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Plant-plant interactions do not result in reproductive costs for *Silene acaulis* across an elevational gradient at Finse, Norway

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Preface

This thesis is the final product of my MSc in Ecology at the Norwegian University of Life Sciences (NMBU). The process has been both educational and interesting.

I want to thank my main supervisor Erik Aschehoug for all the great support, guidance, and advice. I also want to thank my co-supervisor Siri Lie Olsen for the valuable feedback, statistical help, and guidance. Both my supervisors have been motivating me well to work on the project.

Thank you to Finse research station for letting me stay there while I did my field work. And thanks to fellow master students as well, for giving me inspiration and useful feedback along the way.

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Abstract

Plants interact negatively with each other through competition for space, light, or belowground resources, resulting in a reduction in individual survival, growth, or reproduction. Facilitation, on the other hand, is a positive interaction wherein a plant can potentially increase another individual's ecological success. The role of facilitation is predicted to increase along with abiotic levels of stress. *Silene acaulis* is an alpine cushion plant known to facilitate other species in harsh environments, but less is known about the potential costs that *S. acaulis* may incur while facilitating other species.

I investigated the reproductive costs of plant-plant interactions on *S. acaulis* along an elevational gradient at Finse, Norway. Across three elevations, I removed all species growing within 30 of the *S. acaulis* cushion plants and left 30 cushions untreated. I measured the size, number of flowers and number of seed capsules for all cushions. I also counted and weighed the seeds within each seed capsule. Species richness, diversity, percent cover, and composition were compared between untreated cushions and nearby open areas.

I found no evidence for facilitation by *S.* acaulis, but rather weakly competitive effects at all sites. At the low and mid elevation, there was a higher cover of bryophytes in open areas than within untreated cushions, suggesting that bryophytes were outcompeted for space by *S. acaulis*. At the mid and high elevation, there was a higher cover of lichens in open areas than within untreated cushions, implying that *S. acaulis* outcompeted lichens for space. No reproductive costs of plant interactions were found for *S. acaulis* at any elevation.

The lack of a shift in species interactions for *S. acaulis* along an elevational gradient suggests that differences in elevation did not result in a gradient of abiotic stress as expected. It also suggests that the sites were generally less stressful than predicted. The impact of climate change on alpine habitats, which can lead to an increased role of competition in harsher environments, may explain my results. Increased knowledge of how environment impacts alpine ecosystems and species interactions is essential to understanding the long-term persistence of foundational species such as *S. acaulis* and future alpine plant community composition.

Contents

1. Introduction

Interactions among plants are an important determinant of plant community composition and ecosystem function (Aschehoug et al., 2016). Plants can reduce the growth, reproduction, or survival of neighbors through competition for space, light, nutrients, or water (Aschehoug et al., 2016; Casper & Jackson, 1997; Craine & Dybzinski, 2013). In contrast, plants may improve growth, reproduction or survival for one another through facilitation (Bronstein, 2009), where abiotic or biotic stresses are ameliorated (Callaway, 1995).

The degree to which plants compete with or facilitate each other may be determined by environmental conditions (Callaway et al., 2002). The stress-gradient hypothesis proposes that in communities where there are high amounts of physical stress or consumer pressure, positive interactions such as facilitation should be occurring more frequently and with greater importance (Bertness & Callaway, 1994). If stress levels are high, species are more likely to be limited, thereby increasing the role of facilitation (Bertness & Callaway, 1994). Consequently, in lower stress communities competition between species would be more dominant than facilitation (Bertness & Callaway, 1994).

Studies on facilitation, until more recently, have largely focused on the positive effects received by beneficiary species such as increased growth, reproduction and biomass (Callaway et al., 2002). However, strong costs of facilitation through competitive effects of beneficiary species could potentially be experienced by benefactor plants (Cranston et al., 2012), an aspect of plant-plant facilitation that has been explored far less.

Costs of facilitation have been found in alpine plant communities resulting in decreased reproduction (Cranston et al., 2012; Schöb et al., 2014b; Schöb et al., 2014c) and physiological condition (Schöb et al., 2014c), including increased costs across an elevation gradient (Cranston et al., 2012). Yet, we lack a complete understanding of where and when such feedback effects may be experienced by facilitating species (Losapio & Schöb, 2020) and how feedback effects may vary according to environmental stress.

Silene acaulis (moss campion) is an alpine cushion plant that has previously been shown to both facilitate and compete with other plant species (Bonanomi et al., 2016; Kjær et al., 2018). Cranston et al. (2012) observed that *S. acaulis* appears to experience increased feedback effects on reproduction with increases in elevation. However, experimental approaches, rather than observational, may provide more insight into feedback effects.

I explored the potential reproductive fitness costs of facilitation for *S. acaulis* by conducting a removal experiment along an elevational gradient at Finse, Norway. First, I investigated how *S. acaulis* interacts with other plant species, and how the nature of these interactions may change along an elevational gradient. Second, I investigated whether plant interactions result in reproductive costs for *S. acaulis* and if these costs vary along an elevational gradient.

I hypothesize that *S. acaulis* will compete with species at the lowest elevation, interact neutrally with species at the mid elevation, and facilitate species at the highest elevation. Further, I hypothesize that there will be a reproductive cost of competition for *S. acaulis* at the lowest elevation, no reproductive cost of interactions at the mid elevation, and a reproductive cost of facilitation at the highest elevation.

2. Materials and methods

2.1 Study area

I established three study sites within Hallingskarvet National Park at Finse, Norway (Figure 1). The low elevational site was at 1376 meters above sea level (60.612°N; 7.508°E), the mid elevational site at 1523 meters above sea level (60.635°N; 7.509°E) and the high elevational site at 1695 meters above sea level (60.652°N; 7.524°E) (figure 1). Sites were chosen based on the size of *S. acaulis* populations (minimum of 50 individuals per site) and to achieve differences in elevation that reflect a range of stress levels and species interactions for *S. acaulis*. For example, Cranston et al. (2012) found differences for *S. acaulis* in species interactions and costs with a 243 meters difference between their sites, while the difference from the low to high site in this study is 319 meters.

The area surrounding the study sites at Finse is dominated by phyllite bedrock, and can include calcite, limestone, garnet or conglomerate (Askvik, 2008). In 2022, the annual mean temperature at Finsevatn was -0.5℃ (seklima.met.no). The highest monthly mean temperature was 8.9℃ in August and the lowest temperature was -10.7℃ in December (seklima.met.no). The total annual precipitation in 2021 was 756.6 mm, with the highest level on a monthly basis being in October at 154.4 mm and the lowest in August at 21.9 mm (seklima.met.no). Microclimatic variation is an important driver of the species distribution in the heterogenous landscape of Finse (Roos et al., 2022). At Finse, there are heath communities that include the commonly found species *Dryas octopetala*, as well as for instance *Festuca sp., Poa alpina* and *Cerastium alpinum* (Roos et al., 2022).

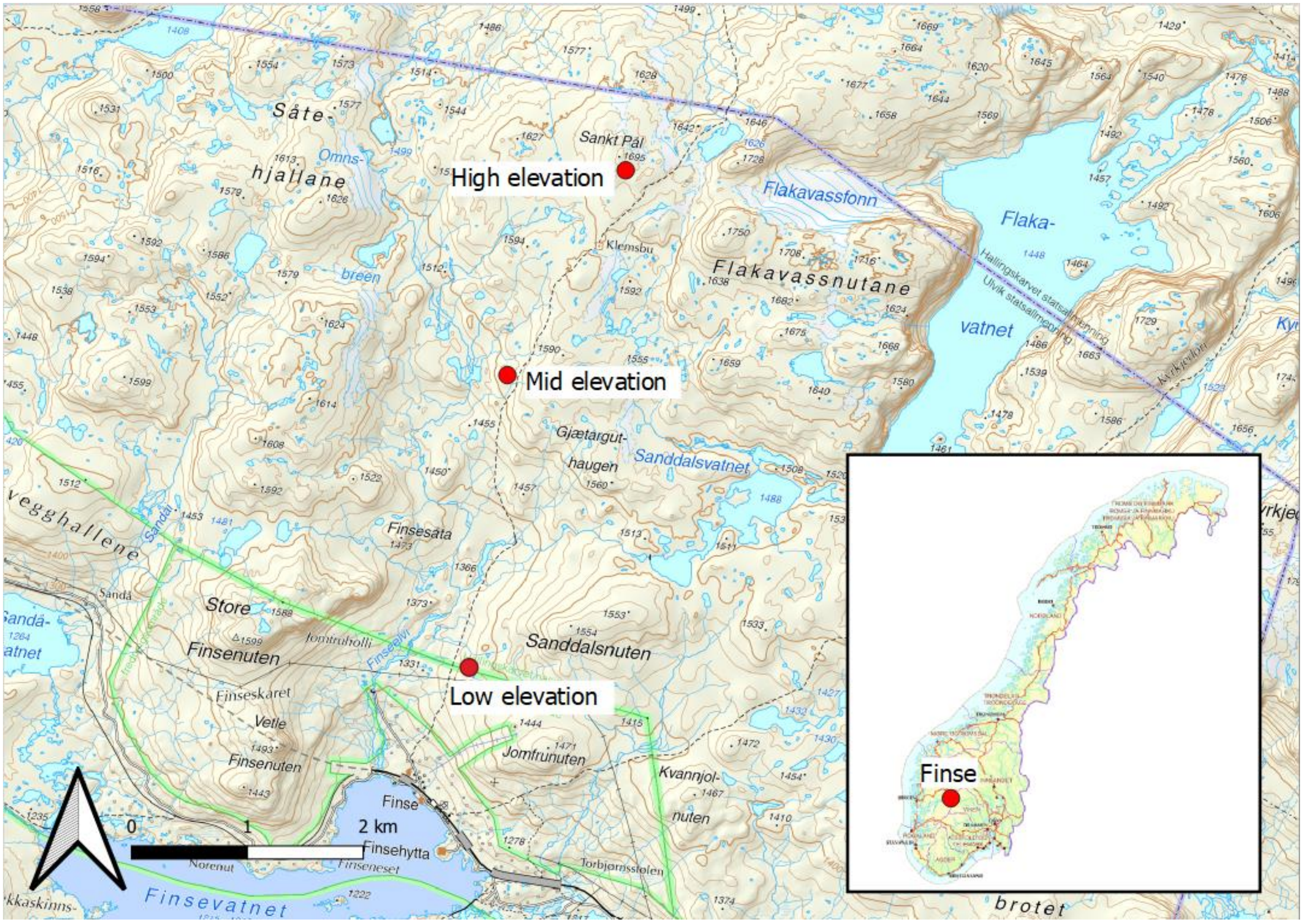

Figure 1: *A map of the three elevational sites established at Finse, Norway. The low elevation was 1376 m a.s.l., the mid elevation was 1523 m a.s.l. and the high elevation was 1695 m a.s.l.. There is also a small map of Norway, showing the location of Finse. The map was made with QGIS 3.16.8-Hannover, using a topographic raster map from ©Kartverket.*

