowers to bloom as soon as the conditions are favorable. Hence, flower preformation could prove advantageous for flower abundance of the species that employ it. The opposing flowering-responses to warming of forbs and graminoids allow for speculation that graminoids might rely more on temperature cues than forbs – providing graminoids with an advantage in a warmer climate.

The differing effects of warming on flower abundance between graminoids and forbs could also at least partly explain the shift in flowering community between the extant alpine climate and the warmed climate found at three of the four study sites. In addition to a general increase in flower production in graminoids under warming, the ordination result suggests a shift in flowering community composition from Poaceae species (i.e., *Agrostis mertensii*, *Avenella flexuosa* and *Festuca ovina*) towards Cyperaceae- and Juncaceae species (i.e., *Carex bigelowii*, *Carex vaginata*, *Trichophorum cespitosum* and *Luzula multiflora*) with warming. This indicates a higher potential for dispersal and genetic recombination for sedges and rushes relative to grasses under a warmer climate, and may thus contribute to a change in grassland character (cf. Klanderud & Birks, 2003). Even though flower production of forbs generally showed weak negative responses to warming, the shift in forb flowering community implies that some species will react positively to warming while other will not. Hence, the reproductive responses to climate warming may be species-specific among forbs.

Flower production of graminoids was unaffected by the presence of competitive novel colonizers. Similarly, previous work found novel competitors to be of weak and non-significant effect on flower production of alpine plants when growing in alpine climates (Alexander et al., 2015). Forbs however, displayed increased flower abundance when interacting with novel competitors in both the extant alpine climate and the warmed climate. Contrarily, previous studies reported reduced flowering for both forbs and graminoids in the presence of range-expanding shrub species (Collins et al., 2019; Macek et al., 2016). However, the transplanted lowland species in this experiment are herbaceous plants, and not woody shrubs, and alpine plants may therefore not respond as strongly to their herbaceous new neighbors as they would to larger, woody shrubs (Elmendorf et al., 2012; Formica et al., 2018). In this study, alpine forbs increased their flower production in the presence of novel competitors despite typically being weaker competitors than the unaffected graminoids (Klanderud & Totland, 2005). This raises the question whether the increased flower production really is a positive response to novel competitive interactions or a stress-response.

As range-expansion of lowland species is facilitated by climate warming (Cahill et al., 2014; Klanderud & Birks, 2003; Lenoir & Svenning, 2015; Steinbauer et al., 2018), it is unlikely that novel competitors will colonize alpine ecosystems without prior temperature increases.

Previous work by Alexander et al. (2015) showed that, contrary to their findings in the extant alpine climate, novel competitors in a warmed climate caused strongly reduced flowering performance of alpine plants. Hence, novel competitors are expected to negatively influence flower production of alpine species (Alexander et al., 2015). Plants can regulate flowering by inducing or accelerating flowering in response to stress – a process known as stress-induced flowering (Takeno, 2016; Wada & Takeno, 2010). Several factors have been reported to cause stress-induced flowering, including high or low light intensity, UV light, high or low temperature, poor nutrition, nitrogen deficiency, drought, low oxygen, crowding, root removal and mechanical stimulation (Takeno, 2016). The novel competitors that were transplanted in this study, namely *Succisa pratensis*, *Carex pallescens* and *Hypericum maculatum*, have resource acquisitive functional traits (Table 2) related to light interception and growth rate (Van Kleunen et al., 2010). The high stature of these novel competitors, particularly that of *S. pratensis*, could cause shading and lower light intensity resulting in stress-induced flowering (Craine & Dybzinski, 2013; Takeno, 2016). Further, crowding caused by the addition of transplanted novel competitors can lead to nutrient stress (Craine & Dybzinski, 2013), which may also result in stress-induced flowering (Takeno, 2016). Thus, stressed alpine plants could be able to produce offspring as an emergency response when they themselves are unable to ontogenetically adapt to unfavorable environmental conditions (Takeno, 2016). Such stress-induced flowering can be considered the ultimate adaptability to stress, as it may result in reproductive success ensuring persistence of the species (Booy et al., 2000; Dorji et al., 2020; Körner, 2021; Takeno, 2016).

#### 4.2 Fecundity's role in the population dynamics of two focal alpine forbs

Despite finding stable or increasing populations of *Veronica alpina* and *Sibbaldia procumbens*, the relative contributions of the different vital rates have consequences for the long-term maintenance of genetic variation in alpine plant populations (Ehrlén & Morris, 2015; Forbis, 2003; Pearson et al., 2014; Töpfer et al., 2018). Fecundity influenced the population dynamics of both the focal alpine species, however, fecundity made relatively large positive contributions to  $\Delta\lambda$  in *V. alpina*, whereas clonality was relatively more important than fecundity for the population dynamics of *S. procumbens*. Therefore, *V. alpina* might be better suited to face the projected climate change than *S. procumbens*. These

findings could have implications for the persistence of populations of the two alpine forb species, as the genetic diversity produced by sexual reproduction enables species to adapt to a changing climate (Booy et al., 2000; Körner, 2021).

