Norwegian University of Life Sciences

Effects of plant-plant interactions on the performance and abundance of Campanula uniflora in Dovre, Norway

Erlend Ekeland

Master of Science in Natural Resource Management

Preface

I hereby present my MSc in Natural resource management at the Norwegian University of Life Sciences (NMBU). It was an interesting and challenging journey departing from an idea, through fieldwork and analysis to a final product. The wonderful sunny days during fieldwork at Dovre was the highlight! First and foremost, I want to thank my main supervisor, Erik T. Aschehoug, and my co-supervisors Kari Klanderud and Ieva Rozite-Arina for always having time for me, giving great feedback, and being supportive and optimistic. I also thank Ieva Rozite-Arina and Thomas Luypaert for patiently helping me with statistics. I have learned a lot from all of you. And a great thanks to my parents, Synnøve Myklebust, and friends who helped me with fieldwork and commenting on the text.

Ås, May 31st, 2021

_____

Erlend Ekeland

Abstract

Anthropogenic environmental changes cause direct and indirect negative effects on alpine ecosystems. Human activities are accelerating the greenhouse effect and fragmenting and changing habitats. Increased temperature has made it easier for species from lower elevations to increase their habitat to higher elevations, which results in novel interactions between species.

Plant-plant interactions are a key process driving plant community composition. Species in plant communities can have negative interactions with a neighbor, and positive interactions with another, affecting a third neighbor indirectly. Plants compete for light, space, water, and nutrients. However, we expect facilitation such as enhanced microclimate and improved water and nutrient availability to be more important than competition in alpine plant communities. The aim of this study is to investigate how competition and facilitation affect the performance, abundance and fine spatial-scale distribution of *Campanula uniflora L.*

In the summer of 2020, I conducted a removal experiment where I compared the performance of individuals growing alone naturally, with individuals growing in intact vegetation, and individuals that had their surrounding vegetation removed. Performance was based on recorded growth variables of 122 individuals of *C. uniflora* from June to August at the mountains Steinhøi and Råtåsjøhøi in the Dovrefjell region of central Norway. The plants occurred in patches on top of wind exposed ridges in calcareous soils. To relate *C. uniflora* to the rest of the vegetation I did a vegetation analysis where I determined the percentage cover of all species present in *C. uniflora*'s habitat. In addition, during the analysis I recorded what substrate each individual of *C. uniflora* grew in. A generalized linear model was used to predict biomass accumulation in different treatments.

C. uniflora showed no significant response to removal of neighboring vegetation. Individuals that grew alone naturally had significantly lower biomass than the control and removal group. The vegetation analysis showed that open ground with no vegetation covered 45-60%, lichens 20-40%, mixed plant community 15-25%, *Silene acaulis* 3.5% and *C. uniflora* 0.3%.

The proportion of *C. uniflora* growing within *S. acaulis* was surprisingly high. Nearly 40% of all *C. uniflora* individuals grew within *S. acaulis* cushions. This finding emphasizes the importance of positive interactions in harsh environments and suggests a strong positive relationship between *S. acaulis* and *C. uniflora*.

Contents

Introduction

Anthropogenic environmental changes such as deforestation, conversion of habitats to agriculture (Feddema et al., 2005), nitrogen deposition (Matson et al., 2002), and strengthening of the greenhouse effect, are contributing to an accelerating rate of biodiversity loss (Butchart et al., 2010; IPCC, 2014). At present, an estimated one million species of animals, plants, and insects are threatened with extinction (Almond et al., 2020). This ongoing global biodiversity loss represents a major threat to ecosystem functioning and is predicted to have strong negative consequences for systems with high levels of species loss (Hooper et al., 2012). Therefore, to minimize future losses in biodiversity, it is essential to study the ecosystems which are most at risk to anthropogenic threats and understand ways to minimize future biodiversity loss.

In Norway, 73 out of 446 red-listed vascular plant species are associated with alpine ecosystems (Henriksen & Hilmo, 2015). Moreover, eight out of 19 threatened habitats on the Norwegian red list of threatened habitats are found above the tree-line (Grytnes et al., 2018). Alpine systems are projected to be heavily impacted by the direct effects of climate change, potentially resulting in an annual average temperature increase of 1-3 °C (IPCC, 2014).

In addition to these direct effects, global warming is also expected to have indirect effects on alpine communities. Pants have either positive, negative, or neutral interactions with adjacent plants. Examples of negative interactions are competition for nutrient, water, space and light (Craine & Dybzinski, 2013). Positive interactions include facilitation through improved resource availability, providing a stable microclimate, or protection from competition (Bruno et al., 2003). The stress-gradient hypothesis states that the frequency of positive interactions increases with physical stress and low productivity (Bertness & Callaway, 1994). As alpine plant species are typically adapted to stressful environments, they tend to display facilitative rather than competitive interspecific interactions (Choler et al., 2001). For instance, alpine cushion species such as *Silene acaulis* are known to function as nurse plants in harsh environments by ameliorating environmental factors and providing beneficial growth and reproduction conditions for the plants they host (Callaway et al., 2002). However, species from lower elevations are projected to shift their range to higher elevations in response to global warming (Chen et al., 2011; Steinbauer et al., 2018). Consequently, novel alpine community assemblages and altered interspecific interactions will be formed (Alexander et al., 2015). If the species that expand their range upslope into alpine environments display competitive rather

than facilitative traits, it is possible these new arrivals will outcompete the existing typical stress-tolerant alpine plant species.

To better understand these potentially negative indirect effects, manipulative experiments are required (Aschehoug & Callaway, 2015). For instance, removal experiments, where all or some of the above-ground vegetation is removed from the area surrounding the species of interest, allow us to study how different groups of species interact with each other under different environmental conditions (Cavieres et al., 2014). Olsen et al. (2016) investigated the impact of a dominant functional group of graminoids on species of subordinate forbs in seminatural grasslands and found that increasing temperature turned the interactions from facilitative to competitive between dominant and subordinate species. This suggests that rising temperatures caused by future global warming may have serious consequences for population dynamics and will likely reduce the survival of subordinate species.

The future threat of climate change in alpine environments and the potential loss of alpine species is of great concern and needs to be further studied (Dirnböck et al., 2011; Kullman, 2010). As such, in this study I investigate how plant-plant interactions affect the rare alpine plant *Campanula uniflora L. C. uniflora* is a perennial sub-nival herb with one to several ramets, and is geologically restricted to areas with calcareous soils, along dry ridges with a high abundance of lichens (Ryvarden, 1994). The species is abundant in many locations within its restricted area (Gjærevoll, 1990). *C. uniflora* is listed as least concern (LC) on the Norwegian red list, however it is nearly threatened (NT) in Svalbard (Henriksen & Hilmo, 2015). By conducting a removal experiment along an elevational gradient, I will elucidate how plant-plant interactions change with increasing abiotic stress and understand how this affects *C. uniflora* performance. Additionally, I will conduct a plant community analysis to relate the study species to its environment, thus better describing its fine-scale spatial distribution and abundance.

In this set of experiments, I will address the following questions: i) How does removal of neighboring vegetation affect the performance of *C. uniflora*? ii) How do the treatment and control group perform compared to individuals with no natural neighbors? iii) How does elevation affect the interaction between *C. uniflora* and neighboring vegetation? iv) How does elevation affect the abundance of *C. uniflora*? v) What is the relationship between the substrates: *S. acaulis*, lichens, and open ground and the performance of *C. uniflora*?

I hypothesize that *C. uniflora* will show a positive response in biomass accumulation following the removal of neighboring vegetation at low elevation sites due to liberation from competition, but a negative effect on biomass at higher elevations due to loss of facilitative interactions (Bertness & Callaway, 1994; Callaway et al., 2002). I predict that individuals growing alone naturally will perform better at a lower elevation than at higher elevations. Furthermore, I predict *C. uniflora* to be least abundant at low elevations and most abundant at high elevations. Finally, I predict that there will be a positive relationship between the nurse plant *S. acaulis* and the performance of *C. uniflora*.

