THE CUSHION PLANT *SILENE ACAULIS*: BIOTIC INTERACTIONS ALONG AN ENVIRONMENTAL GRADIENT AT ALPINE FINSE, SOUTHERN NORWAY

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Preface

This thesis is the final part of my master degree in Natural Resource Management at the Department of Ecology and Natural Resource Management (INA) at the Norwegian University of Life Sciences (UMB).

I would like to thank my main supervisor associate professor Kari Klanderud for her guidance, help and knowledge. My co-supervisor research fellow Siri Lie Olsen helped with the fieldwork, the writing process and much more, thank you. Both of my supervisors have been very positive and they always found time for me. They truly supported me through all the work of this thesis.

Further words of gratitude go to Francesca Jaroszynska who was a fantastic field assistant and always kept the mood up through our long days of work. Lab engineer Annie Aasen helped me with my soil analyses and Maximilian Rohrer proofread my thesis, thanks to both of you.

Finally, I would like to thank Finse Research Station for its great hospitality.

Ås, Mai 10th 2013

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II

Abstract

Plants interact with each other in many ways. Competition for resources and space is well documented among a wide variety of plants. Positive interactions, or facilitation, may also be important for plant survival, especially in physically harsh environments such as alpine regions. *Silene acaulis* and other cushion plants, which are common in the alpine, have been found to facilitate species richness in the most stressful parts of elevation gradients. To my knowledge, nobody has previously examined biotic interactions in cushion plants along successional gradients.

I have studied the effect of *S. acaulis* on the diversity of vascular species, bryophytes, and lichens, as well as on the fertility of vascular species and the growth of *Bistorta vivipara*, along a successional gradient at alpine Finse, southern Norway. The gradient was situated in the glacier foreland of Midtdalsbreen, where physical conditions gradually changed from very harsh near the glacier to more benign further away.

I found that *S. acaulis* facilitated the performance of *B. vivipara* in the harshest parts of the gradient. *B. vivipara* had longer and wider leaves, as well as longer leaf stalk, when growing inside cushions of *S. acaulis* near the glacier. In the other end of the transect no facilitation was found between *S. acaulis* and *B. vivipara*. Here, leaves of *B. vivipara* tended to be wider outside than inside cushions of *S. acaulis*, possibly indicating competition between the two. Species richness showed a weak facilitation from *S. acaulis*. Four species were only found inside cushions, all with low observed numbers of individuals. No facilitation was found when comparing number of species in cushion plots to their paired control plots.

Silene acaulis facilitates the performance of single species under harsh environmental conditions, while only weak interactions between the cushion plant and species richness were found at Finse. Previous studies have documented strong facilitation of species richness by *S. acaulis* in similar environments. For a better understanding of plant interactions in environmental gradients (and especially succession gradients), more research is needed.

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Contents

Introduction

It is well known that plants compete for resources and space. Facilitation, on the other hand, has not received much attention until lately. In the last decades of the 20th century and the beginning of the 21st century, focus on facilitation, or positive interactions, in plant ecology increased (Hunter & Aarssen 1988; Bertness & Callaway 1994; Callaway 1995; Callaway & Walker 1997; Bruno et al. 2003; Brooker et al. 2008). Nevertheless, there is still a need of incorporating facilitation in mainstream ecological theory (Brooker et al. 2008).

Facilitation is broadly defined by Bertness & Callaway (1994) as "*…all non-consumer interactions among two or more species that positively affect at least one of the species involved…*". Positive interactions can be thought of as the opposite of competition. Plants can benefit each other through resource modification, increased light or shade, improved temperature, soil oxygenation, substrate modification, protection from herbivores or improved pollination (Callaway 1995). These mechanisms make it possible for a wider range of species to exist in a given area. Facilitation can be either commensal or mutualistic, benefiting only one of the species involved or both (Callaway 1998). Hacker & Gaines (1997) even suggests that new interaction webs could be created with the presence of a facilitating species.

Positive interactions have been shown to occur within a wide variety of vascular plants (Callaway 1995) such as cushion plants (Cavieres et al. 2002; Arroyo et al. 2003; Antonsson et al. 2009), rushes (Hacker & Bertness 1995), shrubs (Callaway 1992) and trees (Longpre et al. 1994).

The stress gradient hypothesis predicts facilitative interactions to be common in physically harsh environments, as opposed to benign habitats where competition dominates (Bertness & Callaway 1994; Brooker & Callaghan 1998). Salt marshes (Bertness & Shumway 1993), arid desserts (Fowler 1986), alpine areas (Callaway et al. 2002) and arctic tundra (Jonasson 1992) are some examples of environments where facilitation among plants has been documented. Several studies have shown facilitation at high altitudes where the physical conditions are stressful and little or no facilitation at lower altitudes where the environment is more benign (Callaway et al. 2002; Cavieres et al. 2002; Choler et al. 2003; Yang et al. 2010).

Alpine plants face hard climatic challenges such as low temperatures, strong wind and short growing season. Under harsh environmental conditions like these, positive interactions could be important (Bertness & Callaway 1994; Callaway 1997; Brooker & Callaghan 1998;

Michalet et al. 2006). The characteristics of cushion plants make them potential facilitators in alpine environments. Cushions plants have one of the most distinctive growth forms in alpine regions (Körner 2003). They are efficient heat traps, and temperatures can be considerably higher inside the cushion than the surrounding air (Körner 2003). Cushions can also store large amounts of moisture and detritus (nutrients) (Körner 2003), which might become available to other species. As a result, cushion plants are known as "nurse plants", i.e. a sheltering adult plant that supports the growth of seedlings of another species (Callaway 1995). Cavieres et al. (2006) found positive spatial association between the cushion plant *Laretia acaulis* and other vascular species in the Chilean Andes. *Bolax gummifera*, *Azorella monantha* and *Azorella madreporica* are other species which have shown facilitative properties (Cavieres et al. 2002; Cavieres et al. 2008; Quiroz et al. 2009). For a full list of studies regarding cushion plants and facilitation see de Bello et al. (2011).

Few studies have examined the facilitative effects of the cushion plant *S. acaulis*. This widely distributed, circumpolar species (Körner 2003) might have a potentially large impact on other plant species in the northern hemisphere. Antonsson et al. (2009) and Molenda et al. (2012) showed that *S. acaulis* functioned as a nurse plant at high but not at lower altitudes. To my knowledge, *S. acaulis* has not yet been studied with respect to plant-plant interactions along successional gradients. I predict that facilitation from *S. acaulis* can occur in other gradients than elevation gradients, and especially in the environmentally harsh parts.

I studied *S. acaulis*, and plants and lichens growing in its vicinity, in the alpine area Finse, southern Norway. The study area is a succession gradient in the glacier foreland from the retreating glacier Midtdalsbreen to Lake Finsevatnet. I wish to examine whether *S. acaulis* affects other plants in this area and if there are differences in interactions along the gradient. I will study the frequently occurring species *Bistorta vivipara* in order to examine whether or not *S. acaulis* can affect the performance of a single species as well as the diversity of different functional groups.