Contrary to this study, previous demographic studies performed within the Vestland Climate Grid found that fecundity had a negligible influence on the difference in population growth rates both under warming and increased precipitation (Olsen et al., 2016; Töpfer et al., 2018). Since then, the climate has gotten warmer and the mean growing season temperature of the alpine sites has increased from ~6.5 °C to ~7 °C. Although fecundity of *S. procumbens* was not negligible, survival, growth and clonality was relatively more important than fecundity for  $\Delta\lambda$ . For *V. alpina* however, fecundity played a larger role in determining  $\lambda$ -values in the experimental treatments, and does not coincide well with the previous findings within the climate grid. Compared to the previous studies, we found generally higher flowering probabilities and greater numbers of flowers produced for *V. alpina*, as well as an increased number of seeds per capsule and a higher seedling establishment rate (Gya et al., in prep; Töpfer et al., 2018). This suggests that fecundity may become more important for alpine species' population dynamics in a warmer climate, as more seedlings establish and survive where they previously were limited by clonal- and vegetative growth of other neighboring species. Hence, we might expect more genetically diverse alpine populations with the projected climate warming.

The direction of fecundity's contribution, in relation to the other vital rates, varied in response to warming and novel competitors, mainly manifesting through three evident trends: i) opposite direction in the fecundity- and growth contributions, ii) negative fecundity contributions accompanied by negative contributions in all other vital rates, and iii) increased fecundity accompanied by reduced survival. The first trend could be attributed to a change in resource allocation, where the plants allocate more resources to reproduction at the expense of growth (Wenk & Falster, 2015), or the other way around. The second trend is likely a stress-response to increased competitive interactions (cf. Töpfer et al., 2018). The third trend could be an indication of demographic compensation (Villellas et al., 2015). Largely reduced survival might have resulted in a compensatory increase in fecundity as a stress-response – a sort of last resort to try to maintain a viable population (Sheth & Angert, 2018). Such demographic compensation may enable alpine plant populations to persist in a

changing climate, by enhancing their ability to disperse and colonize new ground and by increasing genetic recombination (Villemas et al., 2015). Not only does this finding suggest that climate change may cause increased fecundity through demographic compensation (Villemas et al., 2015), but it also complies with my speculations concerning stress-induced flowering at the community level.

Overall, fecundity contributed positively (more often than negatively) to stable or increasing populations of the two focal alpine species, suggesting that sexual reproduction and flowering plays a part in determining the fate of alpine plant populations. However, if compensatory increases in fecundity is a response to reduced survival, and this continues to be a recurring trend, eventually the alpine plants may not be able to reproductively compensate enough for the reduced survival (Sheth & Angert, 2018). Hence, the positive response in flower production might not be maintained in the long run, and more long-term studies are needed to accurately predict climate effects on future reproduction responses.

#### 4.3 Context dependency related to precipitation regimes

I found no systematic patterns in flower production responses to varying precipitation regimes at the community level. However, other studies have found reduced flower production in drier environments (Galen et al., 1999; Lambrecht & Dawson, 2007; Xie et al., 2016) and increased vegetative propagation under drought stress (Xie et al., 2016). These trends may be caused by the high water loss associated with flowering (Galen et al., 1999) and reduced resource uptake caused by low soil moisture (Lambrecht & Dawson, 2007). Due to the high precipitation levels at the alpine sites (1226 – 3402 mm/year), the systems may not be water-limited. Previous studies performed within the Vestland Climate Grid reported precipitation effects on population growth rate and survival (Olsen et al., 2016) trait distribution (Gya, 2017), and seedling emergence (Meineri et al., 2013). However, other studies within the same climate grid did not detect any precipitation-dependency (Guittar et al., 2016; Skjelstad, 2020). Neither reproductive allocation, nor number of floral displays at the community level, responded significantly to changes in precipitation (Skjelstad, 2020). As suggested by Guittar et al. (2016), a lack of precipitation effects could occur if soil moisture is similar at all sites and/or not limiting at any sites. Soil moisture at the four sites was relatively high and rather similar – around 40-50% volumetric water content at Låvisdalen, Gudmedalen and Skjellingahaugen and ~25% at Ulvehaugen (Gya et al., 2020) – and may

therefore explain why no systematic responses in flower production of the alpine plant community were detected for varying precipitation regimes.

Furthermore, one could also argue that mean annual precipitation is not a sufficient measure for detecting changes in flower production, as it does not account for distribution of precipitation between seasons, nor the type of precipitation (rain- or snowfall).

Nonetheless, precipitation is relatively evenly distributed throughout the year at the sites. Additionally, snowmelt date is a vital determinant for timing of flowering (Inouye et al., 2003). Warming-induced advances in snowmelt have been found to reduce abundance of flowering plants, as well as the total number of flowers per plant (Saavedra et al., 2003), suggesting that the projected climate change will lead to a decrease in genetic recombination and reproductive success of alpine plant communities (Dorji et al., 2020; Körner, 2021).

Although no systematic precipitation effects were detected on the community level, previous work suggests that precipitation-responses may be species-specific (Meineri et al., 2014). Such species-specific responses to precipitation were found for the focal alpine species *Veronica alpina* and *Sibbaldia procumbens*. The vital rates affecting the population dynamics of the two forbs were dependent on precipitation level when exposed to elevated temperatures and novel competitors. Increased precipitation had a positive effect on fecundity of *V. alpina* when interacting with novel competitors under warming, where fecundity contributions to  $\Delta\lambda$  shifted from negative in the dry site to positive in the wet site. However, in the unheated plots with novel competitors the pattern was reversed. For *S. procumbens*, the direction of fecundity contributions was negatively correlated with increasing precipitation for warming and novel competitors alone, but positively correlated with precipitation for warming and novel competitors in concert. Hence, precipitation-dependency is non-additive (cf. Töpper et al., 2018) as the fecundity trends in the single-factor treatments do not add up the combined-factor treatments. Thus, one should not deduce flowering-responses along precipitation gradients from separate studies looking at either warming or novel competitors separately.