2.3 Study species

The moss champion (*Silene acaulis*) is a perennial plant species that forms large, flat, cushions with pink, white or carmine flowers (Jones & Richards, 1962). It is found in the northern and Arctic regions of north America, Asia and Europe (Jones & Richards, 1962). In the mountains, it can commonly be seen on gravel or sandy soils (Mossberg & Stenberg, 2021). *S. acaulis* can become at least 300 years old (Morris & Doak, 1998). It is a compact plant, and has been shown experimentally to tolerate temperatures as low as -80°C and up to 60°C (Larcher et al., 2010). In addition, *S. acaulis* has the capacity to gain a higher leaf temperature than the air temperature, trapping heat in its cushion (Neuner et al., 2000). *S.*

acaulis is gynodioecious (Delph & Carroll, 2001), and it forms seed capsules with an approximately cylindrical shape (Jones & Richards, 1962).

2.4 Selection of cushions and open areas

On July 19th 2022, I selected 20 individual *S. acaulis* cushion plants per elevational site for a total of 60 cushions. The cushions at each site were paired according to size. One plant in each pair was randomly chosen to receive a removal treatment where all individuals growing inside the cushion plant were removed, while the other plant was left untreated as a control plant. Each cushion was marked with a unique ID, elevation, and treatment (Figure 2).

Figure 2. Two *S. acaulis* cushion plants at the high elevation (trip 3), one having received a removal treatment (left) and the other having been left untreated as a control plant (right). Pictures were taken in Finse, Norway, September 2022.

In addition, I selected 10 open vegetated areas without *S. acaulis* cushions per site (30 open vegetated areas total). The 10 open vegetated areas at each site were chosen based on their proximity to a corresponding pair of cushions at the same elevational site. I sized the open vegetated areas by putting a piece of wire around the perimeter of the two corresponding paired plants to estimate the average size of the pair of cushions.

2.5 Measurements and the removal experiment

To measure cushion area, for all cushion plants I measured the diameter of the plant (y), as well as its perpendicular side (x). I also recorded the estimated percentage missing of the cushion from being a perfect ellipse. I used the ellipse formula for a first estimate of the cushion areas:

$$A = \frac{x}{2} \cdot \frac{y}{2} \cdot \pi$$

From this first area estimate, I took the percentages missing recorded for each cushion into account and calculated:

$$A_2 = A \cdot \left(1 - \frac{\%\, missing}{100\%}\right)$$

For each cushion I recorded the number of flowers present. For all plants in the removal treatment, I removed all species (plants, bryophytes and lichens) growing within the cushions carefully by hand.

An August 10th (trip 2), for all *S. acaulis* plants I recorded its number of flowers as well as number of species present within the cushions. In addition, I identified the species growing within each cushion down to species level if possible, and down to family or genus level if not. In those cases where neither the family, genus or species level of a species could be identified, I noted the species as either plant unidentified, bryophyte unidentified or lichen unidentified. Then, I repeated the removal experiment.

On September 1st (trip 3), for all *S. acaulis* cushion plants I recorded the total cover of and number of species growing within the cushions. I again identified species, and this time I recorded the cover of each individual species for all *S. acaulis* cushions. I also recorded the number of seed capsules for each *S. acaulis* cushion plant. For the open areas, I recorded both their total species cover, species richness and the individual cover of each species found within the open area.

2.6 Seed capsule collection and lab work

For each cushion plant, I collected seed capsules wherever possible. For all cushions that had a minimum of 10 seed capsules, I collected between 10 and 15 seed capsules (at random). For cushions that had nine or less seed capsules, I collected all seed capsules. The seed capsules collected were gathered in small paper envelopes marked with date, elevation, treatment and plant ID. I also noted down how many plants without any seed capsules there were per combination of elevation and treatment (table A1). In the lab, I counted and weighed the seeds within each capsule. The seeds that had fallen out of their respective capsule were also weighed and counted, assigned only to the plant they were gathered from and not to a specific seed capsule. For the weighing I used Sartorius ED224S, a 4 decimal balance.

2.7 Data analysis

2.7.1 Seeds and seed capsules

For the response variables number of seeds per capsule, seed mass per capsule and seed mass per seed (for *S. acaulis)*, I estimated mean values and corresponding standard errors for each combination of specific elevations and treatments. For these estimations, the seeds that had fallen out of their respective capsules were included. The plants that had zero seed capsules collected were not included in these calculations. ANOVAs were then run to test the effects of elevation, treatment, and their interactive effect on the response variables number of seeds per capsule, seed mass per capsule and seed mass per seed. Tukey tests were conducted in those cases where the ANOVAs showed significant effects, to see which combinations of elevation (low, mid, high) and treatment (control, removal) affected the response variables.

I calculated a capsules to flowers ratio by taking the total number of seed capsules counted for a cushion plant and dividing it by the maximum number of flowers for that plant. For the three cushions where the capsules to flowers ratio was higher than one, which was due to either errors in counting or counting prior to max flowering, I set the values to one as that is the highest realistically possible value. I used the capsules to flowers ratio value per plant to calculate mean values per combination of elevation and treatment, with corresponding standard errors. To test the effect of elevation and treatment on the capsules to flowers ratio, I ran a generalized linear model (GLM) with zero-inflation and a gaussian distribution, as assumptions for an ANOVA were violated. I chose this model because there were many zero values within the capsules to flowers ratio (figure A1), and because the gaussian distribution fit fine after that was accounted for. I used the glmmTMB package (Mollie E. Brooks, 2017) when making the model. A generalized linear mixed model (GLMM) with plant ID as a random effect was also tested but could not be used as it caused convergence problems.

For the response variables number of seeds per capsule and seed mass per capsule, I performed a simple linear regression analysis with total species cover (trip 3) as the independent variable. I did the regressions in order to test for a significant linear relationship between the included response variables and the cover of other species. The analyses were performed only for control cushions, as the removal cushions already had their cover of species removed. Per elevation (low, mid, high), one regression analysis was performed for each of the included response variables number of seeds per capsule and seed mass per capsule. As the distribution of the response variable capsules to flowers ratio was not normal (figure A1) I ran a Spearman correlation test. One Spearman correlation test was run per elevation to test the possible correlation between the capsules to flowers ratio and total species cover (trip 3).

2.7.2 Species richness, diversity, and cover

As ANOVA assumptions were violated, I performed a Wilcoxon rank sum exact test on both species richness per cm^2 and total species cover found within the cushions. I used the Wilcoxon test to compare median values between treatments (control, removal) within each elevation (low, mid, high). I calculated median species richness per cm^2 as well as the median total species cover by elevation and treatment, along with the corresponding standard errors.

I also performed Kruskal-Wallis rank sum tests on both species richness per cm^2 (trip 3) and total species cover (trip 3) between elevations (low, mid, high) within treatments (control, removal). Dunn's tests with Bonferroni correction for p-values were then performed in the cases of significant Kruskal-Wallis test results for either species richness per cm^2 or total species cover, using the “FSA” package (Derek H. Ogle, 2023). The Dunn’s tests were performed to see which comparisons between elevations (low, mid, high) differed within the specific treatment (control and removal).

For all open areas and control plants, I calculated Shannon diversity index values using percent cover estimates of all species:

$$H = -\sum_{i=1}^{S} p_i ln p_i$$

where H represents the Shannon diversity index values per control plant or open area. The p_i values were calculated per control plant and per open area. I calculated the p_i values by dividing the cover of each individual species by the total species cover for a specific control plant or open area. This gave one H value per control plant or open area. Mean Shannon diversity index values were calculated per elevation and treatment, as well as corresponding standard errors. These calculations made it possible to compare index values between the different combinations of elevation (low, mid, high) and treatment (control, removal). I then ran an ANOVA, testing the effects of elevation and treatment on the Shannon index values.

2.7.3 Functional groups cover

I created a table (table A2), classifying all species into the following functional groups: shrubs, forbs, graminoids, bryophytes and lichens. The few unidentified plants were excluded from this and not sorted into a functional group. As assumptions for an ANOVA were violated (did not have a normal distribution), I ran Wilcoxon rank sum exact tests on the total percentage cover of each functional group. The Wilcoxon rank sum exact tests were each performed within elevation (low, mid, high), comparing the total cover of a functional group between treatments (open, control).

I also performed Kruskal-Wallis rank sum tests for all functional groups. These Kruskal-Wallis tests compared the median values of total percent cover within a treatment (open and control), between different elevations (low, mid, high). Where significant results were found in the Kruskal-Wallis test, I ran Dunn’s tests with Bonferroni correction for p-values. The Dunn’s tests were run in order to find out which contrasts between levels (low, mid, high) of the elevation variable had caused the significant effects in the Kruskal-Wallis test. I estimated the total cover of each functional group per control cushion and open area, along with the median values and corresponding standard errors. I compared median values of functional group cover between all combinations of elevation (low, mid, high) and treatment (control, open).

2.7.4 Species composition

I ran a Canonical Correlation Analysis (CCA) through the anova.cca function in “vegan” (Oksanen et al., 2022). I ran the CCA analysis to test for differences in species composition between treatments (control, open) and elevations (low, mid, high). The data used in the analysis consisted of all the species covers of individual species from trip 3. The interactive term elevation*treatment was excluded from the model, as the interactive effect of elevation and treatment became highly insignificant ($p = 0.997$). This means that the environmental explanatory variables included in the model were elevation and treatment.