My research questions are as follows:

1) Do more vascular plants, bryophytes, lichens or seedlings grow inside cushions of *Silene acaulis* than outside?

2) Are there some vascular plants species only found within the cushions or only outside them?

3) Do vascular plants have higher fertility inside *Silene acaulis* than outside?

4) Does *Silene acaulis* affect the performance of individuals of *Bistorta vivipara*?

5) Is the facilitative effect of *Silene acaulis* higher near the glacier where the environment is harsher and the succession at an earlier stage?

Methods

Study area

The study was conducted three km southwest of Finse, southern Norway (Fig. 1). Finse is situated in a mid-alpine area on Hardangervidda mountain plateau, 1200 m a.s.l. The climate at Finse is slightly oceanic with intermediate amounts of snow (Moen 1998). Annual mean temperature is -2.1 °C, with a monthly mean temperature of -10.1 °C in January and 7.0 °C in July (Norwegian Meteorological Institute 2013). Mean annual precipitation is 1030 mm. April is the driest month and September the wettest with a mean monthly precipitation of 35 mm and 128 mm, respectively (Norwegian Meteorological Institute 2013).
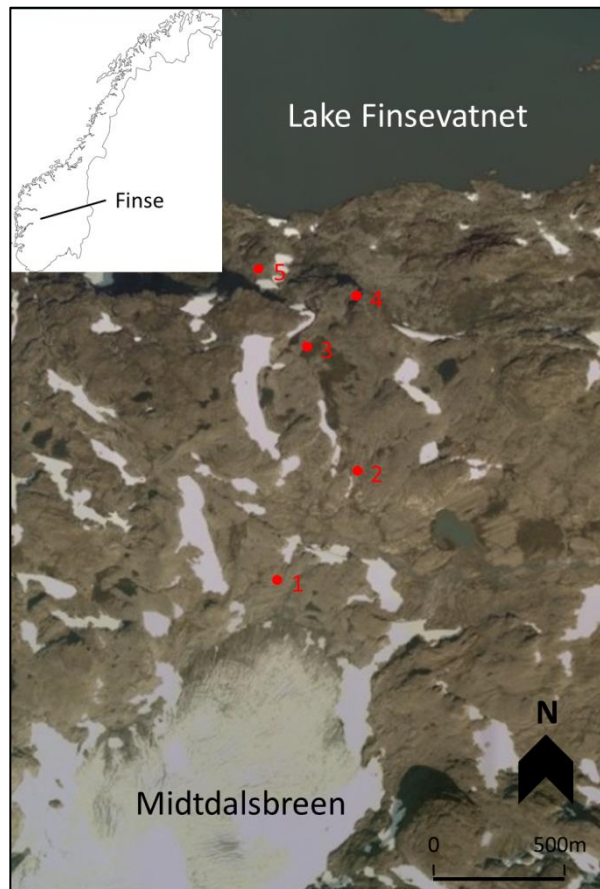
Figure 1: Aerial photo of transect situated between Lake Finsevatnet and glacier tongue Midtdalsbreen. Five locations in the transect are marked in red. Finse's position in Norway showed in upper left corner. Map from Kilden – Skog og landskap (2013), modified after Hågvar et al. (2009).

The study area is located between the glacier tongue Midtdalsbreen and the lake Finsevatnet (between 60°34'29''N 7°28'6''E and 60°35'8''N 7°27'56''E, Fig. 1). The bedrock in the study area consists of medium to coarse-grained granite (Geological Survey of Norway 2013a), with a thin cover of moraine in the southern part (Geological Survey of Norway 2013b). Midtdalsbreen has been receding since A.D. 1750, the end of the Little Ice Age (Dahl & Nesje 1997).

Study species

Silene acaulis is a gynodioecious plant in the family Caryophyllaceae. The plant is perennial and grows in light green cushions with a height of 2-8 cm (Mossberg et al. 1995). Individuals used in this study had a maximum height of approximately five cm. Cushions are compact with a single taproot. The petals are pink, sepals are red, but white flowers can occasionally be found. Leaves are narrow and have stiff hairs on the edges (Lid & Lid 1994). *Silene acaulis* thrives on dry or moist calcareous soil in mountain areas (Mossberg et al. 1995). It has a circumpolar distribution, and is common in the mountains of Norway (including Svalbard), Sweden and Finland as well as in Greenland, North-America and Siberia (Lid & Lid 1994). *Silene acaulis* is highly capable of tolerating extreme temperatures; with winter hardening and a high heat resistance it can survive temperatures from -80 °C to 60 °C (Larcher et al. 2010). The cushions have also shown remarkable heat trapping traits, with leaf temperature being higher than air temperature (Neuner et al. 2000). Estimations show that *S. acaulis* can reach more than 300 years of age (Morris & Doak 1998).

Study design

Data was collected during July 2012. A transect of about 1300 m was established in the study area from Midtdalsbreen towards Lake Finsevatnet. The transect had a weak north-facing slope, with steeper areas in the northern part. Five locations were established at intervals along the transect (Fig. 1). Locations were established with approximately the same distance to the neighbor location (varying from 290 m to 520 m), to cover the variety of the entire successional gradient along the transect. The presence of at least six individuals of *S. acaulis* and roughly the same environmental conditions (flat, exposed and dry) determined the exact position of locations. Location 1 (closest to the glacier) was located at approximately 1380 m a.s.l., location 2 at 1330, location 3 at 1340, location 4 at 1350 and location 5 (closest to the lake) at 1280 m a.s.l. At the top of the transect (location 1) the vegetation was scarce and

gravel dominated the soil. Moving down the transect the vegetation was denser and taller, and the soil seemed to contain more organic material.

I established six paired plots in each location. Each pair consisted of a cushion of *S. acaulis* and a control plot of the same size, without a *S. acaulis* cushion. This gives a total of 60 plots (30 cushions and 30 control plots). Only cushions with a minimum diameter of ten cm and an approximately circular shape were chosen (see Antonsson et al. 2009). Control plots were located two m east of its paired cushion. Sites with more than 10% bare stone were considered inappropriate for a control plot, as it was thought of as unsuitable habitat for *S. acaulis* (gravel was considered to be acceptable). In this case I chose the closest site to the original control plot site, on the line between the cushion and control plot, with less than 10% bare stone.

To determine the size and shape of the control plots I used a soft steel wire. The wire was bent around the cushion of *S. acaulis* to make a figure of the same size and shape (see Cavieres et al. 2002; Antonsson et al. 2009; Cavieres & Badano 2009). The wire was then placed at the site of the control plot to mark the outline of the plot. To find the circumferences of the plot I stretched the metal wire and measured it. Further, I measured the distance across the cushion at the widest point, hereafter referred to as *diameter*.

To study if *S. acaulis* has an impact on plants growing inside it, vegetation analysis was carried out in all *S. acaulis* cushions and control plots. For vascular plants I recorded the number of species, the number of individuals of each species and the number of fertile species. For bryophytes and lichens only the number of species was recorded. It must be noted that lichen fragments caught by the canopy of the cushion (lying on top of it) was observed during the fieldwork. Even though some of them were loose, the chance of the fragments establishing on the cushion was present, hence all fragments were included in the registration. In addition I estimated total cover (%) of bryophytes, lichens, graminoids, litter and bare soil. Number of seedlings was also counted.