#### 4.4 Conclusions

Understanding alpine species' reproductive responses to climate change is essential for predicting how well alpine communities and populations might perform and persist in the future. This study demonstrates that the sexual reproduction of alpine plants may increase with climate change. Experimental warming and the presence of novel competitors triggered higher flower production for graminoids and forbs, respectively. Furthermore, flowering community composition in regard to graminoids shifted from Poaceae species to Cyperaceae- and Juncaceae species with warming, suggesting that the character of grasslands might change under warming. In addition, fecundity clearly contributed to changes in population growth rates ( $\Delta\lambda$ ) of both *Veronica alpina* and *Sibbaldia procumbens*. The population models show that trade-offs in resource allocation between fecundity and vegetative growth may occur and that increased fecundity compensates for reduced survival. Thus, fecundity is strategically used in the ontogeny of alpine plant individuals. These findings suggest that genetic variation in alpine species will be preserved and that alpine plants may persist when influenced by the projected climate warming and range-expansion of lowland competitors. However, as climate warming precedes colonization by lowland species, the increased flowering of graminoids could entail changes in plant community composition if reproduction proves successful. Therefore, the state of the alpine community might already be different before the subsequent colonization sets in, and the positive effect of novel competitors on flowering of forbs might be altered. Further, if the increased sexual reproduction is a means of stress-induced flowering or demographic compensation, these positive reproductive responses might not be maintained in the long run. Hence, more long-term studies are needed to accurately predict how the effects documented in this study play out in the longer run.

## 5 References

- Aerts, R., Cornelissen, J. H. C., Dorrepaal, E., Van Logtestijn, R. S. P., & Callaghan, T. V. (2004). Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. *Global Change Biology*, *10*(9), 1599–1609. <https://doi.org/10.1111/J.1365-2486.2004.00815.X>
- Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature* *2015* 525:7570, *525*(7570), 515–518. <https://doi.org/10.1038/nature14952>
- Anthelme, F., Cavieres, L. A., & Dangles, O. (2014). Facilitation among plants in alpine environments in the face of climate change. *Frontiers in Plant Science*, *5*(AUG), 387. <https://doi.org/10.3389/FPLS.2014.00387/BIBTEX>
- Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jónsdóttir, I. S., Laine, K., Lévesque, E., Marion, G. M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., ... Wookey, P. A. (1999). RESPONSES OF TUNDRA PLANTS TO EXPERIMENTAL WARMING: META-ANALYSIS OF THE INTERNATIONAL TUNDRA EXPERIMENT. *Ecological Monographs*, *69*(4), 491–511. <https://doi.org/10.1890/0012-9615>
- Artsdatabanken. (2015). *Artsnavnebasen*. Norsk Taksonomisk Database. <http://www.artsportalen.artsdatabanken.no/>
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
- Bertrand, R., Riofrío-Dillon, G., Lenoir, J., Drapier, J., De Ruffray, P., Gégout, J. C., & Loreau, M. (2016). Ecological constraints increase the climatic debt in forests. *Nature Communications* *2016* 7:1, *7*(1), 1–10. <https://doi.org/10.1038/ncomms12643>
- Between the Fjords. (2022). *Vestland Climate Grid*. <https://betweenthefjords.w.uib.no/vestland-climate-grid/>
- Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change and the past, present, and future of biotic interactions. *Science*, *341*(6145), 499–504. [https://doi.org/10.1126/SCIENCE.1237184/SUPPL\\_FILE/499.MP3](https://doi.org/10.1126/SCIENCE.1237184/SUPPL_FILE/499.MP3)
- Booy, G., Hendriks, R. J. J., Smulders, M. J. M., Van Groenendael, J. M., & Vosman, B. (2000). Genetic diversity and the survival of populations. *Plant Biology*, *2*(4), 379–395. <https://doi.org/10.1055/S-2000-5958/ID/113>
- Brooker, R. W. (2006). Plant–plant interactions and environmental change. *New Phytologist*, *171*(2), 271–284. <https://doi.org/10.1111/J.1469-8137.2006.01752.X>
- Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Ryu, H. Y., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., & Wiens, J. J. (2014). Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, *41*(3), 429–442. <https://doi.org/10.1111/JBI.12231>
- Callaghan, T. V., & Jonasson, S. (1995). Arctic terrestrial ecosystems and environmental change. *Philosophical Transactions of the Royal Society of London. Series A: Physical and Engineering Sciences*, *352*(1699), 259–276. <https://doi.org/10.1098/RSTA.1995.0069>
- Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire,