I did a Non-metric Multi-dimensional Scaling (NMDS) analysis using the “vegan” package (Oksanen et al., 2022). I did the analysis to visualise the change in species composition over time through a reduced dimensionality, between trip 2 and trip 3, for control cushions. In addition, I used the analysis to see how the species composition of control plants compared to the species composition of the open areas. Presence/absence species data from the second and third trip for the open and control treatments was used. The mean species composition for each combination of treatment (control, open) and elevation (low, min, high) was used in the analysis. Lastly, I quantified per elevation (low, mid, high) which species were only found within the control cushions or within the open areas, but not in both (for trip 3). I did this to explore the differences in species composition between treatments in more depth.

2.7.5 Plots generated and model validations

I did all statistical analyses using R-Studio, in R version 4.2.2 (R Core Team, 2022). Bar plots were generated using the “ggplot2” (Wickham, 2016) and the “dplyr” (Muller, 2022) packages. To check that assumptions for the ANOVAs were not violated, histograms of the distributions of relevant response variables were created as well as QQ plots, and fitted values were plotted against residuals. For the zero inflated mixed model with a gaussian distribution, I used the simulateResiduals function obtained from the "DHARMa" package (Hartig, 2022) to validate the model. For validations of the regression models, I created histograms to check the distributions of the response variables.

3. Results

3.1 Seeds and seed capsules

ANOVA results (table 1) showed that there were significant differences in number of seeds per capsule by elevation (figure 3A). There was no significant impact of the removal treatment or of an interactive effect of treatment and elevation on the number of seeds per capsule. The post-hoc Tukey test (table A3) revealed that plants at the high elevation site had significantly more seeds per capsule than the low elevation, with a 58% increase. In addition, there was a non-significant trend of 42% more seeds per capsule at the mid elevation than at the low elevation.

Table 1. *The test results from the ANOVA done on number of seeds per capsule for S. acaulis. The test included the main effects of elevation (low, mid, high) and treatment (control, removal), as well as the interactive term of elevation and treatment. Significant p values (p<0.05) are highlighted with *.*

Source of variation	df	Sum of squares	Mean squares	F value	p value
Elevation	2	73.89	36.95	4.612	**0.0182***
Treatment	1	0.27	0.27	0.034	0.8549
Elevation x treatment	2	8.63	4.31	0.539	0.5893
Residuals	29	232.31	8.01		
Total	34	315.10	49.54		

The results from the ANOVA (table 2) did not show any significant impact of elevation, treatment or the interactive effect of elevation and treatment on seed mass per capsule (figure 3B). Yet the control and removal error bars at the high elevation were not overlapping, and there was a 56% increase in seed mass per capsule from the control to the removal treatment at the high elevation.

Table 2: *The test results from the ANOVA done on seed mass per capsule for S. acaulis. The test included the main effects elevation (low, mid, high) and treatment (control, removal), as well as the interactive term of elevation and treatment.*

Source of variation	Df	Sum of squares	Mean squares	F value	p value
Elevation	2	0.740	0.3698	0.838	0.443
Treatment	1	0.071	0.0706	0.160	0.692
Elevation x treatment	2	0.727	0.3635	0.824	0.449
Residuals	29	12.797	0.4413		
Total	34	14.335	1.2452		

The ANOVA (Table 3) showed a significant difference in seed mass per seed between elevations (figure 3C). But there was no effect of treatment, nor an interactive effect of elevation and treatment, on seed mass per seed. Yet the control and removal error bars at the high elevation were not overlapping, and there was a 35% increase in seed mass per seed from the control to the removal treatment at the high elevation. A post-hoc Tukey test (table A4) showed that all elevations were significantly different from each other with regards to seed mass per seed. The high elevation had a lower seed mass per seed than the mid (40% decrease) and low (77% decrease) elevation, while the mid elevation had a lower seed mass per seed than the low elevation (27% decrease).

Table 3: *The test results from the ANOVA done on seed mass per seed for S. acaulis. The test included the main effects elevation (low, mid, high) and treatment (control, removal), as well as the interactive term of elevation and treatment. Significant p values (p<0.05) are highlighted with *.*

Source of variation	df	Sum of squares	Mean squares	F value	p value
Elevation	2	0.05734	0.028669	20.126	$\mathbf{3,3 \cdot 10^{-6}}*$
Treatment	1	0.00210	0.002102	1.476	0.234
Elevation x treatment	2	0.00189	0.000945	0.663	0.523
Residuals	29	0.04131	0.00142		
Total	34	0.10264	0.033136		

The generalized linear model (table 4) showed no significant effects of treatment or elevation, nor an interactive effect of elevation and treatment on the capsules to flowers ratio (figure 3D). Yet, there was a non-significant trend of the mid elevation having a higher capsules to flowers ratio than the low elevation (an 86% increase).

Table 4. *The test results from the generalized linear model with zero-inflation and a gaussian distribution done on the capsules to flowers ratio (number of seed capsules divided by the maximum number of flowers) for S. acaulis. The test included the main effects elevation (low, mid, high) and treatment (control, removal), as well as the interactive term of elevation and treatment. p values between 0.05 and 0.1 are marked with (.).*

Source of variation	Estimate	Std. error	Z value	p value
Intercept	0.2015	0.1129	1.785	**0.0742 .**
ElevationMid	0.2832	0.1596	1.775	**0.0760 .**
ElevationHigh	-0.0005	0.1596	-0.003	0.9977
TreatmentRemoval	0.0903	0.1596	0.566	0.5712
ElevationMid:TreatmentRemoval	-0.0394	0.2257	-0.175	0.8612
ElevationHigh:TreatmentRemoval	0.0553	0.2257	0.245	0.8062

There was no significant linear relationship between total cover and the number of seeds per capsule (table A5), nor between the total cover and seed mass per capsule (table A6), at any of the elevations (figure A2). But there was a significant correlation between total species cover and the capsules to flowers ratio at the mid elevation (table A7).

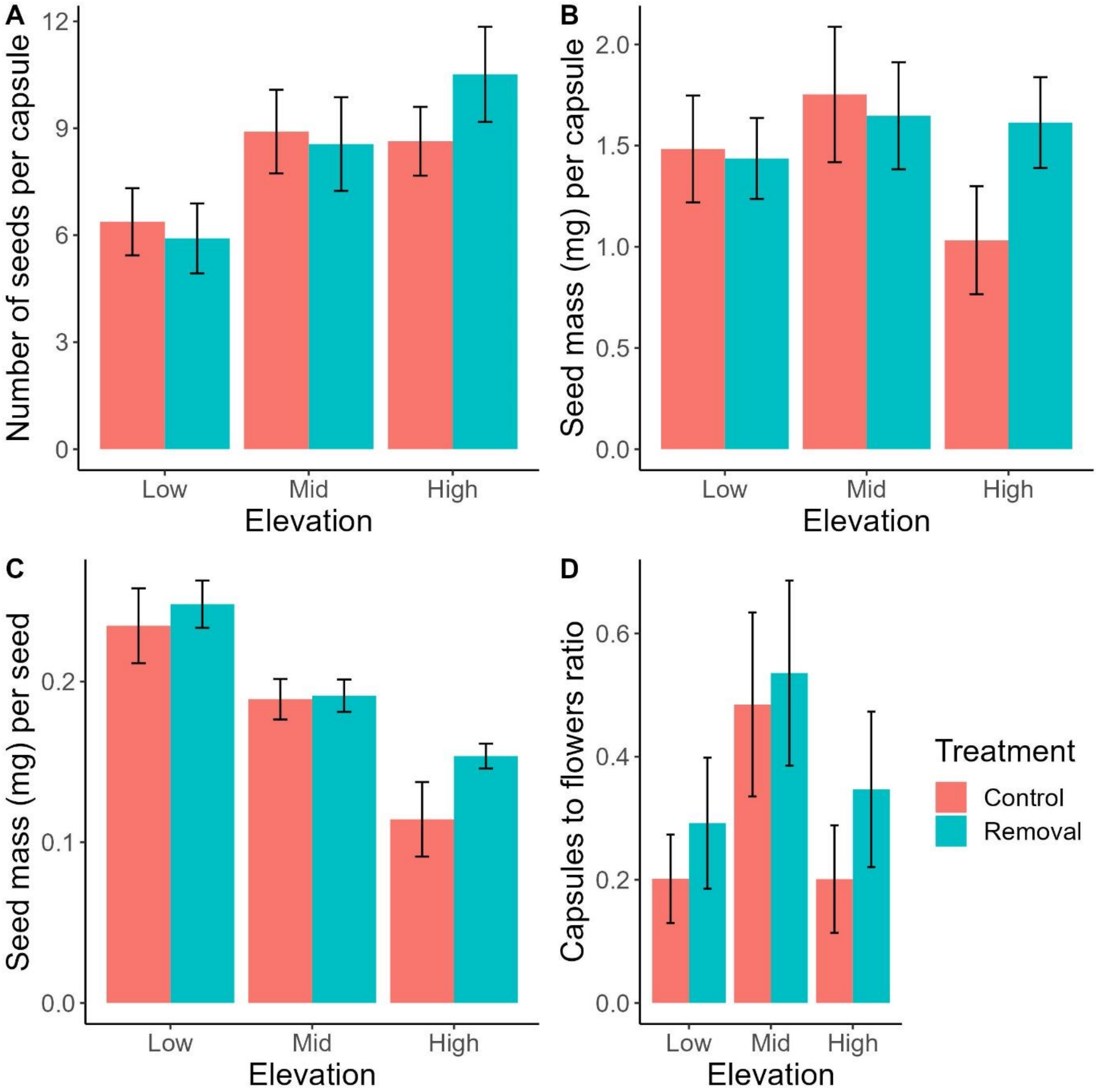

Figure 3. *The average number of seeds per capsule (A), seed mass (mg) per capsule (B), seed mass (mg) per seed (C) and seed capsules per maximum number of flowers (the capsules to flowers ratio) (D) for S. acaulis by elevation (low, mid, high) and treatment (control, removal). The heights of the bars represent mean values, while error bars each represent one standard error.*

3.2 Species richness per area, Shannon diversity index and total percentage cover

The Wilcoxon test (table 5) showed that at the high elevation, median species richness per area was significantly higher for the open areas than for the control cushions (45% increase) (figure 4A). A Kruskal-Wallis rank sum test (table 6) showed that within both treatments, elevation accounted for significant differences in species richness per area (figure 4A).