To study the effect of *S. acaulis* on the performance of a single species, *Bistorta vivipara* was chosen, as it was the species occurring in most plots and in all locations. Three individuals were examined per plot. When less than three individuals were present in a plot, all were examined. On each individual I counted the number of leaves and bulbils, and measured the length and width of the longest leaf, as well as the length of the leaf stalk.

To examine if there were differences in soil moisture between *S. acaulis* cushions and control plots, and along the gradient I measured soil moisture with a Delta-T Devices Moisture Meter type HH2 in all plots. In control plots a sensor was inserted 6-7 cm into the ground and moisture was measured. In the *S. acaulis* plots the sensor was inserted through the cushion and into the ground. This was repeated three times within each plot. All measurements were taken on the same day, in dry weather.

To examine if temperature inside *S. acaulis* differed from outside, temperature was measured with Tiny Tag temperature loggers. Two loggers were placed at each location, one in a *S. acaulis* cushion and one outside *S. acaulis* (in total ten loggers, five inside *S. acaulis* and five outside). For the *S. acaulis* plots, a probe connected to the logger was inserted into the cushion in order to measure the temperature within it. Loggers outside *S. acaulis* were placed, without a probe, on bare ground, measuring air temperature approximately two cm above ground level. Temperature outside *S. acaulis* was assumed to be the same as in control plots. Temperature was logged every hour in the time period 29th of July to 22nd of September.

On two of the Tiny Tag loggers, the cable between the logger and the probe was chewed off (probably by rodents), causing the loggers to stop recording. In the *S. acaulis* plot in location 3 (S3), this happened the second day of logging, and data from this logger could not be used in the analysis. For location 2 it happened on the 20th of September. Thus, I have chosen to use data from all loggers (except S3), from 29th of July to 20th of September.

Soil samples were taken from all plots, after vegetation analyses and measurements were done, to examine if there were differences in pH, organic content and soil moisture along the transect, or inside *S. acaulis* when compared to control plots. In cushion plots, I removed the plant before collecting the soil samples. In control plots, I removed the top layer of vegetation, litter, exposed soil and stones, and took the sample beneath it. Soil was immediately frozen. All samples were taken on the same day, in dry weather.

Soil analyses

From all soil samples I selected a representative subsample, avoiding larger stones. Subsamples were weighed using Sartorius ED Analytical Balance ED224S and dried at 105 °C in Termaks drying oven for 16 hours. I re-weighed the dry subsamples and calculated soil moisture (%) as the weight difference between the wet and dry subsample.

I dried all samples (the remaining material after taking out the subsamples) for 16 hours at 70 °C and cooled them in a desiccator. Dried samples were sifted through a 2-mm sieve. Parts of

each dried sample were saved for pH measurements, the rest were dried at 105 °C for 16 hours and cooled in a desiccator. I weighed all dry samples before burning them at 550 °C for three hours, samples were then cooled in a desiccator. The burned samples were weighed. Further, loss on ignition (LOI) was calculated ((burned material - dried material) / dried material * 100).

I measured pH with a calibrated WTW inoLab pH 720 from 10 ml dried and sifted material mixed with 25 ml distilled water, 16 hours after mixing.

Statistical analyses

Temperature data was checked for normal distribution. Mean temperature outside *S. acaulis* (control plots) was calculated for all locations. I ran a simple linear regression model with *mean temperature* as response variable and *location* as explanatory variable to see if there was a trend in temperature along the transect. I used a one sample t-test to test for differences in daily maximum and minimum temperatures inside and outside *S. acaulis* (null-hypothesis being that the average is equal to zero).

To examine soil moisture, I chose to use the results from the soil samples rather than field measurements, as the instrument used in field gave highly variable measurements within the same plot. *pH*, *LOI* and *soil moisture* were not normally distributed and did not respond well to transformation. I therefore used non-parametric tests to test if these variables differed between *S. acaulis* and control plots and along the transect. I ran Mann-Whitney U-tests with *S. acaulis/control* as explanatory variable and *pH*, *LOI* or *moisture* as response variables in three separate analyses. To check for changes along the transect I ran three separate Kruskal-Wallis tests with *location* as explanatory variable and *pH*, *LOI* or *moisture* as response variables. Mean and standard deviation were calculated for *pH*, *LOI* and *moisture* in *S.acaulis*/control in all locations.

I used Spearmans rank correlation test to examine whether there was a correlation between plot size and location, as this would make the interpretation of the results difficult. I used size as response variable and location as explanatory variable. For size the variables *circumference* and *diameter* were used in separate analyses. For *circumference* ρ (rho) was -0.089 (P = 0.501), and for *diameter* ρ was -0.069 (P = 0.603). Since size of the plots did not change with location, plot size was not considered in further analyses.

I used Generalized Linear Models (GLMs) to test if number of species within different functional groups (*total species*, *vascular species*, *lichen species*, *bryophyte species* and

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fertile vascular species) differed between control plots and *S. acaulis* along the transect. Only *total species* and *vascular species* had normal distributions. For the other groups I used Poisson distributions (in model: "family = poisson"). For each model, number of species within a group was used as the response variable and *S. acaulis/control* and *location* (1-5) were used as explanatory variables. I did not check for differences in number of seedlings as no plots in location 5 and only one plot in location 4 contained seedlings; hence this variable was considered to be insufficient. GLMs were initially run with interaction between *S. acaulis/control* and *location*. There was no significant interaction in any of the models; hence the interaction term was removed in the final models.

I checked data for *B. vivipara* for normal distribution. *Length of leaf* was normally distributed, *width of leaf* was normally distributed when log-transformed, and *number of leaves* had a Poisson distribution. *Length of stalk* did not have a normal distribution, with or without a transformation. For *length of leaf*, *width of leaf* and *number of leaves* I ran GLMs with *S. acaulis/control* and *location*, including their interaction, as explanatory variables with normal distribution, log-transformation and Poisson distribution, respectively. For *number of leaves* there was no significant interaction, and the model was run without interaction term. For *length of stalk* I used non-parametric tests, Kruskal-Wallis test with *location* as explanatory variable and Mann-Whitney U-tests with *S. acaulis/control* as explanatory variable. Few of the plants were developed enough for bulbils to be counted; hence possible differences in reproduction inside and outside cushions were not examined.

All statistical analyses were conducted in R 2.15.2 GUI 1.53 Leopard build 64-bit (6335) (R Core Team 2012).