- F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature* 2002 417:6891, 417(6891), 844–848. <https://doi.org/10.1038/nature00812>
- Choler, P., Michalet, R., & Callaway, R. M. (2001). FACILITATION AND COMPETITION ON GRADIENTS IN ALPINE PLANT COMMUNITIES. *Ecology*, 82(12), 3295–3308. <https://doi.org/10.1890/0012-9658>
- Cleland, E. E., Allen, J. M., Crimmins, T. M., Dunne, J. A., Pau, S., Travers, S. E., Zavaleta, E. S., & Wolkovich, E. M. (2012). Phenological tracking enables positive species responses to climate change. *Ecology*, 93(8), 1765–1771. <https://doi.org/10.1890/11-1912.1>
- Collins, C. G., Bohner, T. F., & Diez, J. M. (2019). Plant-Soil Feedbacks and Facilitation Influence the Demography of Herbaceous Alpine Species in Response to Woody Plant Range Expansion. *Frontiers in Ecology and Evolution*, 7, 417. <https://doi.org/10.3389/FEVO.2019.00417/BIBTEX>
- Craine, J. M., & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, 27(4), 833–840. <https://doi.org/10.1111/1365-2435.12081>
- Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., & Mynsberge, A. R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, 331(6015), 324–327. [https://doi.org/10.1126/SCIENCE.1199040/SUPPL\\_FILE/CRIMMINS.SOM.PDF](https://doi.org/10.1126/SCIENCE.1199040/SUPPL_FILE/CRIMMINS.SOM.PDF)
- Dagleish, H. J., Koons, D. N., Hooten, M. B., Moffet, C. A., & Adler, P. B. (2011). Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, 92(1), 75–85. <https://doi.org/10.1890/10-0780.1>
- De Valpine, P., & Harte, J. (2001). PLANT RESPONSES TO EXPERIMENTAL WARMING IN A MONTANE MEADOW. *Ecology*, 82(3), 637–648. <https://doi.org/10.1890/0012-9658>
- Dickinson, M. G., Orme, C. D. L., Suttle, K. B., & Mace, G. M. (2014). Separating sensitivity from exposure in assessing extinction risk from climate change. *Scientific Reports* 2014 4:1, 4(1), 1–6. <https://doi.org/10.1038/srep06898>
- Dorji, T., Hopping, K. A., Meng, F., Wang, S., Jiang, L., & Klein, J. A. (2020). Impacts of climate change on flowering phenology and production in alpine plants: The importance of end of flowering. *Agriculture, Ecosystems & Environment*, 291, 106795. <https://doi.org/10.1016/J.AGEE.2019.106795>
- Dunnett, N. P., & Grime, J. P. (1999). Competition as an amplifier of short-term vegetation responses to climate: an experimental test. *Functional Ecology*, 13(3), 388–395. <https://doi.org/10.1046/J.1365-2435.1999.00331.X>
- Ehrlén, J., & Morris, W. F. (2015). Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, 18(3), 303–314. <https://doi.org/10.1111/ELE.12410>
- Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., ... Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, 15(2), 164–175. <https://doi.org/10.1111/J.1461-0248.2011.01716.X>
- Evers, S. M., Knight, T. M., Inouye, D. W., Miller, T. E. X., Salguero-Gómez, R., Iler, A. M., & Compagnoni, A. (2021). Lagged and dormant season climate better predict plant vital rates than

- climate during the growing season. *Global Change Biology*. <https://doi.org/10.1111/gcb.15519>
- Fazlioglu, F., & Wan, J. S. H. (2021). Warming matters: alpine plant responses to experimental warming. *Climatic Change*, *164*(3–4). <https://doi.org/10.1007/s10584-021-02996-3>
- Forbis, T. A. (2003). Seedling demography in an alpine ecosystem. *American Journal of Botany*, *90*(8), 1197–1206. <https://doi.org/10.3732/AJB.90.8.1197>
- Formica, A., Farrer, E. C., Ashton, I. W., & Suding, K. N. (2018). Shrub Expansion Over the Past 62 Years in Rocky Mountain Alpine Tundra: Possible Causes and Consequences. *Arctic, Antarctic, and Alpine Research*, *46*(3), 616–631. <https://doi.org/10.1657/1938-4246-46.3.616>
- Fremstad, E. (1997). Vegetasjonstyper i Norge. In *NINA Temahefte* (Vol. 12, Issue 2).
- Fridley, J. D., Lynn, J. S., Grime, J. P., & Askew, A. P. (2016). Longer growing seasons shift grassland vegetation towards more-productive species. *Nature Climate Change* *2016 6:9*, *6*(9), 865–868. <https://doi.org/10.1038/nclimate3032>
- Funk, J. L., & Wolf, A. A. (2016). Testing the trait-based community framework: Do functional traits predict competitive outcomes? *Ecology*, *97*(9), 2206–2211. <https://doi.org/10.1002/ECY.1484>
- Galen, C., Sherry, R. A., & Carroll, A. B. (1999). Are flowers physiological sinks or faucets? Costs and correlates of water use by flowers of *Polemonium viscosum*. *Oecologia* *1999 118:4*, *118*(4), 461–470. <https://doi.org/10.1007/S004420050749>
- Giménez-Benavides, L., Escudero, A., & Iriondo, J. M. (2008). What shapes the altitudinal range of a high mountain Mediterranean plant? Recruitment probabilities from ovule to seedling stage. *Ecography*, *31*(6), 731–740. <https://doi.org/10.1111/J.0906-7590.2008.05509.X>
- Gómez-Rubio, V. (2020). *Bayesian inference with INLA*. Chapman & Hall/CRC Press. <https://becarioprecario.bitbucket.io/inla-gitbook/index.html>
- Gómez-Ruiz, E. P., & Lacher Jr., T. E. (2019). Climate change, range shifts, and the disruption of a pollinator-plant complex. *Scientific Reports*, *9*(1), 14048. <https://doi.org/10.1038/s41598-019-50059-6>
- Grytnes, J. A., Kapfer, J., Jurasinski, G., Birks, H. H., Henriksen, H., Klanderud, K., Odland, A., Ohlson, M., Wipf, S., & Birks, H. J. B. (2014). Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecology and Biogeography*, *23*(8), 876–884. <https://doi.org/10.1111/GEB.12170/SUPPINFO>
- Guittar, J., Goldberg, D., Klanderud, K., Telford, R. J., & Vandvik, V. (2016). Can trait patterns along gradients predict plant community responses to climate change? *Ecology*, *97*(10), 2791–2801. <https://doi.org/10.1002/ECY.1500>
- Gya, R. (2017). *The role of intraspecific variability in driving community trait shifts along temperature and precipitation gradients in alpine and boreal semi-natural grasslands*. University of Bergen.
- Gya, R., Geange, S. R., Lynn, J. S., Spindelböck, J. P., Wallevik, Ø., Zernichow, C., & Vandvik, V. (2020 - Accepted first stage of registered report). A test of local adaptation to drought in germination and seedling traits in populations of two alpine forbs across a 2000 mm/year precipitation gradient. *Ecology and Evolution*. <https://doi.org/10.17605/OSF.IO/H7QAU>
- Gya, R., Töpfer, J. P., Olsen, S. L., Lieungh, E., Berthelsen, S., Skarpaas, O., & Vandvik, V. (in prep). *You have been warmed: novel interactions cancel out positive effects of warming in alpine plants*. Corresponding author: [ragnhild.gya@uib.no](mailto:ragnhild.gya@uib.no)
- Halvorsen, R., & medarbeidere og samarbeidspartnere. (2016). *NiN - typeinndeling og*