A Dunn's test with Bonferroni correction for p-values (table A8) showed that for the control treatment, the high elevation had a significantly lower species richness per area than both the mid (60% decrease) and the low elevation (63% decrease). For the open areas, the high elevation had a significantly lower species richness per area than the mid elevation (60% decrease). Within the open areas, there was a non-significant trend of the high elevation having a lower species richness per area than the low elevation (49% decrease).

Table 5. *The test results from the Wilcoxon rank sum test done on species richness per area (cm^2) (trip 3) found within control S. acaulis cushions and open areas. The contrasts of control-open treatment within each elevation (low, mid, high) are tested for significance with regards to species richness per area (trip 3). Significant p values (p<0.05) are highlighted with *.*

Elevation	W	p value
Low	47	0.8534
Mid	29	0.123
High	22	**0.0355***

Table 6. *The test results from the Kruskal-wallis rank sum test done on species richness per area (cm^2) (trip 3) found within control S. acaulis cushions and open areas. The impact of elevation (low, mid, high) on species richness per area (trip 3) within each treatment (control, open) are tested for significance. Significant p values (p<0.05) are highlighted with *.*

Treatment	Chi-squared	W	p value
Control	9.9897	2	**0.0068***
Open	11.992	2	**0.0025 ***

The ANOVA (table 7) showed a non-significant tendency of an interactive effect between elevation and treatment on Shannon index values (figure 4B).

Table 7: *The test results from the ANOVA done on the Shannon diversity index values for control S. acaulis cushions and open areas. The test included the main effects elevation (low, mid, high) and treatment (control, open), as well as the interactive term of elevation and treatment. Trending p values (p>0.05 but >0.01) are highlighted with (.).*

Source of variation	Df	Sum of squares	Mean squares	F value	p value
Elevation	2	0.1591	0.07955	1.860	0.1655
Treatment	1	0.0153	0.01534	0.359	0.5517
Interaction	2	0.2221	0.11104	2.596	**0.0839 .**
Residuals	54	2.3098	0.04277		
Total	59	2.7063	0.2487		

A Wilcoxon test (table 8) revealed that for all elevations, total species cover was higher in the open areas than within the control treatment (figure 4C). A Kruskal-Wallis rank sum test (table 9) indicated that within both treatments, elevation significantly impacted total species cover (figure 4C). A Dunn's test (table A9) showed that within both treatments, the high elevation had a significantly lower species cover than both the mid and the low elevation.

Table 8. *The test results from the Wilcoxon rank sum test done on total species cover (%) values (trip 3) for S. acaulis cushions and open areas. The contrast of control-open treatments within each elevation (low, mid, high) are tested for significance in total species cover. Significant p values (p<0.05) are highlighted with *.*

Elevation	W	p value
Low	0	$\mathbf{6.20 \cdot 10^{-5}}$ *
Mid	0	$\mathbf{8.69 \cdot 10^{-5}}$ *
High	0	**0.0002***

Table 9. *The test results from the Kruskal-wallis rank sum test done on total species cover (trip 3) for S. acaulis cushions and open areas. The impact of elevation on total species cover (trip 3) within each treatment (control, open) are tested for significance. Significant p values (p<0.05) are highlighted with *.*

Elevation	Chi-squared	df	p value
Control	14.871	2	**0.0006***
Open	21.898	2	$\mathbf{1.757 \cdot 10^{-5}}$*****

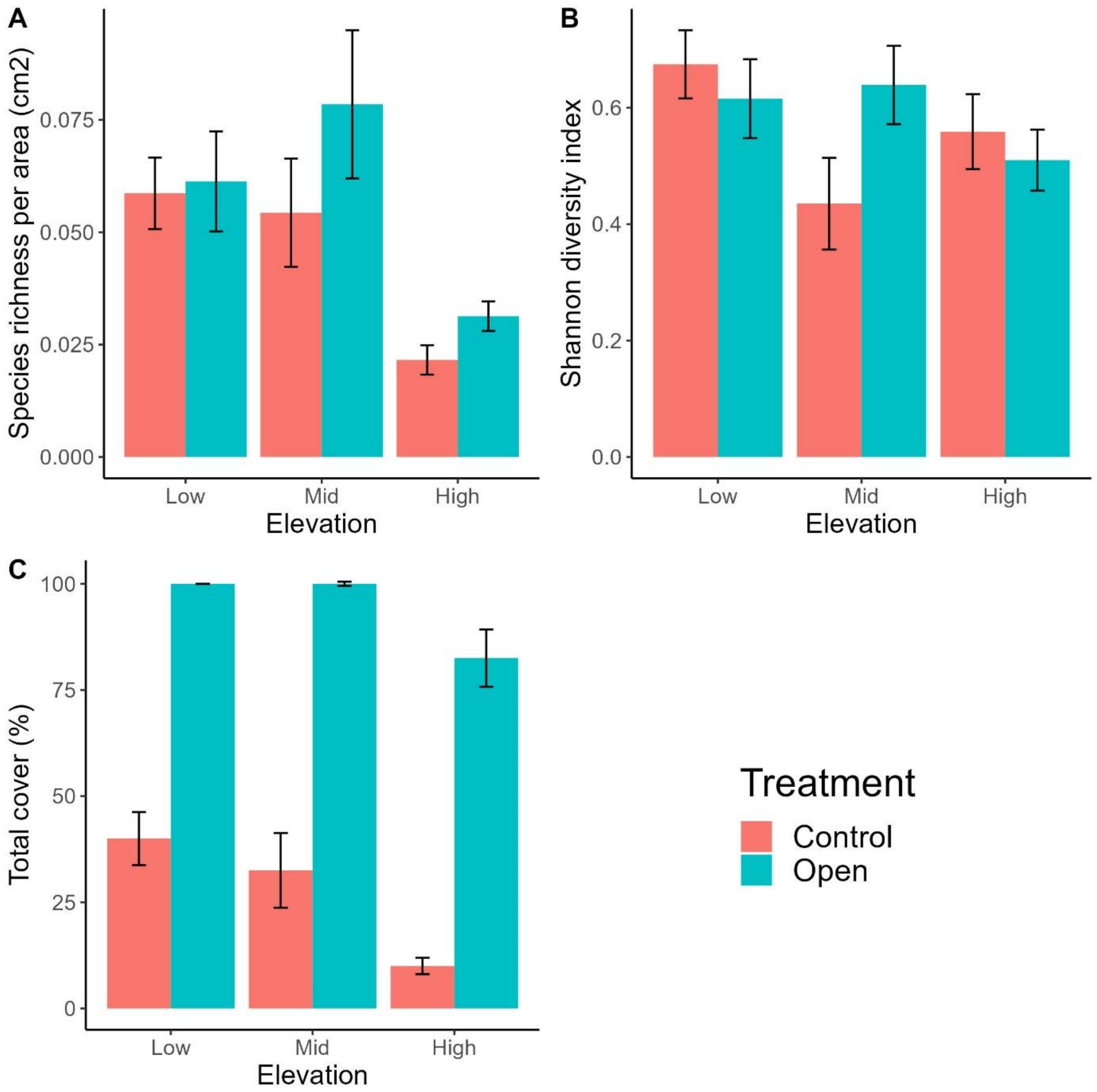

Figure 4. *The median species richness per area (cm^2) (trip 3) (A), the average Shannon diversity index values (B) and the median total species cover (%) values (trip 3) (C) for S. acaulis cushions and open areas, by elevation (low, mid, high) and treatment (control, open). The heights of the bars represent median values for A and C, and mean values for B, while error bars each represent one standard error.*

3.3 Functional group cover

The Wilcoxon tests (table 10) revealed the open areas had a higher cover of lichens than the control cushions at both the mid and the high elevation (figure 5D). The open treatment had a higher cover of bryophytes than the control cushions at the low and mid elevation (figure

5E). There was also a non-significant trend of a difference between treatments for forbs at the high elevation, where the open treatment had a higher cover of forbs than the control treatment (figure 5B).

The Kruskal-Wallis rank sum tests (table 11) revealed no effect of elevation within any of the treatments on cover of shrubs (figure 5A). For the cover of forbs, there was a significant impact of elevation within the control treatment. For graminoids, within both treatments, elevation had a significant impact on the cover (figure 5C). For lichens, within the open treatment, elevation significantly impacted the cover. In addition, within the control treatment there was a non-significant trend of elevation having an effect on the cover of lichens. Within both treatments, there was also a significant impact of elevation on the cover of bryophytes.

The Dunn’s test (table A10) showed that for forbs within the control treatment, the high elevation had a significantly lower cover of forbs than the low elevation. Within the control treatment, the high elevation had a significantly lower cover of graminoids than the low elevation. There was also a non-significant trend for the low elevation to have a higher cover of graminoids than the mid elevation, within the control treatment. Within the open treatment, the low elevation had a significantly higher cover of graminoids than the high elevation.

Within the control treatment, there was a non-significant trend in the high elevation having a higher cover of lichens than the mid elevation. Within the open areas, the low elevation had a significantly lower cover of lichens than both the mid and the high elevation. For bryophytes, within the control treatment, the low elevation had a significantly higher cover of bryophytes than the mid elevation. Also within the control treatment, there was a non-significant trend in the low elevation having a higher cover of bryophytes than the high elevation. Within the open areas, the high elevation had a significantly lower cover of bryophytes than both the mid and the low elevation.