Results

Temperature

Simple linear regression showed a slight increase, although not significant ($R^2 = 0.201$, P = 0.449), in air temperature when moving down the transect and away from the glacier (Fig. 2).
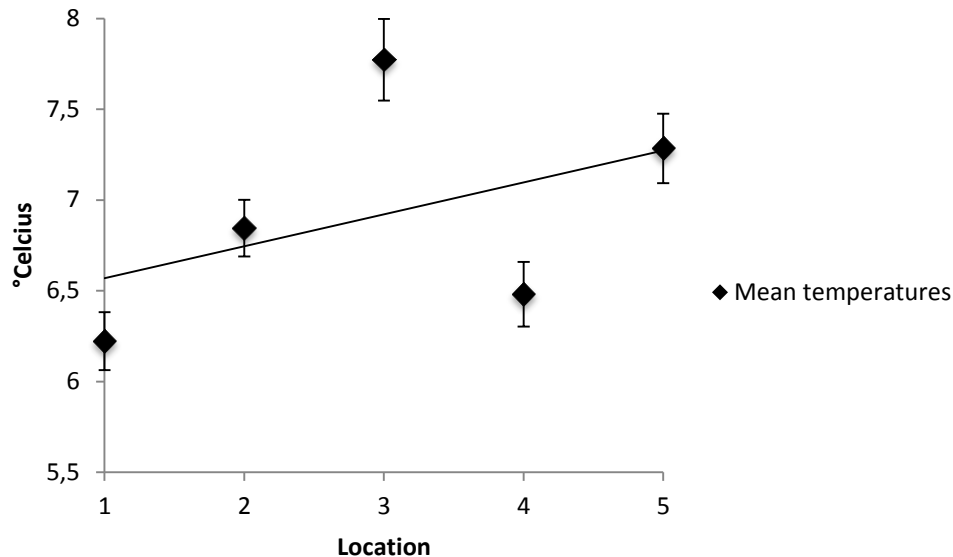

Figure 2: Mean temperature in open air, two cm above ground level, at five locations along a transect from Midtdalsbreen to Lake Finsevatnet (location 1 being closest to Midtdalsbreen and location 5 being closest to Lake Finsevatnet). Error bars represent ± 1 SE. P-value of regression line = 0.449, R^2 = 0.201. Temperature measured in the time period 29th of July to 20th of September 2012.

The highest temperature measured outside *S. acaulis* was 40.6 °C. Inside *S. aculis* the highest measured temperature was 24.6 °C. The lowest temperature was -3.1 °C outside *S. acaulis* and -0.7 °C inside. One sample t-tests showed that there were significant differences (on a 0.05 level) in daily minimum temperature between inside and outside *S. acaulis* cushions for all locations tested (location 1, 2, 4 and 5, P <0.001 for all, Fig. 3a). Daily maximum temperature showed significant differences in location 1, 4 and 5 (P <0.001 for all, Fig. 3b). Location 2 did not have a significant difference between inside and outside *S. acaulis* (P = 0. 891). Daily minimum temperature was higher inside *S. acaulis* than outside, and daily maximum temperature was lower inside than outside (except location 2, Fig. 3); hence the variation in temperature seemed to be lower inside *S. acaulis* than outside.
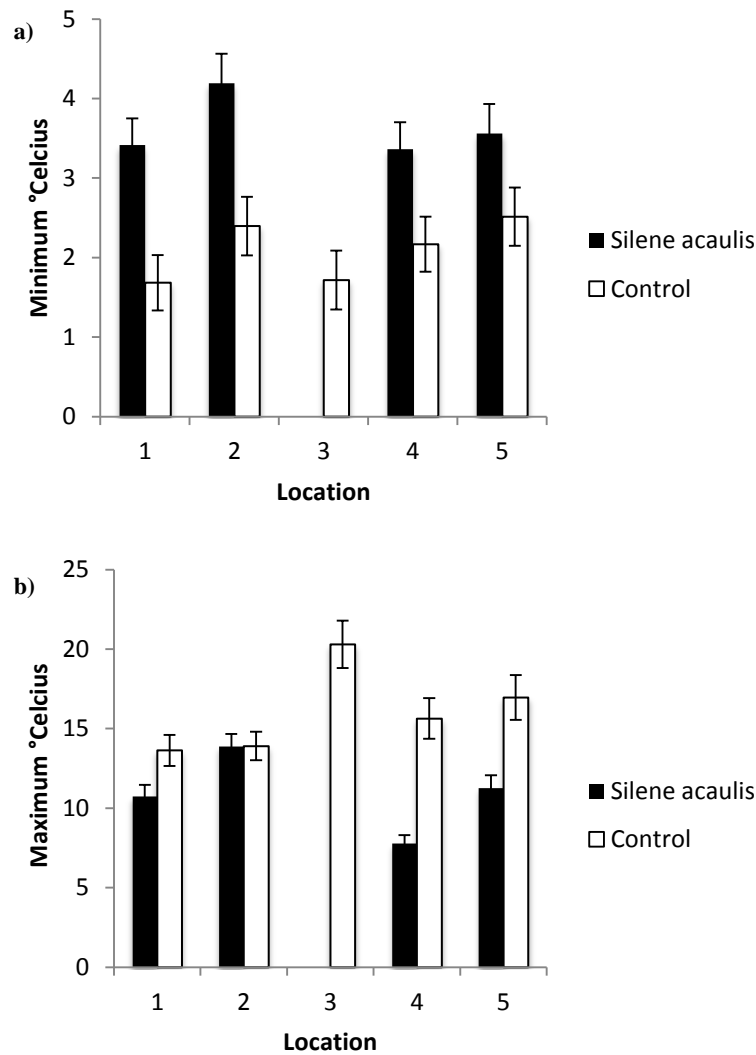
Figure 3: Daily mean minimum temperature a) and daily mean maximum temperature b) in *S. acaulis* and control plots (in open air two cm above ground level) at five locations along a transect from Midtdalsbreen to Lake Finsevatnet (location 1 being closest to Midtdalsbreen and location 5 being closest to Lake Finsevatnet). Error bars represent ± 1 SE. Temperature measured in the time period 29th of July to 20th of September 2012.

Soil samples

Mann-Whitney U-tests showed no significant differences in pH, LOI and moisture between *S. acaulis* and control plots (P = 0.237, 0.485 and 0.959, respectively). Kruskal-Wallis tests showed significant changes in all soil variables along the transect (P <0.001 for all). pH decreased, and LOI and moisture increased with distance to the glacier (Table 1).