beskrivessystem for natursystem-nivået. - *Natur i Norge, Artikkel 3 (versjon 2.1.0)*.  
<http://www.artsdatabanken.no>.

- Harte, J., Torn, M. S., Chang Fang-Ru, Feifarek, B., Kinzig, A. P., Shaw, R., & Shen, K. (1995). Global Warming and Soil Microclimate: Results from a Meadow-Warming Experiment. *Ecological Applications*, 5(1), 132–150. <https://doi.org/10.2307/1942058>
- He, X., Burgess, K. S., Yang, X. F., Ahrends, A., Gao, L. M., & Li, D. Z. (2019). Upward elevation and northwest range shifts for alpine *Meconopsis* species in the Himalaya–Hengduan Mountains region. *Ecology and Evolution*, 9(7), 4055–4064. <https://doi.org/10.1002/ECE3.5034>
- Hollister, R. D., Webber, P. J., & Tweedie, C. E. (2005). The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology*, 11(4), 525–536. <https://doi.org/10.1111/J.1365-2486.2005.00926.X>
- Hulme, P. E., & Bernard-Verdier, M. (2018). Comparing traits of native and alien plants: Can we do better? *Functional Ecology*, 32(1), 117–125. <https://doi.org/10.1111/1365-2435.12982/SUPPINFO>
- Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Lolk, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E., & Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature* 2004 429:6992, 429(6992), 651–654. <https://doi.org/10.1038/nature02561>
- Inouye, D. W., Saavedra, F., Lee-Yang, W., Russek-Cohen, B. B. E., Douglass, L., & Underwood, N. (2003). Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). *American Journal of Botany*, 90(6), 905–910. <https://doi.org/10.3732/AJB.90.6.905>
- Jongejans, E., de Kroon, H., Tuljapurkar, S., & Shea, K. (2010). Plant populations track rather than buffer climate fluctuations. *Ecology Letters*, 13(6), 736–743. <https://doi.org/10.1111/J.1461-0248.2010.01470.X>
- Kikvidze, Z., Pugnaire, F. I., Brooker, R. W., Choler, P., Lortie, C. J., Michalet, R., & Callaway, R. M. (2005). LINKING PATTERNS AND PROCESSES IN ALPINE PLANT COMMUNITIES: A GLOBAL STUDY. *Ecology*, 86(6), 1395–1400. <https://doi.org/10.1890/04-1926>
- Klanderud, K. (2005). Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, 93(1), 127–137. <https://doi.org/10.1111/J.1365-2745.2004.00944.X>
- Klanderud, K., & Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene*, 13(1), 1–6. <https://doi.org/10.1191/0959683603h1589ft>
- Klanderud, K., & Totland, Ø. (2005). SIMULATED CLIMATE CHANGE ALTERED DOMINANCE HIERARCHIES AND DIVERSITY OF AN ALPINE BIODIVERSITY HOTSPOT. *Ecology*, 86(8), 2047–2054. <https://doi.org/10.1890/04-1563>
- Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of Biotic vs. Abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS ONE*, 10(6). <https://doi.org/10.1371/journal.pone.0130205>
- Körner, C. (2021). Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. In *Alpine Plant Life* (3rd ed.). Springer International Publishing. <https://doi.org/10.1007/978-3-030-59538-8>