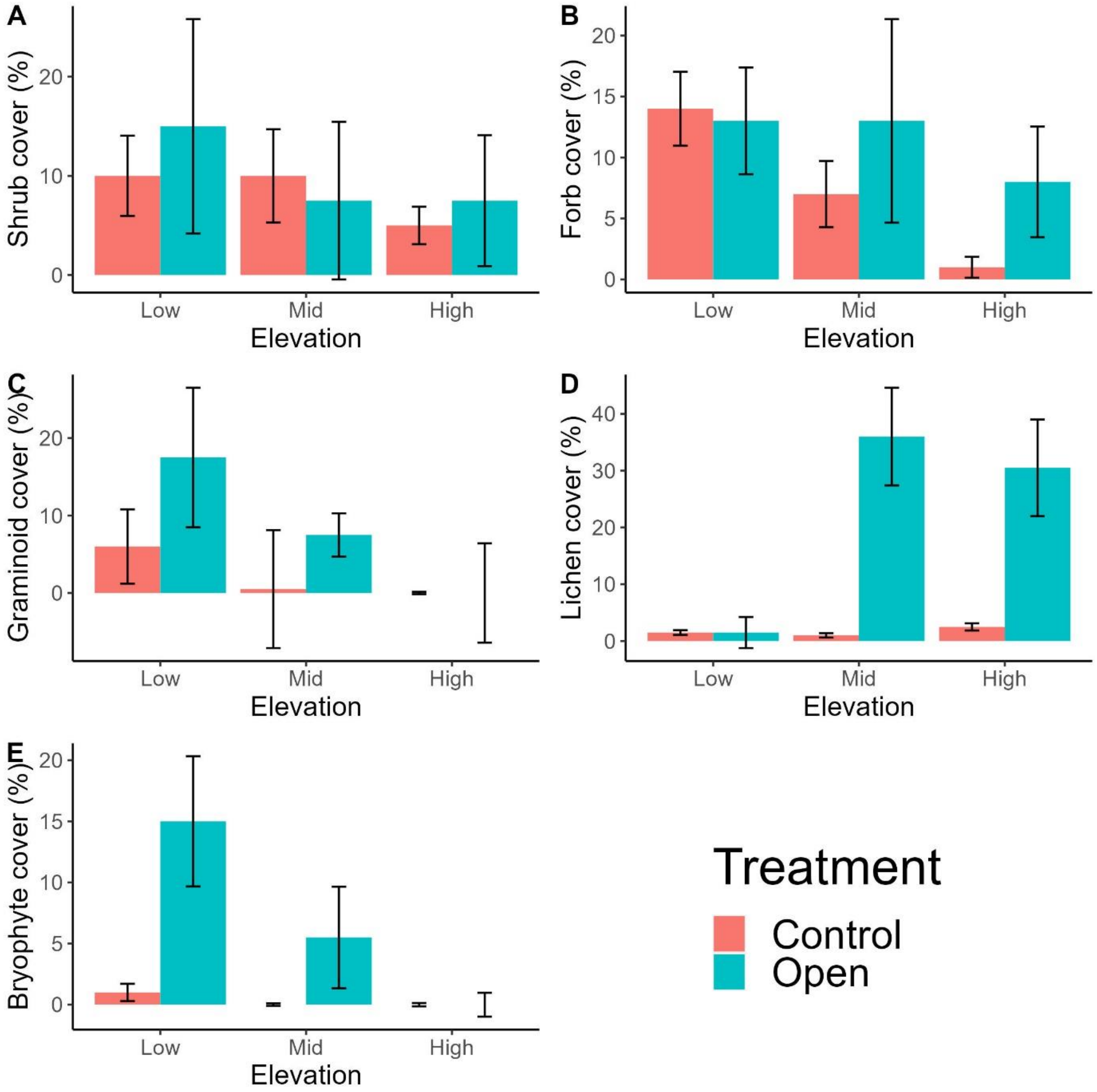

Figure 5. *The median cover (%) values per control S. acaulis cushion or open area of shrubs (A), forbs (B), graminoids (C), lichens (D) and bryophytes (E) by elevation (low, mid, high) and treatment (control, open). The heights of the bars represent median values, while error bars each represent one standard error.*

Table 10. *The test results from the Wilcoxon rank sum tests done on the cover of the functional groups shrubs, forbs, graminoids, lichens and bryophytes for S. acaulis cushions and open areas. The impact of elevation (low, mid, high) on the cover of each of these functional types, within each treatment (control, open), are tested for significance. Significant (*) p values (p<0.05) and trending (.) (p>0.05 but >0.01) are highlighted.*

Functional types/Elevation	**W**	**p value**
Shrubs		
- Low	38.5	0.4014
- Mid	53.5	0.8193
- High	39	0.4177
Forbs		
- Low	54	0.7911
- Mid	35.5	0.2886
- High	28	**0.0969 .**
Graminoids		
- Low	43	0.6204
- Mid	43.5	0.6337
- High	40.5	0.4223
Lichens		
- Low	53.5	0.815
- Mid	0	**0.0002***
- High	4.5	**0.0006***
Bryophytes		
- Low	4.5	**0.0006***
- Mid	7	**0.0006***
- High	39	0.3222

Table 11. *The results from the Kruskal-Wallis rank sum tests done on the cover of the functional groups shrubs, forbs, graminoids, lichens and bryophytes (trip 3) for S. acaulis cushions and open areas. The impact of elevation (low, mid, high) on the cover of each functional type within each treatment (control, open) are tested for significance. Significant (*) p values (p<0.05) and trending (.) p values (p>0.05 but <0.1) are highlighted.*

Functional type/Treatment	Chi-squared	df	p value
Shrubs			
- Control	3.3431	2	0.188
- Open	2.5884	2	0.2741
Forbs			
- Control	13.043	2	**0.0014***
- Open	1.417	2	0.4924
Graminoids			
- Control	13.538	2	**0.0011***
- Open	6.1859	2	**0.0454***
Lichens			
- Control	5.4051	2	**0.0655 .**
- Open	15.906	2	**0.0004***
Bryophytes			
- Control	7.4917	2	**0.0236***
- Open	14.264	2	**0.0008***

3.4 Species composition

Figure 6 visualises the species composition for control cushions and open areas. The cushions and open areas that are close to each other in the plot have more similar species compositions. Species composition was significantly different both between elevations (low, mid, high) and treatments (control, open), although there was no interactive effect of elevation and treatment on the species composition (table 12). The most important species for driving the species composition of control cushions and open areas are shown in figure 7, and the species are coloured based on their functional group. The species (figure 7) with similar axis values to the plants or open areas in figure 8 are important drivers of those plants/open areas. It becomes especially clear that *Flavocetraria Nivalis* is common within the open areas at the high elevation, *Diphasiastrum alpinum* is common within the open areas in the mid elevation and *Empetrum Nigrum* and *Anthoxanthum odoratum* are common in the open areas at the low elevation.

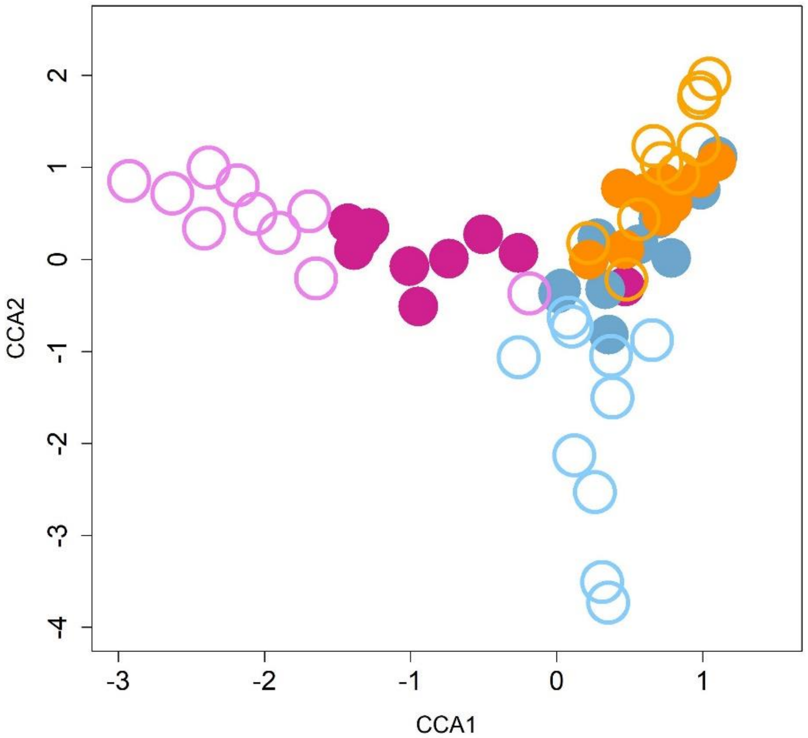

Figure 6. *A CCA ordination plot, visualizing the species composition for all control S. acaulis cushions as well as open areas. Open circles represent open areas, while closed circles represent control cushions. The color purple represents the high elevation, blue represents the mid elevation and orange represents the low elevation. The plot is based on data on the cover of each individual species (trip 3). The species close to each other in species composition are closer in their axis values CCA1 and CCA2.*

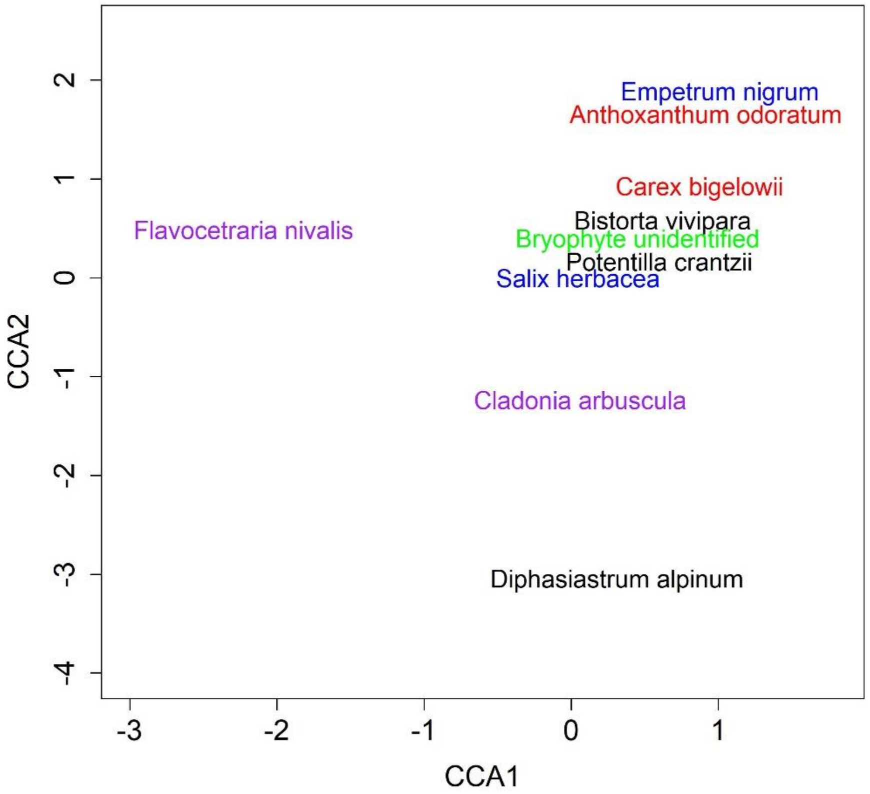

Figure 7: *A CCA ordination plot, visualizing the most important driver species for the species composition of all control S. acaulis cushions as well as open areas. The plot is based on data on the cover of each individual species (trip 3). All species with a total added % cover from all species of at least 100 are included. The species Bistorta vivipara as well as Bryophyte unidentified got their CCA2 axis values changed slightly (to a higher value) to avoid overlap. The colour black represents forbs, red represents graminoids, purple represents lichens, green represents bryophytes and blue represents shrubs. The species with similar axis values as control cushions and open areas in figure 10, are important drivers of those cushions or open areas.*