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Table 1: Mean and standard deviation of pH, LOI (loss on ignition) and moisture in *Silene acaulis* and control plots at five locations along a transect from Midtdalsbreen to Lake Finsevatnet (location 1 being closest to Midtdalsbreen and location 5 being closest to Lake Finsevatnet).
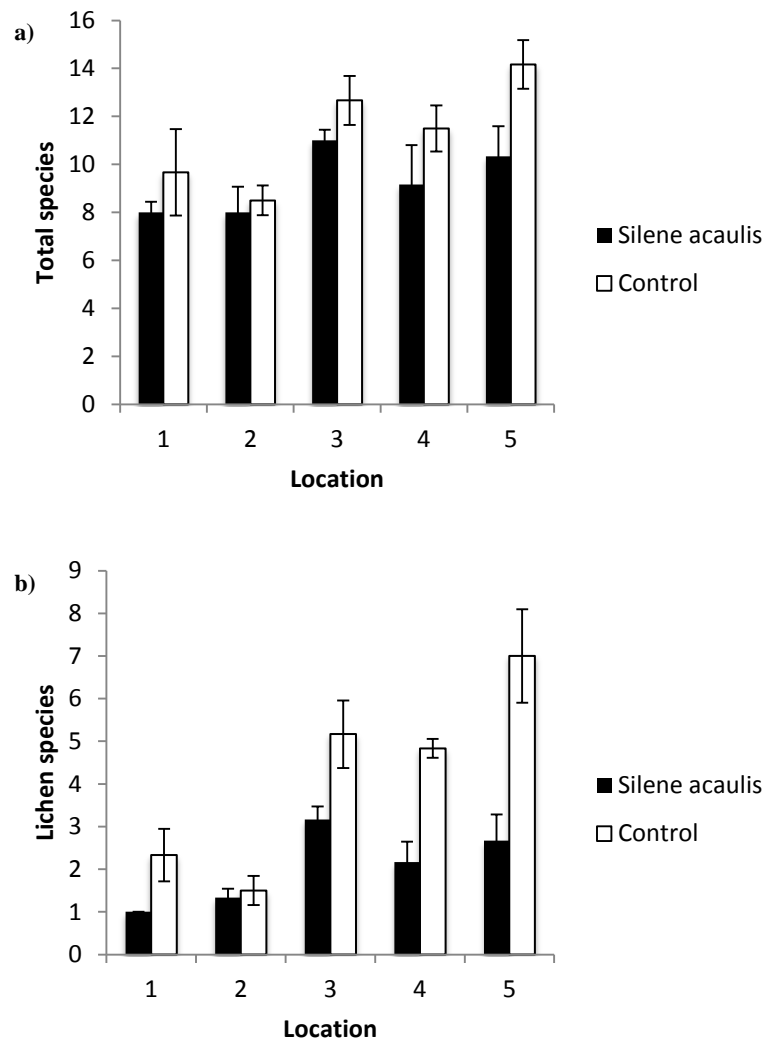
	Location 1		Location 2		Location 3	
	S. aculis	Control	*S. acaulis*	Control	*S. acaulis*	Control
pH	6.8 ± 0.3	6.8 ± 0.6	7.3 ± 0.4	7.6 ± 0.2	5.8 ± 0.5	4.9 ± 0.2
LOI	0.9 ± 0.1	0.7 ± 0.2	2.4 ± 1.3	0.9 ± 0.2	9.1 ± 8.0	8.4 ± 5.5
Moisture	6.5 ± 1.9	6.6 ± 2.6	14.2 ± 3.9	12.1 ± 1.5	21.1 ± 7.4	29.4 ± 9.0

	Location 4		Location 5	
	S. acaulis	Control	*S. acaulis*	Control
pH	4.7 ± 0.2	4.3 ± 0.1	5.1 ± 0.4	4.9 ± 0.5
LOI	39.8 ± 15.2	42.2 ± 23.1	38.5 ± 14.0	39.1 ± 27.6
Moisture	56.4 ± 12.0	55.6 ± 13. 7	52.4 ± 14.0	49.2 ± 18.5

Species richness

In total 34 vascular species were recorded (minimum 1 and maximum 10 per plot, see the appendix for a full list of registered vascular species in *S. acaulis* and control plots). Lichens and bryophytes had minimum 0 and 1 and maximum 10 and 7 species in a plot, respectively. Seedlings were found in 14 plots, nine controls and five *S. acaulis*, with the maximum number of seven seedlings in a plot. Of the vascular species, four species occurred only in *S. acaulis*, never in control plots (*Rhodiola rosea*, *Diphasiastrum alpinum*, *Salix reticulata* and *Thalictrum alpinum*). *Rhodiola rosea* was present in two plots, with one individual in one plot, and two individuals in the other plot. The three other species were registered in one plot each; for *D. alpinum* and *S. reticulata* one individual was found of each, while eight individuals of *T. alpinum* were registered. *Potentilla crantzii* was the only vascular species found only in control plots. It was registered in one plot with two individuals present. Representation of single species of lichens and bryophytes in *S. acaulis*/control plots was not possible to examine as only number of species present was counted.

GLMs showed that there was a significant difference in number of species present in *S. acaulis* compared to control plots for *total species* and *lichen species* (Table 2), with more species being present in control plots than inside *S. acaulis* (Fig. 4). When excluding *lichens* from the group *total species*, there was no significant difference between *S. acauilis* and control (P = 0.859). There was no significant difference in number of *vascular species*, *bryophyte species* and *fertile vascular species* inside and outside *S. acaulis* (Table 2).

Figure 4: Mean number of a) total species and b) lichen species in *Silene acaulis* and control plots in five locations along a transect from Midtdalsbreen to Lake Finsevatnet (location 1 being closest to Midtdalsbreen and location 5 being closest to Lake Finsevatnet). Error bars represent ± 1 SE.

For all groups there was a significant difference in species number between locations (Table 2). *Total species*, *lichen species*, *bryophyte species* and *fertile vascular species* increased in number when moving down the transect (away from the glacier), *vascular species* decreased.

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Table 2: Results from GLMs of species richness in *Silene acaulis* and control plots. Number of species in five groups (total species, vascular species, lichen species, bryophyte species and fertile vascular species) have been tested for differences inside cushion of *S. acaulis* and control plots in five locations along a transect from Midtdalsbreen to Lake Finsevatnet (location 1 being closest to Midtdalsbreen and location 5 being closest to Lake Finsevatnet). "Total species" and "Vascular species" had a normal distribution, for the rest of the response variables Poisson distributions have been used. *Silene acaulis* is compared to control plots, and location 1 is a control for the other locations. Interaction term for the explanatory variables has been removed, as none of them were significant. Bold numbers indicate significant p-values on a 0.05 significance level.

	Total species				Vascular species				Lichen species			
	Estimate	Std. error	t value	P	Estimate	Std. error	t value	P	Estimate	Std. error	Z value	P
Intercept	9.833	0.850	11.563	**<0.001**	5.333	0.527	10.114	**<0.001**	0.801	0.230	3.492	**<0.001**
S. acaulis	-2.000	0.694	-2.880	**0.006**	0.667	0.431	1.548	0.127	-0.701	0.155	-4.514	**<0.001**
Location 2	-0.583	1.098	-0.531	0.597	0.083	0.681	0.122	0.903	-0.163	0.330	-0.493	0.622
Location 3	3.000	1.098	2.733	**0.008**	-0.333	0.681	-0.490	0.646	0.916	0.265	3.463	**<0.001**
Location 4	1.500	1.098	1.366	0.178	-2.167	0.681	-3.183	**0.002**	0.742	0.272	2.731	**0.006**
Location 5	3.417	1.098	3.112	**0.003**	-1.917	0.681	-2.815	**0.007**	1.065	0.259	4.106	**<0.001**

	Bryophyte species				Fertile vascular species			
	Estimate	Std. error	Z value	P	Estimate	Std. Error	Z value	P
Intercept	0.518	0.247	2.095	**0.036**	-0.044	0.303	-0.144	0.886
S. acaulis	-0.239	0.168	-1.418	0.156	0.234	0.217	1.076	0.282
Location 2	-0.325	0.364	-0.894	0.371	-0.956	0.526	-1.816	0.069
Location 3	0.442	0.302	1.462	0.144	0.731	0.338	2.165	**0.030**
Location 4	0.799	0.283	2.813	**0.005**	0.654	0.342	1.912	0.056
Location 5	0.894	0.280	3.195	**0.001**	0.208	0.373	0.556	0.578

Bistorta vivipara

Bistorta vivipara occurred in 37 of 60 plots. Of the 37 plots, 27 had three or more individuals present, with a maximum of 49 individuals in a single plot (location 2). In location 4 only one plot contained *B. vivipara*.