Material and methods

Study area

My study was conducted in the Knutshø landscape conservation area in the eastern part of Dovrefjell in central Norway in Innlandet county. *C. uniflora* was found at 1300-1500-meter elevation on the southward facing slopes of the mountains Steinhøi (62°15'27.7"N 9°51'56.8"E) and Råtåsjøhøi (62°16'19.8"N 9°48'25.0"E; Figure 1). The area is characterized by wide valleys with gentle slopes and mountains with rounded tops (Elven & Fremstad, 1998). The bedrock is lime-rich green slate or phyllite that easily weathers (NGU, 2021) and promotes a rich flora (Artsdatabanken, 2015). The tetra term in 2020 was 10.5 °C and the average total precipitation in the tetra term was 48.6 mm (Yr.no, 2021). The fieldwork took place between June 19, 2020 and August 18, 2020.
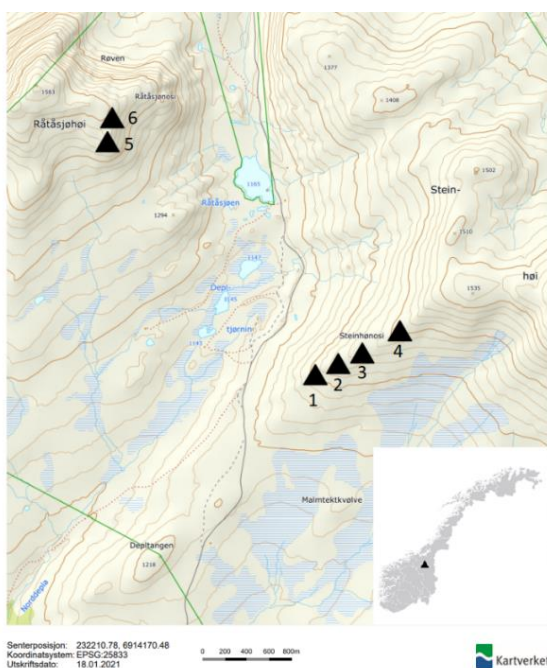

Figure 1. Map over the mountains Råtåsjøhøi and Steinhøi in Einundalen, Norway. The sites are marked with numbers 1-6.

Study species

Campanula uniflora is a perennial herb in the Campanulaceae family. The species has a west arctic distribution, and in Norway, the distribution is bicentric. It is found in Nordland, Troms, and Finnmark in the north, and Jotunheimen, Lom, and Dovre in the south. The plant is exclusively found in alpine areas with calcareous soils (Ryvarden, 1994).

The species is easy to distinguish from other Campanulas because it has only one nodding blue flower at the top of the stem (Figure 2). However stems with several flowers are normal in Greenland (Ægisdóttir & Thórhallsdóttir, 2006). It grows to be 5-10 cm tall and has lancet-shaped leaves. The seeds are wind-dispersed from a relatively large capsule (Ryvarden, 1994). It is considered "Least Concern" (LC) in Norway (Gjærevoll, 1990). At early growing stages it is recognizable by growing prostrate at first, then upwards, and by its vibrant green color. It is usually found around 1500-meter elevation. The species is rhizomatous which can make it hard to identify separate individuals (Lid, 1963).

Figure 2. C. uniflora at site 1 on Steinhøi, a mountain in Einundalen, Norway (Rondane in the background). June 2020. Photo: Erlend Ekeland

Data collection

Campanula uniflora had previously been documented on the two mountains Steinhøi and Råtåsjøhøi by Anders Breili (Artsdatabanken, 2013). I investigated these locations to find populations sufficient to establish sites. A site was defined by individuals at a certain elevation and with the same direction of the slope. At Steinhøi there were four sites (Figure 1), two at low elevation (Site 1 and 2), and two at middle elevation (Site 3 and 4). At Råtåsjøhøi there were two sites at high elevation (Site 5 and 6). There were 13 individuals at site one (1347m), 32 at site two (1357m), 16 at site three (1398m), and 30 individuals at site four (1408m). At site five (1504m) I found 18 individuals and at site six (1521m) I found 15. A GPS was used to record elevation at the different sites.

I used all of the individuals located at each site in order to have the highest possible statistical basis. This resulted in a different number of individuals at the different sites. Before I started the experiment, I excavated a few individuals that were not part of the experiment to understand the range of the rhizomes and the root system. I found that it could be difficult to have full confidence about which ramet belonged to which individual. Based on this, I estimated that plants with a distance >30 cm apart represented different individuals. To ensure that I worked with separate plants in my experiment, I defined individuals >100 cm to the next closest individual as separate.

Each individual was assigned a unique replicate number and individuals were divided into three groups by treatment. The plants in the first group were naturally growing alone (alone group). The plants in the second group were growing in their natural plant- or lichen community (control group). In the third group I removed all of the aboveground vegetation within a 5 cm radius (removal group; Figure 3). The removal treatment was imposed only at the start of the experiment (June 23), since there were no neighbors to remove later in the growing season. Biomass removal has long been a common method for studying interspecific interactions, and there are several different approaches (Díaz et al., 2003). By removing only aboveground material, belowground parts of the plants can still grow. On the other hand, removing belowground biomass may potentially harm the target plant and disrupt soil biota. There are also uncertainties about whether removal experiments have long-term effects on the experimental sites, how big and what shape of removal does the least damage, and what time of the year is least harmful (Aarssen & Epp, 1990).

Figure 3. The removal treatment. 5 cm in radius of aboveground vegetation where removed. Steinhøi 23.06.2020. Photo: Erlend Ekeland

To make sure that there were an equal number of individuals in the control and removal group, I paired individuals that were similar in size and growing conditions.

I recorded the substrate of each individual *C. uniflora* into four categories: 1) within a *Silene acaulis* cushion, 2) in soil with no vegetation, 3) within a lichen community, and 4) within a plant community.

The following growth variables were registered for each stem of the individual, henceforth called ramet. Height was measured from the ground to the sepals to prevent harm to the flower, each leaf was counted, and the ramets were categorized into four different flowering stages. 0: only stem and leaves and no bud, 1: stem and leaves with bud, 2: flowering, 3: finished flowering. These registrations were done three times: at the start (June 23), middle (July 22), and end of the experiment (August 18).

After the last measurements, all of the ramets were harvested. Above-ground plant parts were carefully put into individual envelopes, dried at 40 °C for 72 hours, and weighed. A few ramets still had closed seed capsules. I counted the number of seeds per ramet and weighed them. Unfortunately, not enough ramets had seeds to do reliable statistical analysis.

Vegetation analysis

I did a vegetation analysis at each site to relate *C. uniflora* to the rest of the vegetation. I set up a transect grid with two measuring tapes that served as the X- and the Y-axis. The origin was carefully recorded by GPS (Appendix 1). The X-axis was stationary while the Y-axis was placed at 0m, 3m, 6m, 9m, 12m, and 15m along the X-axis. I used a 0.5m by 0.5m square to identify the percent cover of all species inside the square along the Y-axis. There were ten squares along each of the six transects on alternating sides at 0m, 1.5m, 3m, 4.5m, 6m, 7.5m, 9m, 10.5m, 12m, and 13,5m (Figure 4). This gave me 60 squares of 0.5m by 0.5m at each site, and a total of 360 squares across all sites. See (Appendix 2) for a list of species found in the analysis and their average cover. The vegetation analysis took place July 6 – 8, 2020.
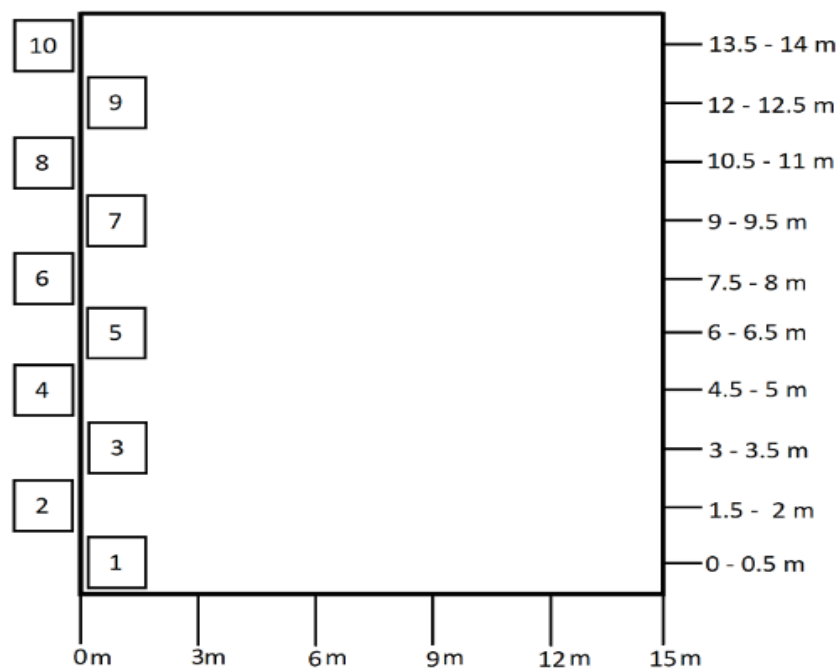

Figure 4. The set up for my vegetation analysis. A transect with ten 0.5m by 0.5m squares where placed along the x-axis at 0, 3, 6, 9, 12 and 15m. The corners of the ten squares along the y-axis is marked on the right side of the figure.