- Kraft, N. J. B., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(3), 797–802. <https://doi.org/10.1073/PNAS.1413650112>
- Kumar, S. V., Lucyshyn, D., Jaeger, K. E., Alós, E., Alvey, E., Harberd, N. P., & Wigge, P. A. (2012). Transcription factor PIF4 controls the thermosensory activation of flowering. *Nature* *2012* *484*:7393, *484*(7393), 242–245. <https://doi.org/10.1038/nature10928>
- Lambrecht, S. C., & Dawson, T. E. (2007). Correlated variation of floral and leaf traits along a moisture availability gradient. *Oecologia*, *151*(4), 574–583. <https://doi.org/10.1007/S00442-006-0617-7/FIGURES/4>
- Larcher, W. (2003). *Physiological plant ecology: ecophysiology and stress physiology of functional groups*. Springer Science & Business Media.
- Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28. <https://doi.org/10.1111/ECOG.00967>
- Lesica, P., & McCune, B. (2004). Decline of Arctic-Alpine Plants at the Southern Margin of Their Range Following a Decade of Climatic Warming. *Journal of Vegetation Science*, *15*(5), 679–690. <http://www.jstor.org/stable/3236595>
- Lindgren, F., & Rue, H. (2015). Bayesian Spatial Modelling with R-INLA. *Journal of Statistical Software*, *63*(19), 1–25. <https://doi.org/10.18637/JSS.V063.I19>
- Liu, Y., Mu, J., Niklas, K. J., Li, G., & Sun, S. (2012). Global warming reduces plant reproductive output for temperate multi-inflorescence species on the Tibetan plateau. *New Phytologist*, *195*(2), 427–436. <https://doi.org/10.1111/J.1469-8137.2012.04178.X>
- Macek, P., Prieto, I., Macková, J., Pistón, N., & Pugnaire, F. I. (2016). Functional plant types drive plant interactions in a mediterranean mountain range. *Frontiers in Plant Science*, *7*(MAY2016), 662. <https://doi.org/10.3389/FPLS.2016.00662/BIBTEX>
- Maindonald, J., & Braun, W. J. (2010). Data Analysis and Graphics Using R: An Example-Based Approach. In *Cambridge Series in Statistical and Probabilistic Mathematics* (3rd ed.). Cambridge University Press. <https://doi.org/DOI:10.1017/CBO9781139194648>
- Marion, G. M. (1996). Temperature enhancement experiments. *ITEX Manual*, 1722.
- 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*(1), 275–286. <https://doi.org/10.1111/JVS.12062>
- 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*(4), 607–619. <https://doi.org/10.1007/S11258-013-0193-Y/FIGURES/5>
- Menzel, C. M., & Simpson, D. R. (2015). Temperatures above 20°C reduce flowering in lychee (*Litchi chinensis* Sonn.). <http://Dx.Doi.Org/10.1080/14620316.1995.11515374>, *70*(6), 981–987. <https://doi.org/10.1080/14620316.1995.11515374>
- Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R., & McMahon, S. M. (2014). Advancing population ecology with integral projection models: a practical guide. *Methods in Ecology and Evolution*, *5*(2), 99–110. <https://doi.org/10.1111/2041-210X.12146>
- Metcalf, C. J. E., McMahon, S. M., Salguero-Gómez, R., & Jongejans, E. (2013). IPMpack: an R package

- for integral projection models. *Methods in Ecology and Evolution*, 4(2), 195–200.  
<https://doi.org/10.1111/2041-210X.12001>
- Nicolè, F., Dahlgren, J. P., 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(5), 1211–1218. <https://doi.org/10.1111/J.1365-2745.2011.01852.X>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O’Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community Ecology Package* (R package version 2.5-7). <https://cran.r-project.org/package=vegan>
- Olsen, S. L., & Klanderud, K. (2014). Biotic interactions limit species richness in an alpine plant community, especially under experimental warming. *Oikos*, 123(1), 71–78.  
<https://doi.org/10.1111/J.1600-0706.2013.00336.X>
- Olsen, S. L., Töpper, J. P., Skarpaas, O., Vandvik, V., & Klanderud, K. (2016). From facilitation to competition: Temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Global Change Biology*, 22(5).  
<https://doi.org/10.1111/gcb.13241>
- Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M. E., Ersts, P. J., Horning, N., Fordham, D. A., Raxworthy, C. J., Ryu, H. Y., Mcneese, J., & Akçakaya, H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change* 2014 4:3, 4(3), 217–221. <https://doi.org/10.1038/nclimate2113>
- Petry, W. K., Soule, J. D., Iler, A. M., Chicas-Mosier, A., Inouye, D. W., Miller, T. E. X., & Mooney, K. A. (2016). Sex-specific responses to climate change in plants alter population sex ratio and performance. *Science*, 353(6294), 69–71.  
[https://doi.org/10.1126/SCIENCE.AAF2588/SUPPL\\_FILE/PETRY-SM.PDF](https://doi.org/10.1126/SCIENCE.AAF2588/SUPPL_FILE/PETRY-SM.PDF)
- R Core Team. (2022). *R: A Language and Environment for Statistical Computing* (R version 4.1.3). R Foundation for Statistical Computing. <https://www.r-project.org/>
- RStudio Team. (2022). *RStudio: Integrated Development Environment for R* (Version 2022.2.1.461). RStudio, PBC. <http://www.rstudio.com/>
- Saavedra, F., Inouye, D. W., Price, M. V., & Harte, J. (2003). Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. *Global Change Biology*, 9(6), 885–894. <https://doi.org/10.1046/J.1365-2486.2003.00635.X>
- Schauber, E. M., Kelly, D., Turchin, P., Simon, C., Lee, W. G., Allen, R. B., Payton, I. J., Wilson, P. R., Cowan, P. E., & Brockie, R. E. (2002). MASTING BY EIGHTEEN NEW ZEALAND PLANT SPECIES: THE ROLE OF TEMPERATURE AS A SYNCHRONIZING CUE. *Ecology*, 83(5), 1214–1225.  
[https://doi.org/10.1890/0012-9658\(2002\)083](https://doi.org/10.1890/0012-9658(2002)083)
- Schneider, S. H., & Thomsson, S. L. (1981). Atmospheric CO<sub>2</sub> and climate: Importance of the transient response. *Journal of Geophysical Research: Oceans*, 86(C4), 3135–3147.  
<https://doi.org/10.1029/JC086IC04P03135>
- Schneider, Stephen H. (1975). On the Carbon Dioxide–Climate Confusion. *Journal of Atmospheric Sciences*, 32(11), 2060–2066. [https://doi.org/10.1175/1520-0469\(1975\)032<2060:OTCDC>2.0.CO;2](https://doi.org/10.1175/1520-0469(1975)032<2060:OTCDC>2.0.CO;2)
- Sheth, S. N., & Angert, A. L. (2018). Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences of the United States of*