Table 12: *The test results from the CCA analysis done on species composition within S. acaulis cushions and open areas. The test included only the main effects of elevation (low, mid, high) and treatment (control, open). Significant p values (p<0.05) are highlighted with *.*

Source of variation	df	ChiSquared	F value	p value
Elevation	2	0.9204	4.3138	**0.001***
Treatment	2	0.3284	1.5390	**0.001***
Residuals	78	8.3209		
Total	82	9.5697		

The species composition of control cushions shifted between trip 2 to trip 3 (figure A3) into being closer to the species composition of open areas. For the low elevation, some species were only found within the control treatment (not in the open areas), but an even higher number of species were only found in open areas (not in control cushions) (table A11). The same trend was also true for the mid elevation (table A12) and for the high elevation (table A13).

4. Discussion

Here, I investigated the potential reproductive costs of plant interactions for *S. acaulis* along an elevational gradient. In contrast to my first hypothesis, I found no change in plant interactions between my elevational sites, only weakly competitive interactions across all three sites. In contrast to my second hypothesis, I found no costs of plant interactions at any of the elevational sites. This suggests that the sites did not differ in abiotic stress as I expected and that the stress levels were generally lower than my prediction. It is possible that my sites have to some degree already been affected by climate change, as global warming has the potential to increase the role of competitive interactions in colder habitats.

4.1 Species interactions

Plants can potentially expand their distribution through facilitation (Bruno et al., 2003), and former studies have shown an increase in the richness (Cavieres & Badano, 2009; Chen et al., 2015; Molenda et al., 2012) and diversity (Cavieres et al., 2014; Sklenář, 2009) of plant communities as a result of facilitation.

At my low site, species cover was higher in open areas than in control cushion plants, indicating competition for space between *S. acaulis* and other species. The only functional group that had a higher cover in the open areas than in the control cushions were bryophytes, indicating that *S. acaulis* competes with bryophytes at the low elevation. At the mid site, species composition seemingly differed between control cushions and open areas, indicating that *S. acaulis* might interact with other species at this site too. The open areas at the mid site had a higher species cover than control cushions, indicating competition between *S. acaulis* and other species. The cover of bryophytes and lichens were higher in the open areas than in the control cushions for the mid elevation, indicating that *S. acaulis* competes with bryophytes and/or lichens at this site. At the high site, species composition also differed between control cushions and open areas, possibly indicating that *S acaulis* interacts with other species at this site too. Both species richness and total cover was higher for the open areas than the control cushions at the high elevation, indicating competition. As the cover of lichens was higher outside the cushions, this indicates competition between *S. acaulis* and lichens. Generally, there were a few species at each elevation that were only found in control cushions and not in open areas. However, the opposite was also true and occurred more often, which strengthens the idea that *S. acualis* competes with rather than facilitates other species across all three elevations.

One possible reason why bryophytes seemingly had a lower competitive ability with *S. acaulis* for space than other functional groups at the low and mid elevation, is that bryophytes are often slower growing (Asplund et al., 2022), smaller, and more sensitive to changes, like temperature, in their external environment (He et al., 2016) than many alpine plants. Competitive ability can depend on size (Bengtsson et al., 1994), and tall species may have an advantage, especially if temperatures and soil nutrients are higher (Klanderud, 2008). Where *S. acaulis*, as a robust and well-adapted plant, grows, other species than bryophytes might have better competitive abilities and are not as easily outcompeted by *S. acaulis*. At the mid and high elevation, it is likely that lichens preferred a different habitat than growing within the cushion of *S. acaulis*. Lichens are also slow growing (Lutzoni & Miadlikowska, 2009), with a low stature, so larger and faster growing species might be more competitive.

The role of facilitation in comparison to competition has been suggested to increase with stress (Bertness & Callaway, 1994), and there has been much support for this i.e. (Armas et al., 2011; Callaway et al., 2002; Michalet et al., 2014; Tewksbury & Lloyd, 2001). At Finse, in particular, another study (Kjær et al., 2018) found a shift in species interactions from neutral to more facilitative with increasing abiotic stress levels. Like me, they also used *S. acaulis* as a study species. But their indicator of stress levels was a primary succession gradient, not an elevational gradient like in my study. As their results do not match mine, this indicates that environment might have been generally less stressful at my sites than at their sites during the time of measure. Also, it might be that the differences between my elevations with regards to levels of abiotic stress were not as great as I expected. This can be backed up by the fact that my mid elevation was not generally shown to be more stressful for species to grow in than the low elevation, as species richness, diversity and total cover were not different between the two sites. Since previous studies have used a greater elevational range between sites (Callaway, 1998; Choler et al., 2001; Duarte et al., 2021), the elevational range and number of sites included may be a limitation of this study.

Still, the high site was likely more stressful for species than my other sites because it had both a lower species richness and cover than the mid elevation, and a lower species richness than the low elevation. This did not, however, result in facilitation at the highest stress level of my study sites. It could of course be that the increase in abiotic stress at the high elevation was not strong enough for facilitation to occur. Yet, a notable difference between my study and Kjær et al. (2018) is in how we measured the effect of plant interactions. In their study, a commonly occurring plant thought to be facilitated was chosen, and its number of leaves as well as leaf size were among the measurements used to assess facilitation. My measurements predicting species interactions were at the community level, not on an individual species level. Thus, although species richness, diversity, composition, and cover did not indicate facilitation by *S. acaulis* at any of my sites, facilitation may still have been occurring on an individual species level.

It may also be that global warming has generally caused a shift in alpine plants moving upwards and increased species richness in alpine areas, as plants adapt to environmental changes based on their own range limits (Pauli et al., 1994; Steinbauer et al., 2018; Walther et al., 2005). In comparison to established species in mountainous areas, the species moving upwards are often larger and more used to higher temperatures which also means they have greater competitive abilities (Steinbauer et al., 2018). Consequently, climate change can affect species interactions in the way that competitive interactions in colder areas occur more frequently (Klanderud & Totland, 2005). In addition, increased temperatures in initially cold alpine areas could mean that the need for being facilitated for some plants decreases due to lower stress levels, in line with the stress gradient hypothesis (Bertness & Callaway, 1994). Thus, since there was a lesser difference between two of my sites in species richness than expected, and as I found indications of weak competition at all sites, it is possible that this is partly because climate change has started to affect the sites. Also, the role of facilitation or competition may vary even within a growing season, as facilitative interactions may be more common when it’s drier (Kikvidze et al., 2006). Consequently, weather variation both within a season and between years can be considered sources of uncertainty for my results.

One example of a study that did find similar results as me is Dvorský et al. (2013), a study on the cushion plant *Thylacospermum caespitosum* in the Trans-Himalaya, India, along an elevational gradient. Across all elevations, they found a higher species richness and abundance in open areas than within cushions, indicating competitive interactions and no facilitation. Yet, this study was conducted along a very high elevational gradient (4850-5850 m), while my study was at 1376-1695 m. The median species cover in the open areas at their lowest elevational site was below 40%, while my open areas at the low site were fully covered by other species, suggesting their study sites were generally more stressful for species than mine. Their results could possibly be explained by a model proposed by Michalet et al. (2006) saying there is a point under extreme stress conditions where only the most stress tolerant species exist, and being facilitated is not enough for the less stress-tolerant species when it comes to enduring these environments. In my case though, it is unlikely that all three of my elevational sites were extreme to this degree, especially since facilitation has been found at Finse before (Kjær et al., 2018; Klanderud, 2005; Klanderud & Totland, 2005).

4.2 Costs of species interactions

Most studies on the feedback effects that beneficiary species can have on their benefactor plants have found reproductive fitness costs of facilitation (Cranston et al., 2012; García et al., 2016; Schöb et al., 2014a; Schöb et al., 2014b; Schöb et al., 2014c). One of these studies (Cranston et al., 2012) focused on *S. acaulis* and found that facilitation along with its costs (less flowers per plant and seeds per fruit, as well as smaller leaves) increased with abiotic stress and a higher elevation.

My findings are not in line with most previous studies including Cranston et al. (2012), in the sense that the role of facilitation along with facilitative costs did not increase with elevation. Instead, I found weakly competitive interactions between *S. acaulis* and other species at all sites with no apparent costs. Without any indications of facilitation at my sites, I cannot assess whether facilitating other species would have come at a cost for *S. acaulis* at Finse. The lack of reproductive costs for *S. acaulis* at my sites, however, can instead mean that there were no competitive effects between *S. acaulis* and other species strong enough to induce a cost on *S. acaulis*. One limitation of my study though, would be that I measured a single season of the effects of plant interactions on the reproductive costs of *S. acaulis*, not multiple seasons, or other long-term metrics of *S. acaulis* performance such as growth or survival. Thus, while I found no effects of plant interactions on reproduction of *S. acaulis* in my study, costs may still emerge over longer periods of time. This underscores the need to study not just short term feedback effects for long-lived benefactor plants, but also long-term effects (Armas & Pugnaire, 2005; Raath-Krüger et al., 2023).

It is worth mentioning that although I found no costs of species interactions for *S. acaulis*, the high elevation had a 56% higher seed mass per capsule and a 35% higher seed mass per seed for the removal cushions than the controls. The high elevation was also the elevation with the most plants (11 out of 20) with no seed capsules. In addition, there was no difference between control and removal cushions with regards to the capsules to flowers ratio but interestingly, a significant negative relationship between the capsules to flowers ratio and the cover of species inside the cushion at the mid elevation. Therefore, the cost of species interactions at the mid elevation may be dependent of the degree of species cover. Thus, given the general trend in species moving upwards in alpine environments increasing species richness (Pauli et al., 1994; Steinbauer et al., 2018; Walther et al., 2005), it is possible that there will be a cost of species interactions at the mid elevation in the future.