Crustose lichen species and *Umbilicaria*, were considered a part of the rock and not a part of the plant community. If a species was present but covered less than five percent, I recorded it as 1 percent. In addition, for every *C. uniflora* ramet that was recorded inside a square, I noted the X and Y coordinates, the substrate, and the flowering stage.

Data analysis

Statistical tests and analysis were conducted using R-Studio and R version 4.0.3 (RCoreTeam, 2020). The response variable biomass per ramet was calculated based on the measured dry mass. The total plant dry mass was divided by the number of ramets to account for individual size.

To check the biomass data distribution, I used a Shapiro-Wilk normality test. The data were not normally distributed (p-value = 4.243e-06). I transformed the data using a logarithmic scale and re-tested for normality (p-value = 0.1055; Appendix 3). To further investigate the data distribution, I ran a QQ-plot where I compared distribution types using the packages "fitdistrplus" (Delignette-Muller & Dutang, 2015) and "flexsurv" (Jackson, 2016). My dataset was gamma distributed (Appendix 4). The assumptions were met using a Gamma model with a logarithmic transformation link.

The global model consisted of the response variable biomass per ramet, and the predictor variables elevation, substrate, and treatment. I conducted a model selection process using the "dredge" function from the package "MuMIn" (Barton, 2020). The "dredge" function tries all possible combinations of predictor variables from the global model and ranks them based on delta score, weights and AICc (Akaike Information Criterion for small sample sizes; Appendix 5). The final model consisted of the response variable biomass per ramet and the predictor variable treatment. To test the effects of treatment on the performance of *C. uniflora*, I used a generalized linear model (GLM) with gamma distribution and a logarithmic link function (Table 1). The GLM was fitted using the "lme4" package (Bates et al., 2015).

I plotted the vegetation analysis and the total number of individuals that grew inside the different vegetation types to show the connection between vegetation types and the abundance and distribution of C. uniflora.

Post hoc analysis and contrasts were done on the GLM using pairwise comparison from the package "emmeans" (Lenth, 2020). The packages "Car" (Fox & Weisberg, 2019) and "Multicomp" (Hothorn et al., 2008) were also used to run the post hoc and contrast (Appendix 6). All figures were made using the "ggplot2" package (Wickham, 2016).

Results

I found a total of 235 individuals of *C. uniflora:* 90 individuals at Steinhøi and 32 individuals at Råtåsjøhøi. In addition, I recorded 122 individuals in the vegetation analysis, nine of them were also part of the experiment. The vegetation analysis was conducted later in the growing season than the experimental setup. At this point in time the plants were much easier to identify, thus the reason I found many additional individuals at the experimental sites.

I tried several different model types to test the effect of substrate type on the abundance of *C. uniflora*. The GLM's with family "poisson", "quasipoisson", and negative binomial models were all suffering from model convergence issues. In addition, the chi-square test on the number of individuals growing in different substrates (p = 0.3632), and on the number of individuals at different elevations (p = 0.4115) were not significant. I did not have enough data to do reliable statistical tests. However, I plotted the number of individuals that grew in different substrates at each site and combined it with the data from the vegetation analysis (Figure 5) to visualize abundance across the elevation gradient of *C. uniflora*.

At the lowest elevation site (1347m), *C. uniflora* had the lowest recorded abundance, with a total of 16 individuals. Most of the individuals grew in the open (56%), and some within lichens (25%) and *S. acaulis* (19%; Figure 5). I recorded 26 individuals at site two (1357m). Few individuals grew within *S. acaulis* cushions (15.2%). The other individuals were equally distributed in the open (41%), and within lichen communities (43.5%; Figure 5). At the middle elevation site (1398m), 31 individuals were recorded. Individuals grew mainly within *S. acaulis* (77.5%), some in lichens (16%), and few grew in the open (6.5%; Figure 5). Site four (1408m) had the highest abundance with 56 individuals. Individuals grew mostly within *S. acaulis* (68%), some in lichen communities (30%) and very few in the open (2%; Figure 5). At site five at high elevation (1504m) were 36 individuals recorded. The majority grew within lichens (77.7%), and few grew within *S. acaulis* (13.8%) and in the open (8%; Figure 5). At the highest elevation site (1521m), 40 individuals were recorded. Half of the individuals grew in lichen communities, and some grew within *S. acaulis* (30%) and in the open (20%; Figure 5).
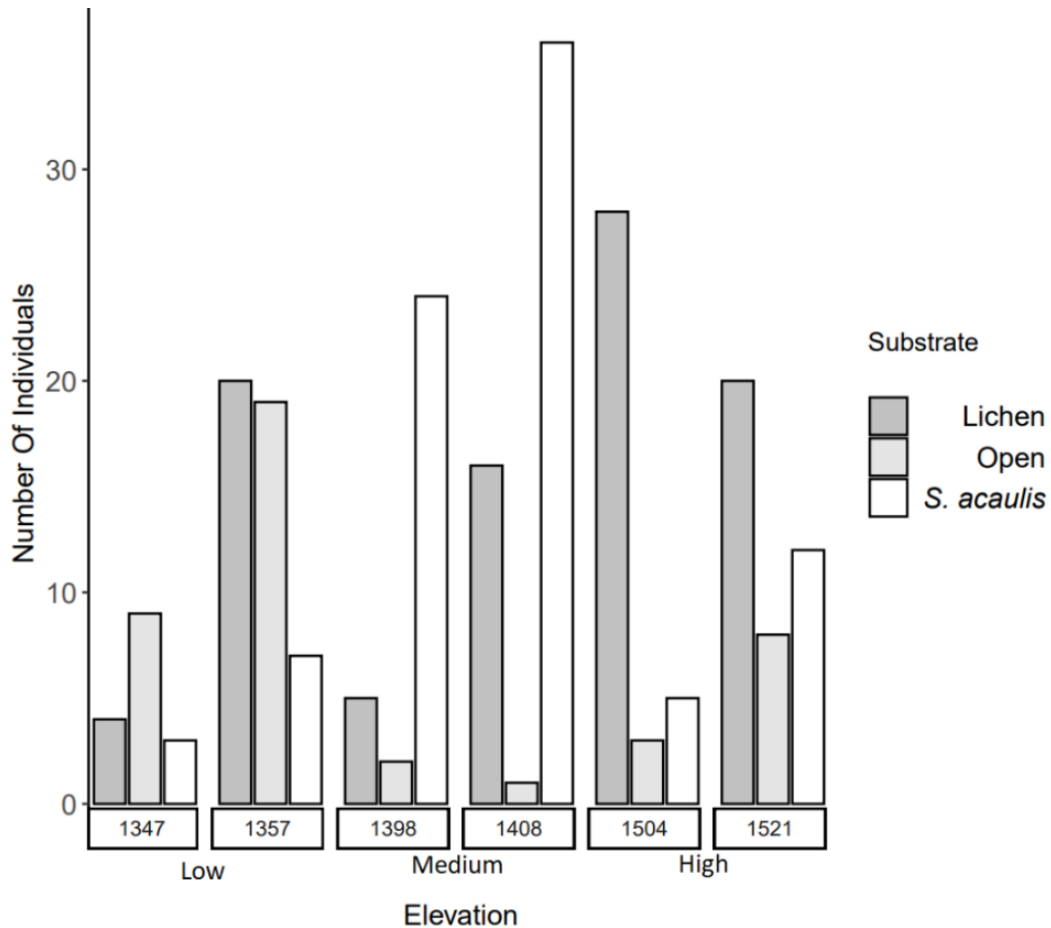
Figure 5. Total number of individuals that grew in the different substrates across the elevation gradient. The number of individuals is the combination of plants recorded in the experiment and the plants found in the vegetating analysis. The sites at elevations 1347 – 1408 is located at Steinhøi, and the sites at elevations 1504 and 1521 is at Råtåsjøhøi.

Individuals that grew alone had significantly lower biomass per ramet compared to the control and removal groups (Table 1). Removing neighboring vegetation had no significant effect on the biomass of *C. uniflora* (Table 1). Although, the interaction between treatment and elevation was not significant and was therefore excluded from the model, there was an indication of individuals in the removal group accumulating slightly more biomass per ramet across middle and high elevations during the growing season than individuals in the control group (Figure 6).