- America*, 115(10), 2413–2418. <https://doi.org/10.1073/PNAS.1715899115>
- Skjelstad, G. (2020). *Reproductive allocation and floral traits of insect pollinated forbs along climatic gradients in semi-natural grasslands*. University of Bergen.
- Sletvold, N., Dahlgren, J. P., 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(9), 2729–2738. <https://doi.org/10.1111/GCB.12167>
- Sjøgaard, L. F. (2020). *The effects of climate on resource allocation and traits of alpine and boreal herbaceous plants*. University of Bergen.
- Spindelböck, J. P., & Olsen, S. L. (2013). Prolonged dormancy in three common Norwegian plant species: strategy or cost? *Blyttia*, 71(4), 235–240. <http://www.nhm.uio.no/botanisk/nbf/blyttia/>
- Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg, S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V. A., ... Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* 2018 556:7700, 556(7700), 231–234. <https://doi.org/10.1038/s41586-018-0005-6>
- Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J., Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., ... Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101(1), 58–67. <https://doi.org/10.1111/1365-2745.12025>
- Takeo, K. (2016). Stress-induced flowering: the third category of flowering response. *Journal of Experimental Botany*, 67(17), 4925–4934. <https://doi.org/10.1093/jxb/erw272>
- Töpper, J. P., Meineri, E., Olsen, S. L., Rydgren, K., Skarpaas, O., & Vandvik, V. (2018). The devil is in the detail: Nonadditive and context-dependent plant population responses to increasing temperature and precipitation. *Global Change Biology*, 24(10), 4657–4666. <https://doi.org/10.1111/GCB.14336>
- Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J. B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353(6304). [https://doi.org/10.1126/SCIENCE.AAD8466/SUPPL\\_FILE/URBAN.SM.PDF](https://doi.org/10.1126/SCIENCE.AAD8466/SUPPL_FILE/URBAN.SM.PDF)
- Urban, M. C., Tewksbury, J. J., & Sheldon, K. S. (2012). On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B: Biological Sciences*, 279(1735), 2072–2080. <https://doi.org/10.1098/RSPB.2011.2367>
- Van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13(2), 235–245. <https://doi.org/10.1111/J.1461-0248.2009.01418.X>
- Vandvik, V., Skarpaas, O., Klanderud, K., Telford, R. J., Halbritter, A. H., & Goldberg, D. E. (2020). Biotic rescaling reveals importance of species interactions for variation in biodiversity responses to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 117(37), 22858–22865. <https://doi.org/10.1073/PNAS.2003377117>
- Villellas, J., Doak, D. F., García, M. B., & Morris, W. F. (2015). Demographic compensation among

- populations: what is it, how does it arise and what are its implications? *Ecology Letters*, *18*(11), 1139–1152. <https://doi.org/10.1111/ELE.12505>
- Wada, K. C., & Takeno, K. (2010). Stress-induced flowering. *Plant Signaling & Behavior*, *5*(8), 944–947. <https://doi.org/10.4161/psb.5.8.11826>
- Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jónsdóttir, I. S., Klein, J. A., Magnússon, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., ... Wookey, P. A. (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*(5), 1342–1346. <https://doi.org/10.1073/PNAS.0503198103>
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature* *2002* *416*:6879, *416*(6879), 389–395. <https://doi.org/10.1038/416389a>
- Wang, N., Quesada, B., Xia, L., Butterbach-Bahl, K., Goodale, C. L., & Kiese, R. (2019). Effects of climate warming on carbon fluxes in grasslands— A global meta-analysis. *Global Change Biology*, *25*(5), 1839–1851. <https://doi.org/10.1111/GCB.14603>
- Wenk, E. H., & Falster, D. S. (2015). Quantifying and understanding reproductive allocation schedules in plants. *Ecology and Evolution*, *5*(23), 5521–5538. <https://doi.org/10.1002/ECE3.1802>
- Williams, A. L., Wills, K. E., Janes, J. K., Vander Schoor, J. K., Newton, P. C. D., & Hovenden, M. J. (2007). Warming and free-air CO<sub>2</sub> enrichment alter demographics in four co-occurring grassland species. *New Phytologist*, *176*(2), 365–374. <https://doi.org/10.1111/J.1469-8137.2007.02170.X>
- Williams, J. W., Blois, J. L., Gill, J. L., Gonzales, L. M., Grimm, E. C., Ordonez, A., Shuman, B., & Veloz, S. D. (2013). Model systems for a no-analog future: species associations and climates during the last deglaciation. *Annals of the New York Academy of Sciences*, *1297*(1), 29–43. <https://doi.org/10.1111/NYAS.12226>
- Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J., & Davis, C. C. (2008). Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(44), 17029–17033. <https://doi.org/10.1073/PNAS.0806446105>
- Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., Pau, S., Regetz, J., Davies, T. J., Kraft, N. J. B., Ault, T. R., Bolmgren, K., Mazer, S. J., McCabe, G. J., McGill, B. J., Parmesan, C., Salamin, N., Schwartz, M. D., & Cleland, E. E. (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature* *2012* *485*:7399, *485*(7399), 494–497. <https://doi.org/10.1038/nature11014>
- Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J., & Hungate, B. A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, *17*(2), 927–942. <https://doi.org/10.1111/J.1365-2486.2010.02302.X>
- Xie, L., Guo, H., & Ma, C. (2016). Alterations in flowering strategies and sexual allocation of *Caragana stenophylla* along a climatic aridity gradient. *Scientific Reports* *2016* *6*:1, *6*(1), 1–8. <https://doi.org/10.1038/srep33602>