GLMs showed that *length* and *width* (log-transformed) of the longest leaf differed significantly inside and outside *S. acaulis* (Table 3, Fig. 5a and 5b). Along the transect there was significant change in *length* and *width*, both increasing with distance to the glacier (Table 3, Fig. 5a and 5b). Significant interactions between *S. acaulis/control* and *location* on leaf length suggested that the relationship between leaf length in *S. acaulis* and control plots differed between location 3 (close to significant) and 5, compared to location 1 (used as control in the GLM, Table 3). Significant interactions between *S. acaulis/control* and *location* on leaf width suggested that the relationship between leaf width in *S. acaulis* and control plots differed between location 2, 3 and 5, compared to location 1 (Table 3).

Both *width* and *length* were longer in *S. acaulis* than control near the glacier (location 1 and 2) while there was no difference between inside and outside *S. acaulis* in the lower end of the transect (location 3 and 5), except leaf width which tended to be larger in control than in *S. acaulis* in location 3 (Fig. 3a and 3b).

Table 3: Results from GLMs of measurements of performance on *Bistorta vivipara* in *Silene acaulis* and control plots in five locations along a transect from Midtdalsbreen to Lake Finsevatnet (location 1 being closest to Midtdalsbreen and location 5 being closest to Lake Finsevatnet). In each plot "length of leaf" and "width of leaf" of the longest leaf of three individuals was measured. "Length of leaf" had a normal distribution; width of leaf is log-transformed and then normally distributed. *Silene acaulis* is compared to control plots, and location 1 is a control for the other locations. Bold numbers indicate significant p-values on a 0.05 significance level.

	Length of leaf				Width of leaf			
	Estimat	Std.	t value	P	Estimat	Std.	t value	P
Intercept	0.708	0.342	2.071	**0.041**	-1.101	0.134	-8.217	**<0.001**
S. acaulis	1.025	0.484	2.119	**0.037**	0.947	0.190	4.996	**<0.001**
Location 2	0.717	0.395	1.815	**0.073**	0.366	0.155	2.366	**0.020**
Location 3	2.207	0.433	5.100	**<0.001**	1.098	0.170	6.479	**<0.001**
Location 4	2.067	0.905	2.284	**0.025**	0.417	0.355	1.175	0.243
Location 5	2.600	0.453	5.741	**<0.001**	0.947	0.177	5.341	**<0.001**
S.acaulis : location 2	-0.792	0.559	-1.417	0.160	-0.928	0.219	-4.241	**<0.001**
S.acaulis : location 3	-1.173	0.592	-1.981	0.051	-1.110	0.232	-4.782	**<0.001**
S.acaulis : location 4	NA	NA	NA	NA	NA	NA	NA	NA
S.acaulis : location 5	-1.513	0.621	-2.437	**0.017**	-0.961	0.243	-3.950	**<0.001**

Mann-Whitney U-test showed significant differences in length of stalk on longest leaf between *S. acaulis* and control plots ($P = 0.006$), with longer stalks inside *S. acaulis* (Fig. 5c). Kruskal-Wallis test showed significant differences in length of stalk along the transect ($P < 0.001$), with increasing stalk length when moving down the transect (Fig. 5c). There was no significant difference in number of leaves on each individual inside and outside *S. acaulis* or along the transect.
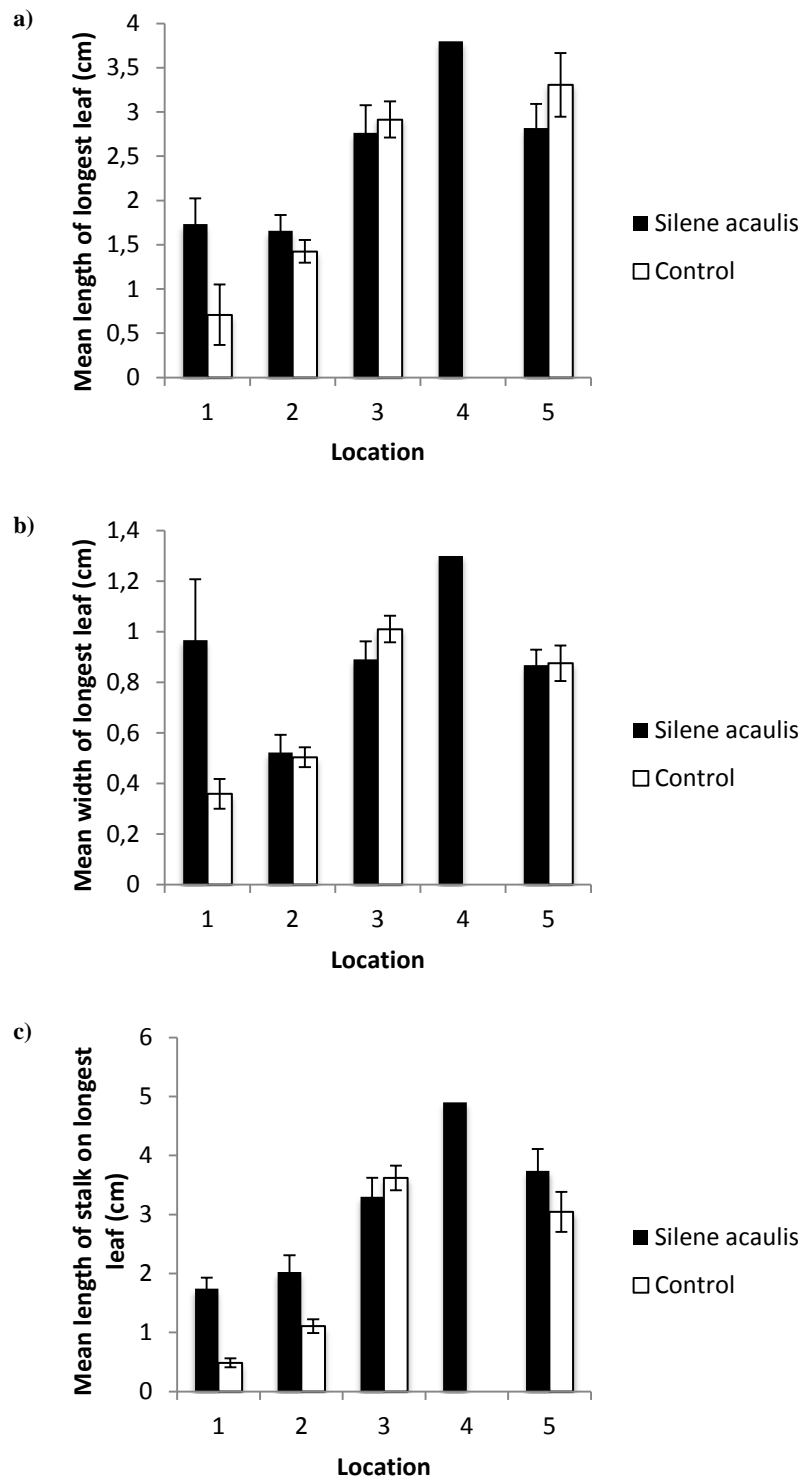
a)

b)

c)