Table 1. Summary output from the generalized linear model (GLM), with biomass per ramet as response variable and treatment as explanatory variable. The group is showing that "Control" and "removal" were not significantly different from each other, and that "Alone" were significantly different from "Control" and "Removal".

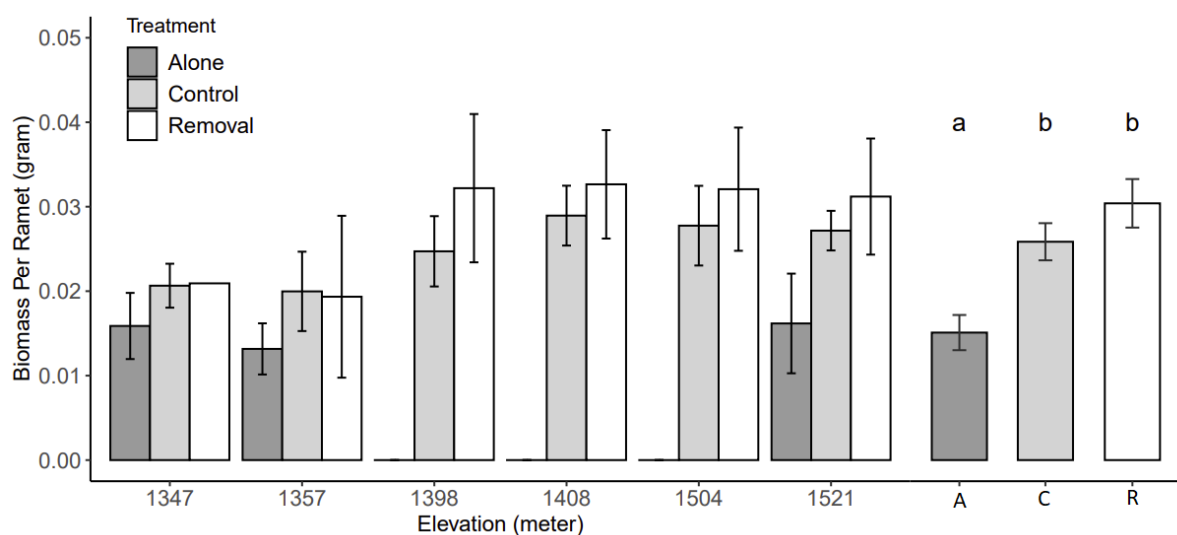| Treatment	Estimate	Std. Error	t - value	p - value	Group
Alone	-4.2275	0.1337	-31.619	< 2e-16	a
Control	0.5782	0.1582	3.655	0.000418	b
Removal	0.7488	0.1630	4.594	1.31e-05	b

Figure 6. Effects of the treatments "alone" (no natural neighbors), "control" and "removal" (natural neighbors removed) and elevation (m) on average biomass per ramet (g) in the growing season 2020. Error bars shows means and standard errors. "A", "C" and "R" is the average biomass per ramet across the elevation gradient for the treatments "Alone", "Control" and "Removal". The significant letters "a" and "b" shows that "A" is significant different from "C" and "R".

The individuals at low elevation sites in both control and removal groups accumulated less biomass compared to middle and high elevation sites. Plants in the alone group performed poorly across the elevation gradient compared to control and removal groups (Figure 6).

Substrate had no significant effect on *C. uniflora*'s biomass and was excluded from the final model (Appendix 5). However, there was an indication of a shift from greatest biomass when the plants were growing in a lichen community at low elevation to greatest biomass when the plants grew inside *S. acaulis* at high elevation (Figure 7).
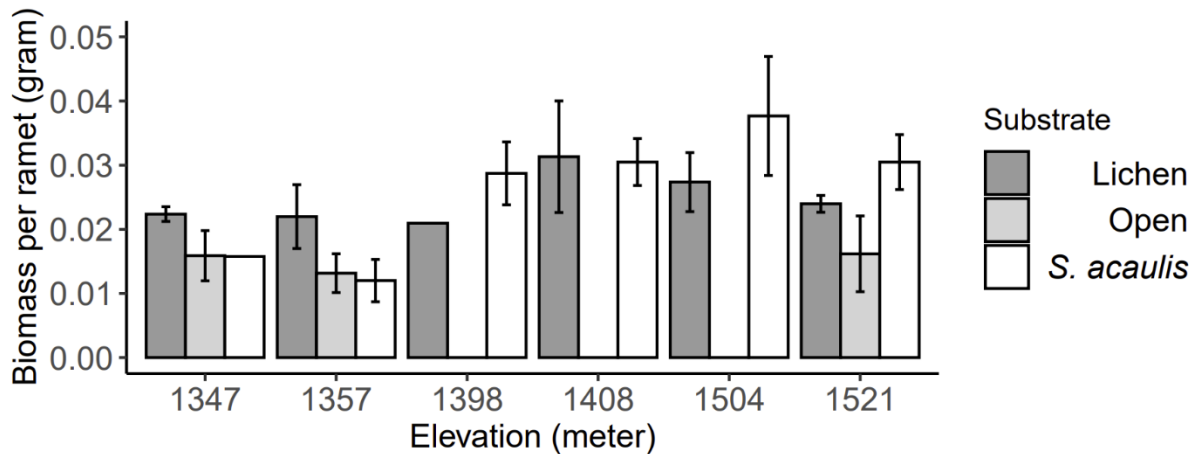
Figure 7. Effects of the substrates "Lichen" (growing inside a lichen community), "Open" (Growing alone naturally and are the same individuals who is addressed "alone") and "S. acaulis" (Growing inside the cushion) and elevation (m) on average biomass per ramet (g) in the growing season 2020. The Lichen and S. acaulis bars is the combined average of the plants in the control and removal groups. Bars shows means and standard errors.

The vegetation analysis showed that no vegetation (open) was the most common cover type at the two mountains (45 – 60%), lichens were the dominant vegetation group covering 20 – 40 %, and mixed plant communities (other) covering 15 – 25%. Both *S. acaulis* and *C. uniflora* were relatively rare species, covering 3.5% and 0.3% on average respectively (Figure 8).

S. acaulis was most abundant at middle and high elevation. The number of *C. uniflora* growing within *S. acaulis* was highest at middle elevation. The proportion between vegetation percentage cover and the number of *C. uniflora* individuals that grew inside *S. acaulis* is strikingly high at both middle and high elevation (Figure 5 and Figure 8). Approximately 15% of the individuals grew within *S. acaulis* cushions at low elevation, where *S. acaulis* covered less than two percent. *S. acaulis* covered less than ten percent at middle and high elevation (Figure 5 and Figure 8). Yet, about 75% grew within *S. acaulis* at 1398m elevation, and 50% at 1408m elevation. At the high elevation sites, roughly 15% grew within *S. acaulis* at 1504 and 33% at 1521m. *S. acaulis* covered less than ten percent at middle and high elevation (Figure 5 and Figure 8).
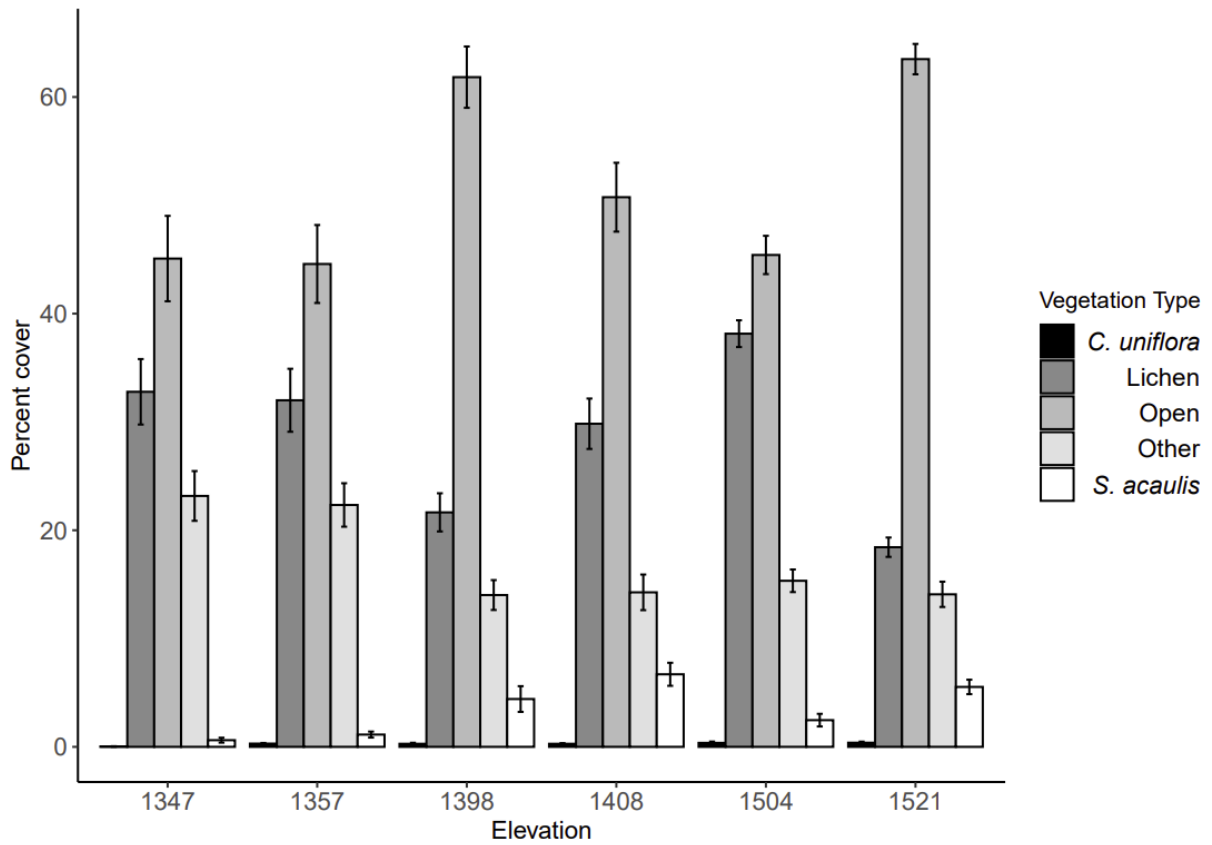
Figure 8. The average percentage cover of vegetation types across the elevation gradient at both mountains combined. Bars represent means and standard errors. Open refers to area with no vegetation. Other refers to a mixed plant community.