## 6 Appendix

*Table A1: An overview of all the flowering species registered in the experimental plots during the peak growing season, between 26th of July and 20th of August 2021. All species are listed together with their respective family and order, following the taxonomy specified by the Norwegian Biodiversity Information Centre (Artsdatabanken, 2015). Flower production was measured differently, depending on the species' inflorescence type. Each species was assigned to a functional group; either forbs or graminoids.*

<b>Species</b>	<b>Family</b>	<b>Order</b>	<b>Measurement type</b>	<b>Functional group</b>
<b>Agrostis capillaris</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Agrostis mertensii</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Alchemilla alpina</b>	Rosaceae	Rosales	Percent cover	Forb
<b>Alchemilla spp.</b>	Rosaceae	Rosales	Percent cover	Forb
<b>Anthoxanthum odoratum</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Astragalus alpinus</b>	Fabaceae	Fabales	Flower count	Forb
<b>Avenella flexuosa</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Bistorta vivipara</b>	Polygonaceae	Caryophyllales	Length of inflorescence	Forb
<b>Campanula rotundifolia</b>	Campanulaceae	Asterales	Flower count	Forb
<b>Carex bigelowii</b>	Cyperaceae	Poales	Number of reproductive inflorescence units	Graminoid
<b>Carex capillaris</b>	Cyperaceae	Poales	Number of reproductive inflorescence units	Graminoid
<b>Carex flava</b>	Cyperaceae	Poales	Number of reproductive inflorescence units	Graminoid
<b>Carex norvegica</b>	Cyperaceae	Poales	Number of reproductive inflorescence units	Graminoid
<b>Carex vaginata</b>	Cyperaceae	Poales	Number of reproductive inflorescence units	Graminoid
<b>Carex vaginata cf.</b>	Cyperaceae	Poales	Number of reproductive inflorescence units	Graminoid
<b>Cerastium cerastoides</b>	Caryophyllaceae	Caryophyllales	Flower count	Forb
<b>Cerastium fontanum</b>	Caryophyllaceae	Caryophyllales	Flower count	Forb
<b>Coeloglossum viride cf.</b>	Orchidaceae	Asparagales	Flower count	Forb
<b>Deschampsia cespitosa</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Epilobium anagallidifolium</b>	Onagraceae	Myrtales	Flower count	Forb
<b>Euphrasia spp.</b>	Orobanchaceae	Lamiales	Number of flowering individuals	Forb
<b>Festuca ovina</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Festuca vivipara</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Gentiana nivalis</b>	Gentianaceae	Gentianales	Flower count	Forb
<b>Geum rivale</b>	Rosaceae	Rosales	Flower count	Forb
<b>Juncus trifidus</b>	Juncaceae	Poales	Flower count	Graminoid
<b>Leontodon autumnalis</b>	Asteraceae	Asterales	Flower head count	Forb
<b>Luzula multiflora</b>	Juncaceae	Poales	Number of reproductive inflorescence units	Graminoid
<b>Nardus stricta</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Omalotheca supina</b>	Asteraceae	Asterales	Flower head count	Forb
<b>Parnassia palustris</b>	Celastraceae	Celastrales	Flower count	Forb

<b>Phleum alpinum</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Pinguicula vulgaris</b>	Lentibulariaceae	Lamiales	Flower count	Forb
<b>Poa alpina</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Potentilla erecta</b>	Rosaceae	Rosales	Flower count	Forb
<b>Pyrola minor</b>	Ericaceae	Ericales	Flower count	Forb
<b>Ranunculus acris</b>	Ranunculaceae	Ranunculales	Flower count	Forb
<b>Rhinanthus minor</b>	Orobanchaceae	Lamiales	Flower count	Forb
<b>Rumex acetosa</b>	Polygonaceae	Caryophyllales	Length of inflorescence	Forb
<b>Sagina saginoides</b>	Caryophyllaceae	Caryophyllales	Flower count	Forb
<b>Sibbaldia procumbens</b>	Rosaceae	Rosales	Flower count	Forb
<b>Taraxacum spp.</b>	Asteraceae	Asterales	Flower head count	Forb
<b>Thalictrum alpinum</b>	Ranunculaceae	Ranunculales	Flower count	Forb
<b>Trichophorum cespitosum</b>	Cyperaceae	Poales	Flower count	Graminoid
<b>Trientalis europaea</b>	Primulaceae	Ericales	Flower count	Forb
<b>Trisetum spicatum</b>	Poaceae	Poales	Length of inflorescence	Graminoid
<b>Veronica alpina</b>	Plantaginaceae	Lamiales	Flower count	Forb
<b>Viola biflora</b>	Violaceae	Malpighiales	Flower count	Forb
<b>Viola palustris</b>	Violaceae	Malpighiales	Flower count	Forb