Figure 5: Mean number of a) length, b) width and c) length (cm) of stalk on the longest leaf on individuals of *Bistorta vivipara* in *Silene acaulis* and control plots in five locations along a transect from Midtdalsbreen to Lake Finsevatnet (location 1 being closest to the Midtdalsbreen and location 5 being closest to Lake Finsevatnet). Error bars represent ± SE.

Discussion

Interactions affecting the performance of *Bistorta vivipara*

Silene acaulis had a positive effect on growth of *B. vivipara*, near the glacier. Leaves were longer and wider inside *S. acaulis* than in control plots, indicating facilitation by *S. acaulis* on the performance of *B. vivipara*. When moving into more benign environment down the transect, there was no facilitation by *S. acaulis*. Here, leaf size was the same in cushions and control, or slightly wider in control plots, indicating neutral/no effect, or possibly a negative effect from *S. acaulis* on *B. vivipara*.

Totland & Esaete (2002) found positive effects of *Salix lapponum* on the performance of single species at Finse. Nine species had higher above-ground biomass when growing inside canopies of *S. lapponum* than outside. In addition, mean leaf number was higher inside than outside for two species, and total seed number was higher inside than outside for one species. Positive associations have been documented between *Carex bigelowii* and the dwarf shrubs *Cassiope tetragona* and *Empetrum hermaphroditum* as well as the mat forming moss *Racomitrium lanuginosum* (Carlsson & Callaghan 1991). When *C. bigelowii* was growing in close proximity to the shrubs or the moss, leafs were longer and culms were higher compared to individuals >2 cm away from the shrubs or outside the moss mat. My results show that *S. acaulis* can affect the performance of *B. vivipara* positively, under harsh physical conditions, like Totland & Esaete (2002) showed for *S. lapponum*.

In many studies related to species interactions and cushion plants, the target species is studied at different elevations (Callaway et al. 2002; Cavieres et al. 2006; Yang et al. 2010). It is often found that interactions change with harshness of the environment, and facilitation increases with environmental stress. For instance, Yang et al. (2010) found positive interactions between the cushion plant *Arenaria polythrichoides* and other species to be higher at 4700 m a.s.l. than at 4500 m a.s.l. They explained this by higher levels of nutrients inside cushions than outside, and this difference increased with elevation. Even though these studies looked at species richness, facilitative effect on the performance of a single species can be expected to behave the same way. The results from Finse suggest that there is a change from facilitation of *B. vivipara* to neutral/no effect or weak competition between *B. vivipara* and *S. acaulis* when moving from a stressful environment near the glacier and into more benign conditions down the transect. This is in line with the stress gradient hypothesis, and the model proposed by Brooker & Callaghan (1998) explaining the relationship between

facilitation and competition in disturbance gradients. Callaway (1997) suggests that the same plant species can have neutral or negative effects on neighbors at one point in an environmental gradient and positive effects at another point, like *S. acaulis* affects *B. vivipara.*

Length and width of leaves, as well as length of leafstalk, increased with distance to the glacier. This is as expected when moving into more benign conditions. It must be noted that the sample size of *B. vivipara* was small, and number of individuals varied between locations. Thus, results must be interpreted carefully.

Interactions affecting the survival of specific species

When studying interactions and possible facilitation by a nurse plant, both the species richness in nurses and open areas must be assessed, as well as the number of species added to the community due to the presence of the nurse (Cavieres & Badano 2009). In this study I found four vascular species occurring only within *S. acaulis*, never on bare ground. Each were found in a maximum of two plots, and represented by a very low number of individuals.

Cavieres et al. (2002) reported a total of 24 vascular species inside cushions of *Bolax gummifera* and 13 species outside at 900 m a.s.l. Of these, 15 were found only within cushions and three were found only outside cushions. The positive association between *B. gummifera* and several vascular species indicates an addition of species to the entire community due to the presence of *B. gummifera*.

Like in Cavieres et al. (2002) vascular species were added to the plant community in Finse because of a cushion plant, a sign of survival of specific species due to the presence of *S. acaulis*. Because of the low observed number of individuals and species interpretations should be done carefully, as the presence of these plants could be caused by coincidence. Still, the total number of vascular species in the entire study area is raised from 30 to 34 when including these observations, indicating a weak facilitation from *S. acaulis*.

On the other hand, species found only outside cushions might indicate a competitive relationship with *S. acaulis*. However, as only one species was found exclusively on bare ground, and in low numbers, there is little indication of competition from *S. acaulis* on specific vascular species.

Interactions between *S. acaulis* and functional groups

There was no difference in number of species between inside and outside cushions of *S. acaulis* for vascular species, bryophytes, or the fertility of vascular species. This suggests that *S. acaulis* has no effect or a neutral effect on these groups.

Total species had a significantly higher number of species in control plots than in cushions of *S. acaulis,* indicating competition between *S. acaulis* and other species. When looking at each of the functional groups separately, only lichens had significantly more species in control plots than in *S. acaulis*. When excluding *lichen species* from *total species*, there was no difference between control plots and *S. acaulis* in number of species present. Results indicate a negative effect on lichens from *S. acaulis*. Cushion plants are probably not a favorable habitat of lichens; hence these results were as expected.

My results are contrasting to those of Molenda et al. (2012), who studied *S. acaulis* on Whistler Mountain in British Columbia, Canada. They found that plant species richness and abundance, but not Simpson's diversity index, was higher inside cushions than outside, indicating facilitation. Antonsson et al. (2009) studied the effect from *S. acaulis* on vascular plant species along an altitudinal gradient in the subarctic Scandes in Sweden. They found facilitation from *S. acaulis* above 1280 m a.s.l. in Sweden. Below this altitude, there was no or a slightly negative effect of *S. acaulis*. Their study area was located between 1150 and 1447 m a.s.l. with mean annual temperature and precipitation of -2.0 °C 839 mm, respectively. These conditions are quite similar to those of the study area in Finse. The location of the transect near the glacier front probably makes my study area environmentally harsher. My findings are therefore surprising compared to Antonsson et al. (2009), as one would expect the same result in quite similar environments, or possibly even a stronger facilitation if the environment is harsher (Bertness & Callaway 1994; Brooker & Callaghan 1998).