Eight individuals died between the first and second measurements. Two in the alone group, two in the control group, and three in the removal group. Five individuals died between the second and the last measurement. One in the alone group, one in the control group, and three in the removal group. In total three individuals died in both the alone and control group and seven died in the removal group. All individuals were partly or completely colored brown/red by anthocyanin as a response to sun exposure (Field observation).

Discussion

Removal of neighboring vegetation did not significantly affect the performance of *C. uniflora* (Figure 6). However, individuals with neighbors or those which had neighbors removed performed significantly better than individuals that grew alone naturally (Figure 6). This trend was strongest at high elevation. Interestingly, in contrast to my hypothesis, there was no difference in performance at low elevation sites among individuals growing alone naturally, with neighbors, or had neighbors removed (Figure 6), where competition was expected to negatively affect the performance of *C. uniflora*. This suggests that neighboring vegetation has a neutral interaction with *C. uniflora* at low elevations. On the other hand, the average mass per ramet of individuals at low elevation was less than individuals at middle or high elevations (Figure 6). This suggests that environment has a negative effect on individual performance at low elevation, and that facilitation has a strong positive effect at middle and high elevation sites, which is in line with the stress gradient hypothesis (Bertness & Callaway, 1994).

In contradiction to my hypothesis, the removal of neighboring vegetation at high elevation sites did not reduce the performance of *C. uniflora* (Table 1). On the other hand, individuals in both the control and removal groups performed significantly better than individuals in the alone group at high elevation sites, suggesting that *C. uniflora* is facilitated by neighboring vegetation. Surprisingly, individuals growing alone naturally at the high elevation sites performed the same as in low elevation sites (Figure 6), opposite of my prediction. None-the-less, increased performance of *C. uniflora* when growing with neighbors at the middle and high elevation sites indicates a positive interaction between *C. uniflora* and its neighbors because of increasing abiotic stress. This further suggests that positive interactions are important for the persistence of *C. uniflora*. This trend was also found in a large-scale experiment on the effect of positive interactions (Callaway et al., 2002). Few studies have been conducted with a focus on *C. uniflora*, but relatable studies on other alpine specialist species (Olsen et al., 2016) suggest that facilitation had stronger effects on the performance than temperature, which explains why the alone group performed the same along the elevation gradient.

Elevation was a determining factor for the abundance of *C. uniflora*. Low elevation sites had the lowest abundance. At these sites, the majority of the individuals were found growing in the open, less within lichens and a few grew within S. acaulis (Figure 5). This suggests that while competition doesn't appear to affect the performance of established individuals of *C. uniflora*, competition may have a negative effect on the recruitment of *C. uniflora*, leading to smaller,

less stable populations at low elevations. Middle elevation sites had the highest abundance of *C. uniflora* of all sites. The majority of the individuals were found within in *S. acaulis* cushions (Figure 5). At high elevation sites, *C. uniflora* was almost as abundant as in middle elevation sites. The majority shifted to grow within lichen mats (Figure 5). These two shifts in substrates suggest that *C. uniflora* is facilitated mainly by *S. acaulis* cushions at middle elevations and mainly lichens at high elevations and that the abundance of *C. uniflora* changes along the stress gradient in response to plant-plant interactions.

Recent studies have concluded that plant-plant interactions change along the stress gradient, with interactions going from mainly competitive where resources are the limiting factor to mostly facilitative where abiotic factors limit plant growth (Callaway et al., 2002; He et al., 2013; Kjaer et al., 2018; Olsen et al., 2016). Although, no significant effects were found in this study, the observed trend in biomass per ramet suggests that *C. uniflora* shifted from performing slightly better when living inside lichen mats at low elevation, to performing equally at middle elevation, and best within *S. acaulis* at high elevation (Figure 7), which is in line with my prediction. The shift in performance suggests that *S. acaulis* is a superior facilitator of *C. uniflora* when stress exceeds a threshold. Similar to my results, Kjær et al. (2018) found that *S. acaulis* shifted from facilitating *Bistorta vivipara* when the stress was high, to neutral interactions when stress was lower. Taken together, these finding show that the interaction between *S. acaulis* and other species is dependent upon abiotic stress levels.

Interestingly, despite the potential increased performance in terms of biomass per ramet within *S. acaulis* at higher elevations, the abundance of *C. uniflora* found within lichens was 2-5 times higher than that found in *S. acaulis*. This result suggests that at high elevation sites lichens could have an important facilitative impact on the abundance of *C. uniflora,* but the effect of *S. acaulis* may be more important concerning the performance of the plant. Additionally, plants which were subject to the removal treatment did not perform worse than the control group at middle and high elevations. This result is opposite to what Olsen et al (2016) found. The alpine species *Veronica alpina* and *Viola biflora* had a negative response to neighbor removal compared to their control.

The number of individuals that were found growing within *S. acaulis* cushions (Figure 5) was disproportionately high compared to the average percent cover of *S. acaulis* (Figure 8). For instance, of the recorded individuals at middle and high elevations, 48 % grew within *S. acaulis* (Figure 5) – despite *S. acaulis* proportionally contributing much less to the percent vegetation cover (Figure 8). Even at low elevation sites, where *S. acaulis* was almost as rare as *C. uniflora*,

both species occurred together 16% of the time (Figure 5). Lichens, on the other hand, constituted the dominant vegetation type covering 20 – 40%, but were found to grow proportionally less with *C. uniflora* as a direct neighbor. Across the elevation gradient, 42% of the individuals grew with lichens as their only neighbor (Figure 5), which is likely the result of lichens constituting the dominant vegetation type.

Cavieres et al. (2007a) found that seedling survival was significantly higher for their three study species within the cushion plant *Laretia acaulis* compared to those in the open. This can explain the high proportion of individuals within *S. acaulis* in my study. Firstly, vegetation analysis showed that 40-60% of the ground at the two sites was without vegetation (Figure 8). However, very few individuals were found in the open, and the GLM showed that plants growing alone generally perform worse than those in lichens or *S. acaulis* cushions (Table 1), suggesting that seeds ending up in the open are less likely to germinate and survive. Secondly, the chance of seeds getting stuck in *S. acaulis* cushions on the wind-exposed ridges is noticeable. Combined with the enhanced microclimate and refuge from competition *S. acaulis* provides, these cushions might present ideal germination conditions for seeds of *C. uniflora*.

Based on field observations, I hypothesize that the sites at middle elevation had more optimal growing conditions for *C. uniflora*. The sites were situated at the edge of a terrace with a lower slope angle than the other sites, which could mean that rainwater carries away fewer nutrients and less soil. Combined with the increased abiotic stress caused by wind and temperature, the stress levels are high enough to prevent competitive plant groups from establishing, unlike lower elevation sites. Additionally, *C. uniflora* was not found in flat areas with deep soil where grasses and sedges were dominant, but instead grew exclusively in dry and crusted soils with minimal vegetation. Combined with its adaptation to avoid competition, I posit the plant does not cope well in moist environments over time.