5. Conclusion

I found weakly competitive interactions for space between *S. acaulis* and other species, mainly bryophytes and lichens, at all sites along an elevational gradient in my study. Further, I found no indications of facilitation, and no reproductive costs for *S. acaulis* from species interactions.

The lack of facilitative interactions found at my study sites suggests that the sites, at the time of measure, were not experiencing high degrees of abiotic stress. Temporary and seasonal environmental conditions could have played a role in determining the plant interactions and the short-term reproductive effects on *S. acaulis*. Yet it is also possible that the study sites have already been affected by global warming, because in colder areas, changes in species interactions from facilitative to more competitive may be driven by changes in climate.

This experimental study was conducted at a high latitude and across an elevational gradient. As my results differed from my predictions and from most other studies, it emphasizes the importance of studying species interactions, and their costs, within and across wide ranges of environments, latitudes and elevations. In addition, future research is needed to further unravel the effects of climate change on species interactions and fitness costs for known facilitating plants. This could help explain more of the variation in species interactions and potential costs within and across environmental gradients.

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Appendix

Table A1. *All S. acaulis cushion plants that had zero seed capsules are counted for each combination of elevation (low, mid, high) and treatment (control, removal).*

Elevation/Treatment	Number of plants (out of 10) with zero seed capsules
Low, control	4
Low, removal	4
Mid, control	3
Mid, removal	3
High, control	6
High, removal	5

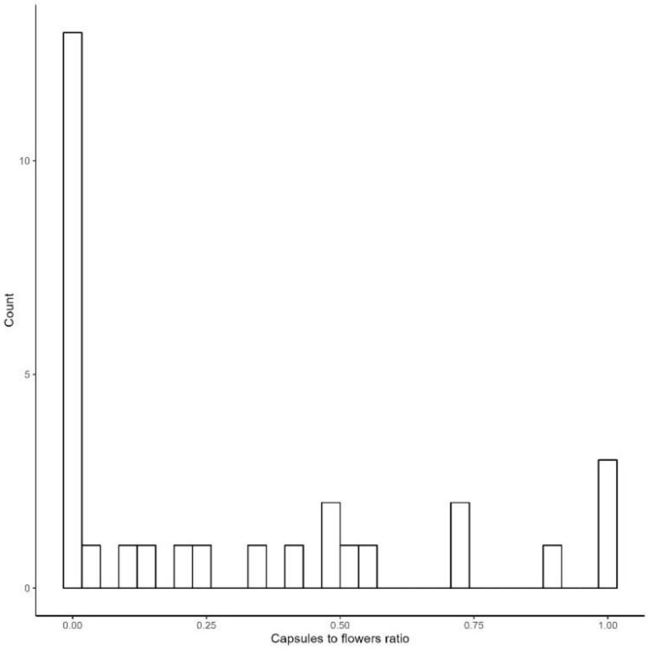

Figure A1. *Histogram showing the distribution of the capsules to flowers ratio values. The histogram includes data from all elevations (low, mid, high) and the treatments control and removal.*

Table A2. All species found within control plots, *S. acaulis* removal cushions and *S. acaulis* control cushions and their corresponding functional group.

Species	**Functional group**
Antennaria alpina	Forbs
Antennaria sp.	Forbs
Anthoxanthum odoratum	Graminoids
Astragalus alpinus	Forbs
Bartsia alpina	Forbs
Bistorta vivipara	Forbs
Brodoa oroarctica	Lichens
Carex bigelowii	Graminoids
Careax sp.	Graminoids
Carex vaginata	Graminoids
Cerastium alpinum	Forbs
Cetraria sp.	Lichens
Cladonia arbuscula	Lichens
Cladonia sp.	Lichens
Cladonia uncialis	Lichens
Deschampsia alpina	Graminoids
Diphasiastrum alpinum	Forbs
Empetrum nigrum	Shrubs
Equisetum sp.	Forbs
Erigeron sp.	Forbs
Euphrasia wettsteinii	Forbs
Festuca rubra	Graminoids
Festuca sp.	Graminoids
Festuca vivipara	Graminoids
Flavocetraria nivalis	Lichens
Gentiana sp.	Forbs
Hieracium alpinum	Forbs
Luzula spicata	Graminoids

Omalotheca supina	Forbs
Ophioparma ventosa	Lichens
Peltigera sp.	Lichens
Poa alpina	Graminoids
Polytrichastrum sexangulare	Bryophytes
Polytrichum sp.	Bryophytes
Potentilla crantzii	Forbs
Rhizocarpon sp.	Lichens
Rhodiola rosea	Forbs
Rhytidium sp.	Lichens
Salix herbacea	Shrubs
Saussurea alpina	Forbs
Saxifraga oppositfolia	Forbs
Sibbaldia procumbens	Forbs
Stereocaulon sp.	Lichens
Taraxacum sp.	Forbs
Thalictrum alpinum	Forbs
Trisetrum spicatum	Graminoids
Vaccinium vitis-idaea	Shrubs
Veronica alpina	Forbs
Vulpicida pinastri	Forbs
Bryophyte unidentified	Bryophytes
Lichen unidentified	Lichens
Plant unidentified	NA

Table A3. *Estimated differences in means of number of seeds per capsule, and the corresponding standard error as well as p value. The Tukey test was based on an ANOVA that included number of seeds per capsule as a response variable, elevation and treatment as main effects and an interactive effect between elevation and treatment. Only the contrasts in elevation are shown in this table. Significant p-values (p<0.05) are marked with *.*

Contrast	Estimate	p value
mid – low	2.5883	0.0682
high – low	3.5333	**0.0221***
high – mid	0.9451	0.7172

Table A4. *Estimated differences in means of seed mass (mg) per seed for elevation*treatment, and the corresponding standard error as well as p value. The Tukey test was based on an ANOVA with seed mass (mg) per seed as a response, elevation and treatment as main effects and an interactive effect between elevation and treatment. Only the contrasts in elevation are shown in this table. Significant p-values (p<0.05) are marked with *.*

Contrast	Estimate	p value
mid – low	-0.0513	**0.0047***
high – low	-0.1053	**0.0000***
high – mid	-0.0540	**0.0062***

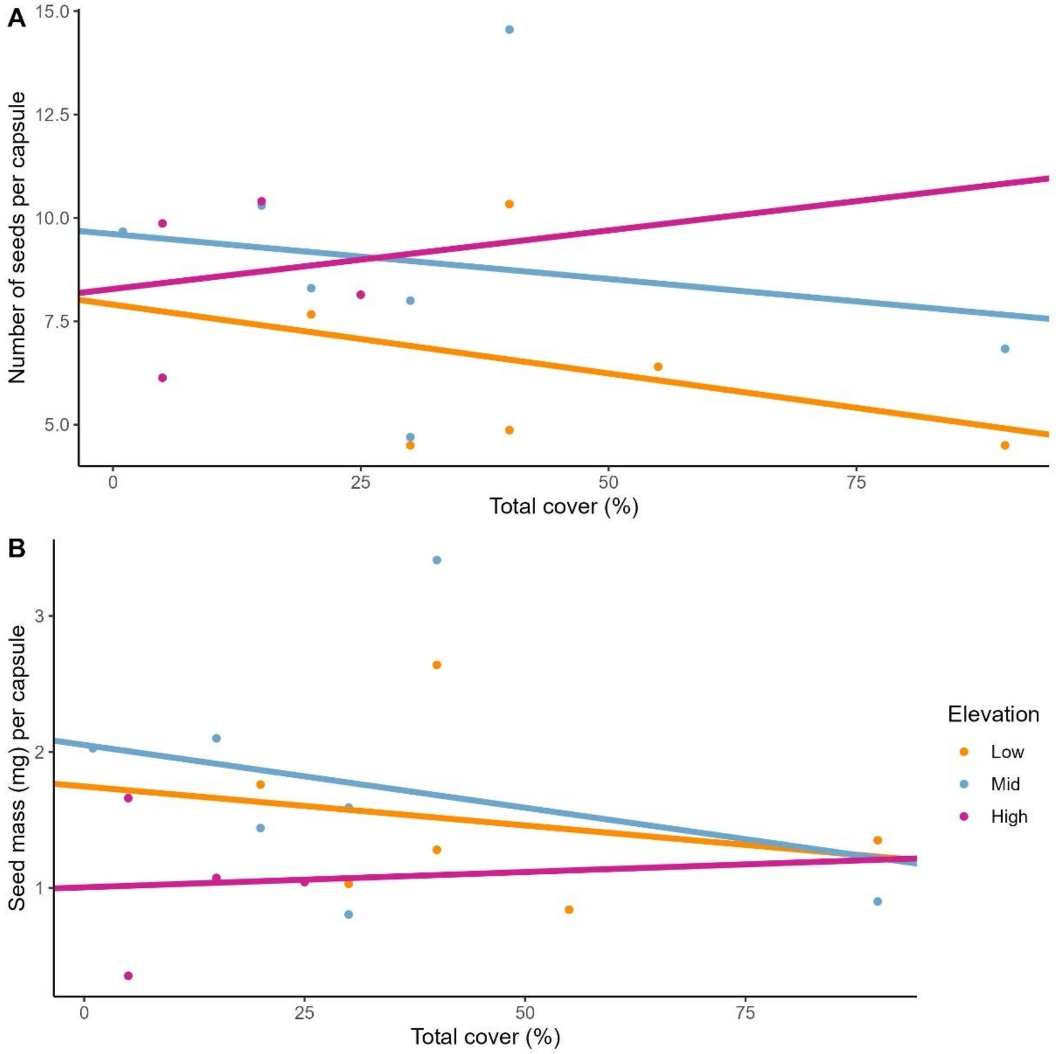

Figure A2. *A figure showing the linear regressions done on the number of seeds per capsule (A) and seed mass per capsule (B) for S. acaulis control cushions in relation to total species cover (trip 3). The low elevation is represented by the color orange, the mid elevation is represented by the color blue and the high elevation is represented by the color purple.*