The cushion plant *Thylacospermum caespitosum* has been found to not facilitate other species under extremely dry conditions in very high altitudes (5900 m a.s.l.) (De Bello et al. 2011). This is in line with a model proposed by Michalet et al. (2006), claiming that under extreme environmental severity facilitation decreases, and only stress-tolerant species will survive. However, it seems unlikely that conditions at Finse are too extreme for facilitation to species richness to occur.

All the functional groups showed changes in species richness along the transect. *Total species*, *lichen species*, *bryophyte species* and *fertile species* increased in numbers when moving away from the glacier. This could be due to the increase in air temperature, organic material and moisture, which all indicate the stress gradient in the transect. *Vascular species*, on the other hand, decreased in richness when moving down the transect, possibly caused by competition dominating over facilitation in more benign environment, causing the richness to decrease (see Brooker & Callaghan 1998). This is in line with Callaway (1998), who argued that facilitative effects do not occur apart from competition. Plants grew larger, and space-requiring species such as *Empetrum nigrum hermaphroditum*, *Vaccinium vitis-idaea* and *Salix* sp. increased in density down the transect, possibly outcompeting smaller individuals of other species. Plots in Finse were small (diameter between 12 and 37 cm); hence large individuals could possibly fill the plot, giving a vegetation registration that did not represent the plant community.

Abiotic factors

Silene acaulis seems to be a buffer of extreme temperatures, possibly explaining the observed facilitation of *B. vivipara* and the weak facilitation of vascular plants. Maximum temperatures were lower inside *S. acaulis* than outside, and never reached more than 25 °C, while bare ground temperatures reached more than 40 °C on sunny days. Minimum temperatures were higher inside cushions than outside, the lowest measured temperature being -0.7 °C inside and -3.1 °C on bare ground.

Molenda et al. (2012) found that cushions of *S. acaulis* buffered high, but not low, temperature extremes. In addition it buffered low humidity drops, retaining higher moisture levels relative to the surroundings on dry days. A study done on the cushion plant *Laretia acaulis* showed buffering of high temperatures at 2800 m a.s.l. While ground temperatures (measured two cm below soil surface) reached up to 45 °C, cushion temperatures hardly exceeded 25 °C (Cavieres et al. 2006). Cavieres et al. (2008) found that the cushion plants *Laretia acaulis* and *Azorella monantha* both buffered high, but not low, temperatures.

I found that *S. acaulis* can buffer both high and low extreme temperatures, and hence gives a lower variation of temperature inside the cushion. As suggested by Cavieres et al. (2006), buffering of extremely high temperatures can be important directly on survival of plants as well as on the evaporative effect of the soil and plants, giving facilitation. The temperature buffer found in Finse possibly has an effect on the performance of *B. vivipara* near the glacier

where the harshest climate in the transect is found. It does not seem to have an effect on the species richness in cushions of *S. acaulis*. The buffer might not be strong enough to make a difference on community level between cushions and bare ground. An alternative is that the positive effect is neutralized by interspecific competition between species which all benefit from this buffer.

It must be noted that in this study temperature for control plots was measured in open air, close to ground level. Measurements in the soil would probably have given a better comparison to temperatures inside the cushion, and is a more common method. For instance, Cavieres et al. (2006), Cavieres et al. (2008) and Yang et al. (2012) inserted a probe two cm into the ground in control plots and two cm into the cushion in cushion plots. An alternative would be to measure control plot temperature under litter or vegetation (Molenda et al. 2012) to avoid direct solar radiation. However, I still recognize my results as comparable and valid, as they at least give a hint about what is happening inside *S. acaulis* cushions.

There were no differences in pH, LOI and moisture between *S. acaulis* and control plots, indicating similar soil conditions for species growing inside and outside *S. acaulis*, possibly contributing to species richness and composition being similar between the two. All the soil variables showed changes between locations. Moisture and LOI both increased down the transect. These results indicate that the transect is a stress gradient. Thus, one could expect to find ecological changes along it, including changes in the interactions among plants as found between *S. acaulis* and *B. vivipara*.

Conclusion

Silene acaulis facilitated the performance of *Bistorta vivipara* in the harshest parts of the succession gradient. Closest to the glacier, *B. vivipara* grew larger inside than outside cushion of *S. acaulis*. Lower temperature variation inside cushions (compared to surrounding air) probably modifies the microclimate enough to positively affect the performance of *B. vivipara*. In more benign parts of the gradient, there was no facilitation to the performance of *B. vivipara*. There was a trend of wider leaves in control plots compared to *S. acaulis*, possibly indicating competition from the cushion. Thus, *S. acaulis* can promote the growth of species that are already established inside cushions in harsh environment, while in milder conditions no/neutral effect or negative interactions are likely to occur.

There were weak indications of facilitation from *S. acaulis* affecting the survival of specific vascular species. A few species were found only within cushions, and the presence of *S.*

acaulis can be crucial for their survival in the study area. There were no differences in number of species inside and outside *S. acaulis*, except for lichens, which thrived better outside *S. acaulis*. The fertility of vascular species was also the same inside and outside cushions. It seems that *S. acaulis* has little influence of species richness on community level, and this pattern is the same through the succession gradient.

Other studies have documented clear facilitation by *S. acaulis* on community level, increasing with stress in elevation gradients. Facilitation of the performance of *B. vivipara* in stressful environment is in accordance with this, while on community level, there is no clear evidence of facilitation at Finse. *Silene acaulis* is not a nurse plant for species richness, but can facilitate the performance of single species. Further research on plant interactions in succession gradients is needed to understand more about plant facilitation in stressful environments.

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Appendix

List of registered vascular species with number of *Silene acaulis* and control plots containing each of them.

	Silene acaulis	Control
Antennaria dioica	4	4
Bartsia alpina	6	4
Bistorta vivipara	20	16
Cassiope hypnoides	3	2
Carex bigelowii	4	4
Cerastium alpinum	2	2
Deschampsia alpine	5	5
Diphasiastrum alpinum	1	0
Empetrum nigrum hermaphroditum	7	10
Euphrasia frigida	1	1
Festuca vivipara	10	9
Hieracium alpinum	4	2
Juncus trifidus	3	2
Leontodon autumnalis	1	1
Luzula spicata	4	3
Minuartia biflora	2	1
Omalotheca supine	2	2
Oxyria digyna	3	2
Poa alpine	13	6
Potentilla crantzii	0	1
Rhodiola rosea	2	0
Salix herbacea	25	25
Salix lanata	6	3
Salix reticulate	1	0
Saxifraga oppositifolia	8	4

Saussurea alpine	1	1
Sibbaldia procumbens	1	1
Silene acaulis	0*	3
Thalictrum alpinum	1	0
Taraxacum sp.	1	1
Trisetum spicatum	3	5
Vaccinium uliginosum	2	5
Vaccinium vitis-idaea	5	6
Veronica alpina	4	1

* *Silene acaulis* was not registered in cushion plots.