About 25% of the ground at low elevation sites was covered by plant communities, compared to about 15% at middle and high elevation. Klanderud & Totland (2007) found that intact vegetation can prevent recruitment of new species in alpine ecosystems. *C. uniflora* was very rare within the low elevation sites. The low elevation sites in my study are situated at the lower end of recorded elevation for *C. uniflora* in southern Norway (Gjærevoll, 1990), suggesting the species dispersed from higher elevations. Therefore, I suspect recruitment of *C. uniflora* was constrained by competition at low elevation sites, hence affecting the local distribution and abundance negatively.

The distribution of *C. uniflora* was associated most closely with topography. The habitat of *C. uniflora* is limited by calcareous and base-rich soils and sites at alpine elevation with minimal competition. The species is wind-dispersed and relies on landing in suitable habitats to germinate (Gjærevoll, 1990). *C. uniflora* populations may be limited in size and distribution because of a lack of available micro-sites for germination. In a seed addition experiment in the Alps, Frei et al. (2012) made vegetation gaps by removing above-ground vegetation and scarifying the soil, to investigate germination and seedling survival of the rare alpine species *Campanula thyrsoides* L. They found that germination and seedling performance was significantly higher in disturbed plots than undisturbed, and that seed addition to new habitats was successful. In addition, previous studies on the breeding system of *C. uniflora*, showed that seeds kept in an incubator in a solution of Gibberellic Acid resulted in very high germination rates (Ægisdóttir & Thórhallsdóttir, 2006). Based on both findings I suggest that future research should explore dispersal and site limitation of *C. uniflora* through seed addition experiments in situ.

Following the stress gradient hypothesis (Bertness & Callaway, 1994), cushion plants such as *S. acaulis* and *Azorella* are known to facilitate other species in harsh environments and become neutral or negative for plant communities with decreasing stress (Choler et al., 2001). Cushion plants have several positive functions for their nursed species. They provide a stable microclimate, balancing the temperature and water availability within the cushion and increases the soil organic matter under the cushion (Cavieres et al., 2007b; Kikvidze et al., 2015; Molenda et al., 2012), increases nutrient availability (Anthelme et al., 2012), all of which provides them shelter from stress (Kikvidze et al., 2015). Cushion plants also have a higher pollinator diversity and more pollinator visits compared to non-cushion plants (Reid & Lortie, 2012). In addition, *S. acaulis* can function as a seed catcher using its soft canopy (Cavieres et al., 2007a).

When *C. uniflora* was growing in the substrate of lichens, it was possible to remove the above-growing vegetation without destroying the roots of the plant. When growing within *S. acaulis*, I discovered that the roots of *C. uniflora* were totally entangled with the roots of *S. acaulis*. I could only remove the above-ground plant material without severely damaging *C. uniflora* plants. *C. uniflora* still grew well within the remaining cushion plant after the removal treatment (Figure 3). I suspect that remnants of *S. acaulis* provided soil bound by remaining roots, water access, stable temperature, and nutrients. This may explain why the removal of aboveground plant material did not affect the performance. Further, this may be a flaw with the removal

method in experiments involving cushion plants and should be considered in future experiments.

It can take several growing seasons to clearly see the effect of removal experiments, and the results from long-term experiments give unique perspectives on complex systems and interactions (Brown et al., 2001). In comparison, my experiment took place during one growing season. It is possible that if my experiments were continued over several years or even just an additional growing season, a negative effect of neighbor removal may emerge.

Alpine ecosystems are expected to see direct and indirect effects of anthropogenic environmental change (IPCC, 2014). Increased temperature can potentially change the interaction between *C. uniflora* and other species (Klanderud & Totland, 2005a; Klanderud & Totland, 2005b). My results indicate that there is a gradual transition in plant-plant interactions from mainly neutral and competitive at lower elevation sites, to strong facilitation at middle and high elevation sites. This is in accordance with the stress gradient hypothesis (Bertness & Callaway, 1994). Competition appeared to limit abundance and distribution, and facilitation appeared to be important for increasing the performance of *C. uniflora*. Since competitive plants are expected to expand their habitat upward as a response to climate change (Steinbauer et al., 2018), *C. uniflora* and other stress-adapted species may be at risk of being outcompeted. Since *C. uniflora* rarely grew where competition occurred, I predict that novel interspecific interactions will have strong negative effects on the abundance and distribution of the species. Experimental warming experiments from Finse, Norway have shown that graminoids and forbs are increasing their abundance with increased temperatures (Klanderud & Totland, 2005b; Klanderud & Totland, 2007). This response to climate change is consistent worldwide in cold ecosystems (Elmendorf et al., 2012) and suggests that stress-adapted rare species in alpine ecosystems are at tremendous risk of extinction. *C. uniflora* may be at particular risk because it is known to be cleistogamous and has a strong self-compatible breeding system as an adaption to harsh and unpredictable environments where it is beneficial to produce a large number of seeds at a low cost (Warming, 1886; Ægisdóttir & Thórhallsdóttir, 2006). Self-pollinated species are especially at risk due to less genetic variation, which can lead the species into an extinction vortex (Tanaka, 2000). However, as long as benefactor species such as lichens and *S. acaulis* remain dominant members of alpine plant communities, C. *uniflora* may be able persist. To be able to draw more precise conclusions, further monitoring, and experiments on species and functional groups with increasing upward distribution and their impact on alpine ecosystems are needed.

Conclusions

This study highlights the importance of positive interactions in harsh environments. Competition appeared to constrain where *C. uniflora* could grow at low elevation sites, resulting in a negative effect on the abundance of the species. In contradiction to my hypothesis, removal of neighboring vegetation did not increase the performance at low elevation, nor did it decrease performance at high elevation. Individuals that grew alone performed the same across the elevation gradient, opposite of my prediction. The interaction between *C. uniflora* and neighboring vegetation at middle and high elevation was strongly facilitative. In contrast to my prediction, abundance of *C. uniflora* was highest at middle elevation. The strikingly high number of *C. uniflora* individuals that grew within *S. acaulis* cushions confirmed my prediction and provides further support for cushion plants as nurse species in alpine ecosystems.

C. uniflora is currently listed as "LC" in Norway, however the narrow niche of the species in addition to self-pollination makes it vulnerable to rapid environmental changes and it is therefore of interest from a conservation perspective. *C. uniflora* is also a specialist species in alpine ecosystems that appears to rely on facilitation by species such as *S. acaulis*. Therefore, changes to alpine ecosystems that results in the loss of nurse plant species may also result in the loss of biodiversity and reduced ecosystem function. My results contribute to the growing body of evidence that highlights the important consequences of anthropogenic changes to alpine ecosystems.

References

Alexander, J. M., Diez, J. M. & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, 525 (7570): 515-8. doi: 10.1038/nature14952.

Almond, R., Grooten, M. & Peterson, T. (2020). *Living Planet Report 2020-Bending the curve of biodiversity loss*: World Wildlife Fund.

Anthelme, F., Buendia, B., Mazoyer, C. & Dangles, O. (2012). Unexpected mechanisms sustain the stress gradient hypothesis in a tropical alpine environment. *Journal of Vegetation Science*, 23 (1): 62-72. doi: 10.1111/j.1654-1103.2011.01333.x.

Artsdatabanken. (2013). *Detaljert funninformasjon*. Available at: https://www.artsobservasjoner.no/Sighting/11641612.

Artsdatabanken. (2015). *kalkinnhold*. Available at: https://artsdatabanken.no/Pages/179743/Kalkinnhold.

Aschehoug, E. T. & Callaway, R. M. (2015). Diversity Increases Indirect Interactions, Attenuates the Intensity of Competition, and Promotes Coexistence. *Am Nat*, 186 (4): 452-9. doi: 10.1086/682901.

Barton, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. . Available at: https://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. . *Journal of Statistical Software*, 67 (1): 1-48. doi: 10.18637/jss.v067.i01

Bertness, M. D. & Callaway, R. (1994). Positive interactions in communities. *Trends Ecol Evol*, 9 (5): 191-3. doi: 10.1016/0169-5347(94)90088-4.

Brown, J., Whitham, T., Ernest, S. K. M. & Gehring, C. (2001). Complex species interactions and the dynamics of ecological systems: Long-term experiments. *Science (New York, N.Y.)*, 293: 643-50.

Bruno, J. F., Stachowicz, J. J. & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, 18 (3): 119-125. doi: https://doi.org/10.1016/S0169-5347(02)00045-9.