Table A5. *Statistics table on the linear regressions done on the number of seeds per capsule for S. acaulis control cushions in relation to total species cover (trip 3). Significant p-values (p<0.05) are marked with *, while trending values (p<0.10) are marked with (.).*

Elevation	Adjusted R^2	Estimate	Std. Error	t value	p value
Low	-0.0930				
Intercept		7.9035	2.2407	3.527	**0.0243***
Total cover		-0.0333	0.0439	-0.758	0.4906
Mid	-0.1526				
Intercept		9.6086	1.9925	4.822	**0.0048***
Total cover		-0.0217	0.0479	-0.453	0.6693
High	-0.4703				
Intercept		8.2818	2.1129	3.920	**0.0594 .**
Total cover		0.0283	0.1409	0.201	0.8593

Table A6. *Statistics table on the linear regressions done on seed mass (mg) per capsule for S. acaulis control cushions in relation to total species cover (trip 3). Significant p-values (p<0.05) are marked with *, while trending values (p<0.10) are marked with (.).*

Elevation	Adjusted R^2	Estimate	Std. Error	t value	p value
Low	-0.1907				
Intercept		1.7461	0.6555	2.664	**0.0562 .**
Total cover		-0.0057	0.01285	-0.446	0.6785
Mid	-0.0947				
Intercept		2.0514	0.5545	3.700	**0.014***
Total cover		-0.0093	0.0133	-0.693	0.519
High	-0.4976				
Intercept		1.0042	0.5916	1.698	0.232
Total cover		0.0023	0.0394	0.057	0.960

Table A7. Statistics table on the *Spearman correlation tests done on the capsules to flowers ratio (the number of seed capsules divided by the maximum number of flowers) for S. acaulis cushions in relation to the total % cover (trip 3). Significant p-values (p<0.05) are marked with *.*

Elevation	S	rho	p value
High	153.77	0.0680	0.8519
Mid	301.76	-0.8289	**0.0030***
Low	193.2	-0.1709	0.6369

Table A8. *The test results from the Dunn's test done on species richness per area (cm^2). The impacts of the three elevational contrasts high-low, high-mid and low-mid on species richness per area within each treatment (control, open) are tested for significance. Significant p-values (p<0.05) are marked with *.*

Treatment/Contrast	Z value	p value unajusted	p value adjusted
Control			
- high-low	-2.9464	**0.0032***	**0.0096***
- high-mid	-2.4638	**0.0137***	**0.0412***
- low-mid	0.4826	0.6294	1.0000
Open			
- high-low	-2.1336	0.0329	0.0986
- high-mid	-3.4290	0.0006	0.0018
- low-mid	-1.2954	0.1952	0.5855

Table A9. *The test results from the Dunn's test done on the median total species cover (%) values (trip 3). The impacts of the three elevational contrasts high-low, high-mid and low-mid on total species cover within each treatment (control, open) are tested for significance. Significant p-values (p<0.05) are marked with *.*

Treatment/Contrast	Z value	p value unajusted	p value adjusted
Control			
- high-low	-3.6600	**0.0003***	**0.0008***
- high-mid	-2.8821	**0.0040***	**0.0119***
- low-mid	0.7779	0.4366	1.0000
Open			
- high-low	-4.2089	$\mathbf{2.567 \cdot 10^{-5}}$ *****	$\mathbf{7.700 \cdot 10^{-5}}$ *****
- high-mid	-3.8758	$\mathbf{1.063 \cdot 10^{-4}}$ *****	$\mathbf{3.188 \cdot 10^{-4}}$ *****
- low-mid	0.3331	0.7391	1.0000

Table A10. *The test results from the Dunn's test done on the median total species cover (%) of the five functional groups shrubs, forbs, graminoids, lichens and bryophytes. The impacts of the three elevational contrasts high-low, high-mid and low-mid on total species cover within each treatment (control, open) are tested for significance. Significant p-values (p<0.05) are marked with * while p values between 0.10 and 0.05 marked with (.).*

Treatment/Contrast	Z value	p value unajusted	p value adjusted
<u>Shrubs</u>			
Control			
- high-low	-1.6086	0.1077	0.3231
- high-mid	-1.5571	0.1194	0.3583
- low-mid	0.0514	0.9589	1.0000
Open			
- high-low	-1.4743	0.1404	0.4212

- high-mid	0.1795	0.8576	1.0000
- low-mid	1.2949	0.1954	0.5861
Forbs			
Control			
- high-low	-3.6114	**0.0003***	**0.0009***
- high-mid	-1.8249	**0.0680 .**	0.2041
- low-mid	1.7866	**0.0740 .**	0.2220
Open			
- high-low	-1.0434	0.2968	0.8903
- high-mid	-1.0179	0.3087	0.9261
- low-mid	0.0254	0.9797	1.0000
Graminoids			
Control			
- high-low	-3.6537	**0.0003***	**0.0008***
- high-mid	-1.4509	0.1468	0.4404
- low-mid	2.2028	**0.0276***	**0.0828 .**
Open			
- high-low	-2.4697	**0.0135***	**0.0406***
- high-mid	-0.9800	0.3271	0.9812
- low-mid	1.4896	0.1363	0.4089
Lichens			
Control			
- high-low	1.5869	0.1125	0.3376
- high-mid	2.2763	**0.0228***	**0.0685 .**
- low-mid	0.6894	0.4906	1.0000

Open			
- high-low	3.2323	**0.0012***	**0.0037***
- high-mid	-0.4072	0.6838	1.0000
- low-mid	-3.6395	**0.0003***	**0.0008***
<u>Bryophytes</u>			
Control			
- high-low	-2.1287	**0.0333***	**0.0998 .**
- high-mid	0.4257	0.6703	1.0000
- low-mid	2.5544	**0.0106***	**0.0319***
Open			
- high-low	-3.7168	**0.0002***	**0.0006***
- high-mid	-2.4391	**0.0147***	**0.0442***
- low-mid	1.2776	0.2014	0.6041

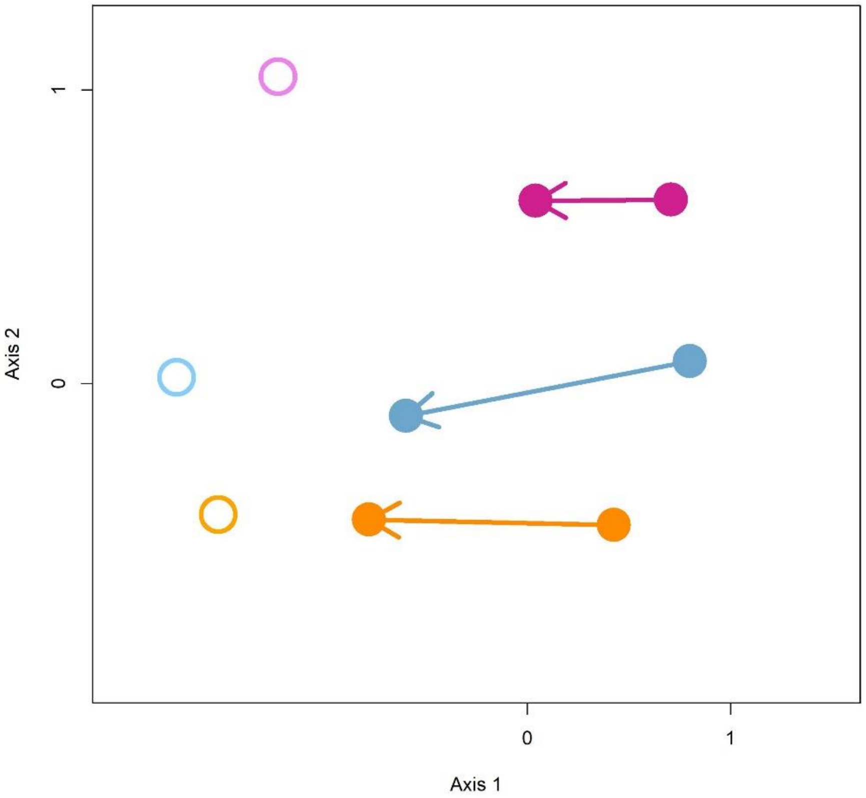

Figure A3. *An NMDS ordination plot showing how the species composition of the S. acaulis control cushions changed between visit two and three to Finse, as well as showing the species composition of the open areas on the third visit to Finse. The open areas are represented in the figure by open circles, while the S. acaulis control cushions are represented by closed circles. The second visit to Finse is represented by the start of the arrow, while the end of the arrow represents the third visit to Finse. The color purple represents the high elevation, blue represents the mid elevation and orange represents the low elevation. The figure is based on presences/absence data of species (trip 2 and 3).*

Table A11. *The total added cover per treatment S. acaulis control cushion or open area of the species that were found in only one treatment (control, open) at the high elevation (trip 3).*

Species	**Control**	**Open**
Brodoa oroarctica	0	17
Cladonia uncialis	0	11
Luzula spicata	0	10
Ophioparma ventosa	0	5
Peltigera sp.	1	0
Poa alpina	1	0
Polytrichastrum sexangulare	0	1
Rhizocarpon sp.	0	2
Rhodiola rosea	2	0
Trisetrum spicatum	0	6
Vulpicida pinastri	0	20

Table A12. *The total added cover per treatment S. acaulis control cushion or open area of the species that were found in only one treatment (control, open) at the mid elevation (trip 3).*

Species	**Control**	**Open**
Bartsia alpina	2	0
Cladonia sp.	0	6
Cladonia uncialis	0	25
Deschampsia alpina	0	25
Diphasiastrum alpinum	0	115
Erigeron sp.	0	10
Festuca rubra	1	0
Hieracium alpinum	0	10
Peltigera sp.	1	0
Polytrichum sp.	0	21
Rhytidium sp.	0	40
Sibbaldia procumbens	7	0
Trisetrum spicatum	30	0
Lichen unidentified	0	5

Table A13. *The total added cover per treatment S. acaulis control cushion or open area of the species that were found in only one treatment (control, open) at the low elevation (trip 3).*

Species	**Control**	**Open**
Anthoxanthum odoratum	0	95
Careax sp.	0	25
Diphasiastrum alpinum	0	5
Empetrum nigrum	0	150
Equisetum sp.	0	1
Festuca vivipara	1	0
Gentiana sp.	1	0
Luzula spicata	0	5
Omalotheca supina	1	0
Lichen unidentified	0	1

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