Butchart, S. H., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P., Almond, R. E., Baillie, J. E., Bomhard, B., Brown, C., Bruno, J., et al. (2010). Global biodiversity: indicators of recent declines. *Science*, 328 (5982): 1164-8. doi: 10.1126/science.1187512.

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., et al. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417 (6891): 844-8. doi: 10.1038/nature00812.

Cavieres, L. A., Badano, E. I., Sierra-Almeida, A. & Molina-Montenegro, M. A. (2007a). Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high andes of central Chile. *Arctic Antarctic and Alpine Research*, 39 (2): 229-236. doi: Doi 10.1657/1523-0430(2007)39[229:Mmocpa]2.0.Co;2.

Cavieres, L. A., Quiroz, C. L. & Molina-Montenegro, M. A. (2007b). Facilitation of the non-native Taraxacum officinale by native nurse cushion species in the high Andes of central Chile: are there differences between nurses? *Functional Ecology*, 0 (0): 070917205248001-??? doi: 10.1111/j.1365-2435.2007.01338.x.

Cavieres, L. A., Brooker, R. W., Butterfield, B. J., Cook, B. J., Kikvidze, Z., Lortie, C. J., Michalet, R., Pugnaire, F. I., Schob, C., Xiao, S., et al. (2014). Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecol Lett*, 17 (2): 193-202. doi: 10.1111/ele.12217.

Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B. & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333 (6045): 1024-6. doi: 10.1126/science.1206432.

Choler, P., Michalet, R. & Callaway, R. M. (2001). Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82 (12): 3295-3308. doi: Doi 10.1890/0012-9658(2001)082[3295:Facogi]2.0.Co;2.

Craine, J. M. & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, 27 (4): 833-840. doi: https://doi.org/10.1111/1365-2435.12081.

Delignette-Muller, M. L. & Dutang, C. (2015). fitdistrplus: An R Package for Fitting Distributions. . *Journal of Statistical Software*, 64 ((4)): 1-34.

Díaz, S., Symstad, A. J., Stuart Chapin, F., Wardle, D. A. & Huenneke, L. F. (2003). Functional diversity revealed by removal experiments. *Trends in Ecology & Evolution*, 18 (3): 140-146. doi: 10.1016/s0169-5347(03)00007-7.

Dirnböck, T., Essl, F. & Rabitsch, W. (2011). Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, 17 (2): 990-996. doi: https://doi.org/10.1111/j.1365-2486.2010.02266.x.

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H. & Day, T. A. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology letters*, 15 (2): 164-175.

Elven, R. & Fremstad, E. (1998). *Botaniske verdier i Dovrefjell-området, Hedmark*, 2/98.

Feddema, J. J., Oleson, K. W., Bonan, G. B., Mearns, L. O., Buja, L. E., Meehl, G. A. & Washington, W. M. (2005). The importance of land-cover change in simulating future climates. *Science*, 310 (5754): 1674-8. doi: 10.1126/science.1118160.

Fox, J. & Weisberg, S. (2019). An {R} Companion to Applied Regression, Third Edition. . In *Sage*. Available at: https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gjærevoll, O. (1990). *Maps of Distribution of Norwegian Vascular Plants*. Alpine Plants, vol. 2. Trondheim: Tapir Publishers.

Grytnes, J.-A., Evju, M., Høitomt , T. & Ihlen, P. G. A., P. A. (2018). *Fjell og berg. Norsk rødliste for naturtyper 2018. Artsdatabanken.* Available at: https://www.artsdatabanken.no/Pages/258605 (accessed: 11.05.21).

He, Q., Bertness, M. D. & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett*, 16 (5): 695-706. doi: 10.1111/ele.12080.

Henriksen, S. & Hilmo, O. (2015). *Norsk rødliste for arter 2015. Artsdatabanken, Norge*.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L. & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486 (7401): 105-108. doi: 10.1038/nature11118.

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, 50 (3): 346-363.

IPCC. (2014). *IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.*

Jackson, C. (2016). flexsurv: A Platform for Parametric Survival Modeling in R. . *Journal of Statistical Software,*, 70 ((8)): 1-33. doi: doi:10.18637/jss.v070.i08

Kikvidze, Z., Brooker, R. W., Butterfield, B. J., Callaway, R. M., Cavieres, L. A., Cook, B. J., Lortie, C. J., Michalet, R., Pugnaire, F. I., Xiao, S., et al. (2015). The effects of

foundation species on community assembly: a global study on alpine cushion plant communities. *Ecology*, 96 (8): 2064-9. doi: 10.1890/14-2443.1.

Kjaer, U., Olsen, S. L., Klanderud, K. & Pugnaire, F. (2018). Shift from facilitative to neutral interactions by the cushion plantSilene acaulisalong a primary succession gradient. *Journal of Vegetation Science*, 29 (1): 42-51. doi: 10.1111/jvs.12584.

Klanderud, K. & Totland, O. (2005a). The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, 93 (3): 493-501. doi: 10.1111/j.1365-2745.2005.01000.x.

Klanderud, K. & Totland, O. (2005b). Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology*, 86 (8): 2047-2054. doi: Doi 10.1890/04-1563.

Klanderud, K. & Totland, Ø. (2007). The relative role of dispersal and local interactions for alpine plant community diversity under simulated climate warming. *Oikos*, 116 (8): 1279-1288. doi: https://doi.org/10.1111/j.0030-1299.2007.15906.x.

Kullman, L. (2010). A Richer, Greener and Smaller Alpine World: Review and Projection of Warming-Induced Plant Cover Change in the Swedish Scandes. *AMBIO*, 39 (2): 159-169. doi: 10.1007/s13280-010-0021-8.

Lenth, R. V. (2020). emmeans: Estimated Marginal Means, aka

Least-Squares Means. R package version 1.5.3. Available at: https://CRAN.R-project.org/package=emmeans.

Lid, J. (1963). *Norsk og svensk FLORA*. 3 ed. Oslo: Det norske samlaget.

Matson, P., Lohse, K. A. & Hall, S. J. (2002). The globalization of nitrogen deposition: consequences for terrestrial ecosystems. *Ambio*, 31 (2): 113-9. doi: 10.1579/0044-7447-31.2.113.

Molenda, O., Reid, A. & Lortie, C. J. (2012). The alpine cushion plant Silene acaulis as foundation species: a bug's-eye view to facilitation and microclimate. *PLoS One*, 7 (5): e37223. doi: 10.1371/journal.pone.0037223.

NGU. (2021). *Berggrunnskart*. Available at: https://geo.ngu.no/kart/berggrunn_mobil/

Olsen, S. L., Topper, 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. *Glob Chang Biol*, 22 (5): 1915-26. doi: 10.1111/gcb.13241.

RCoreTeam. (2020). R: A language and environment for statistical computing. . Available at: http://www.R-project.org/

Reid, A. M. & Lortie, C. J. (2012). Cushion plants are foundation species with positive effects extending to higher trophic levels. *Ecosphere*, 3 (11). doi: Artn 96

10.1890/Es12-00106.1.

Ryvarden, L. (1994). *Norges planter*. Norges planter, vol. 4: J. W. Cappelens Forlag as.

Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., et al. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556 (7700): 231-234. doi: 10.1038/s41586-018-0005-6.

Tanaka, Y. (2000). Extinction of populations by inbreeding depression under stochastic environments. *Population Ecology*, 42 (1): 55-62. doi: https://doi.org/10.1007/s101440050009.

Warming, E. (1886). *Om Bygningen ogden formodede Bestøvningsmaade af nogle grønlandske Blomster*.

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis.

Yr.no. (2021). *Einunndalen*. Available at: https://www.yr.no/nb/historikk/graf/1-179701/Norge/Innlandet/Folldal/Einunndalen.

Ægisdóttir, H. H. & Thórhallsdóttir, T. E. (2006). Breeding System Evolution in the Arctic: a Comparative Study of Campanula uniflora in Greenland and Iceland. *Arctic, Antarctic, and Alpine Research*, 38 (3): 305-312. doi: 10.1657/1523-0430(2006)38[305:Bseita]2.0.Co;2.

Aarssen, L. W. & Epp, G. A. (1990). Neighbor Manipulations in Natural Vegetation - a Review. *Journal of Vegetation Science*, 1 (1): 13-30. doi: Doi 10.2307/3236049.
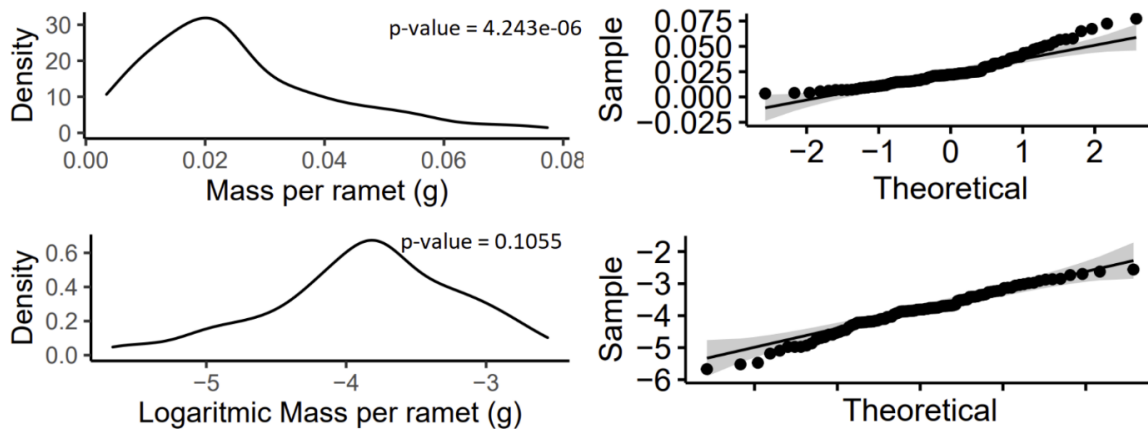
Appendix

Appendix 1. The origins of the transects used in the vegetation analysis. The x- and y-axis represents the angle on the measuring tapes when the compass was facing north.

| Mountain	Transect ID	Moh	GPS	32V UTM	x-axis	y-axsis
Steinhøi	1	1344	544186	6902264	260w	170s
Steinhøi	2	1361	544314	6902966	240w	155s
Steinhøi	3	1398	544635	6903125	245w	155s
Steinhøi	4	1407	544687	6903175	240w	150s
Råtåsjøhøi	5	1508	541865	9604863	230w	140s
Råtåsjøhøi	6	1519	541735	9604957	220w	130s

Appendix 2. List of species identified during vegetation analysis and their average percentage cover. "open" is ground with no vegetation.

Species:	Average percent cover:
open	51.861
Alectoria nigricans	5.050
Alectoria ochroleuca	6.064
Antennaria dioica	0.280
Arctostaphylos alpinus	0.347
Astragalus alpinus	0.097
Betula nana	0.497
Bistorta vivipara	0.158
Bryophyta	1.219
Campanula uniflora	0.275
Carex	4.475
Cerastium	0.038
Cetraria islandica	0.044
Cetrariella delisei	0.102
Cladonia	0.036
Cladonia arbuscula	0.405
Cladonia rangiferina	0.144
Cladonia stellaris	0.252
Diphasiastrum alpinum	0.017
Draba alpina	0.005
Dryas octopetala	1.936
Empetrum nigrum subsp. hermaphroditum	1.772
Festuca	2.475
	0.469
Flavocetraria nivalis	15.250
Hieracium alpinum agg.	0.014
Juncus trifidus	1.942
Kalmia procumbens	0.008

Luzula	0.055
Omalotheca supina	0.008
Parmelia saxatilis	0.302
Pedicularis palustris	0.150
Poa alpina	0.061
Ranunculus glacialis	0.319
Rhodiola rosea	0.013
Salix herbacea	0.766
Silene acaulis	3.478
Solidago virgaurea lapponica	0.069
Solorina crocea	0.044
Stereocaulon	0.016
Thalictrum alpinum	0.114
Thamnolia vermicularis	0.619
Vaccinium vitis-idaea	0.316
Vaccinum uliginosum	0.042

Appendix 3. Shapiro-Wilk normality test. The data met assumptions when logarithmically scaled.

Q–Q plot
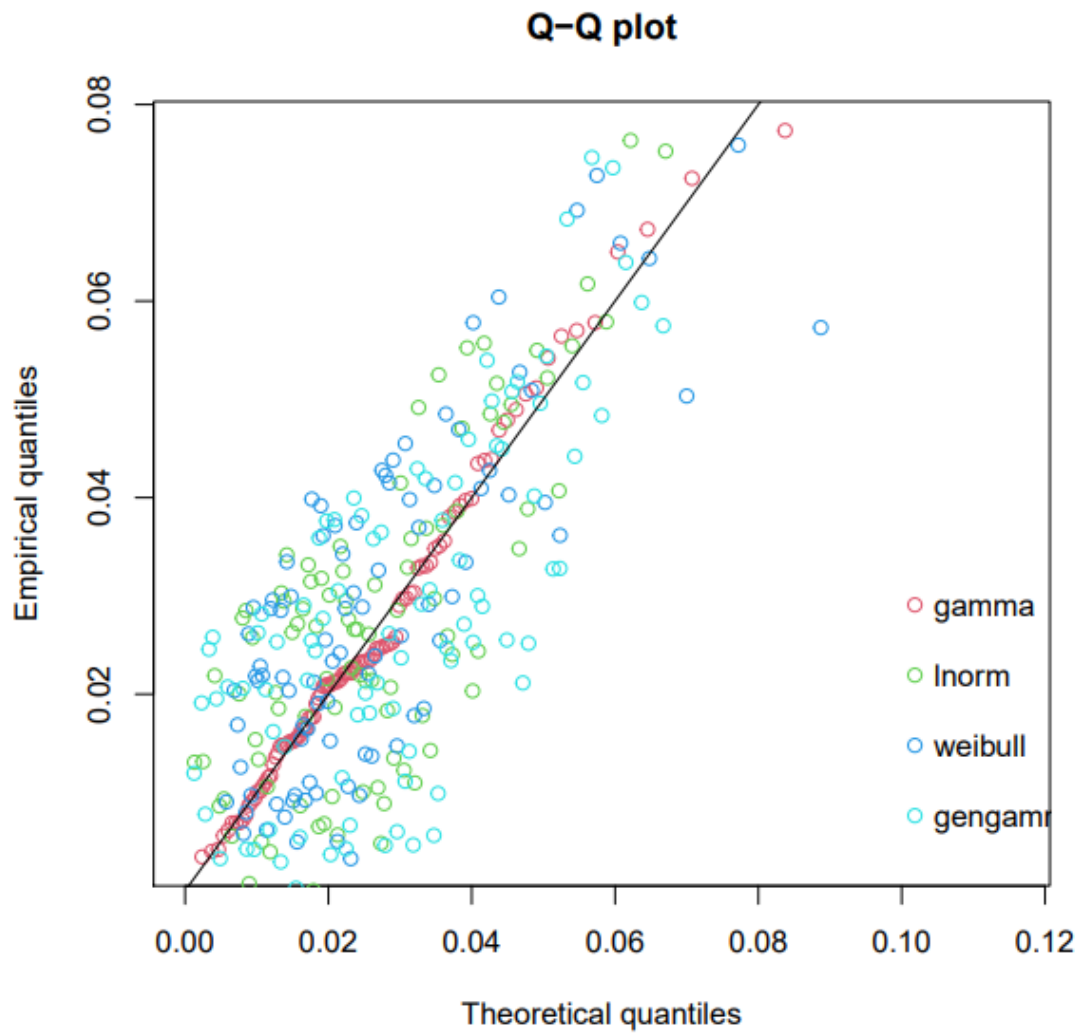
Appendix 4. Output from the (flexsurv) package. The line shows normal distribution, and the red dots describes the line best, indicating my data is gamma distributed.

Appendix 5. Model selection table. Model 5 were chosen due to most weight, and best delta and AICc score (Akaike Information Criterion for small sample sizes). The + symbols indicate variables that were included in the model. Only weighted models are included in the table. elv=elevation, sub=substrate, trt=treatment. The : symbol between variables means interaction.

Model ID	elv	sub	trt	elv:sub	elv:trt	sub:trt	AICc	delta	Weight
5			+				-582.9	0.00	0.443
3		+					-581.8	1.07	0.259
7		+	+				-581.3	1.60	0.199
39		+	+			+	-579.0	3.85	0.065
6	+		+				-576.0	6.86	0.014
4	+	+					-574.9	8.01	0.008
2	+						-574.2	8.65	0.006
8	+	+	+				-573.7	9.21	0.004
40	+	+	+			+	-571.2	11.70	0.001
1							-569.4	13.48	0.001

Appendix 6. Contrast analysis of the explanatory variable treatment. The contrast is based on the generalized linear model.

Contrast	Estimate	SE	p-value
Alone – Control	-0.578	0.158	0.0008
Alone – Removal	-0.749	0.163	<0.0001
Control - Removal	-0.171	0.126	0.3647