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Effect of Elevation Differences in Alpine Insect Activity on *Silene Acaulis* at Finse, Norway

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Preface

This thesis is the results of my five years of studying biology at the Norwegian University of Life Sciences (NMBU). I have always been interested in biology, and ever since I was a kid I have been flipping over rocks and tree trunks to look for insects. It therefore felt natural for me to study and write about something that has always fascinated me. To be able to combine this with something as important as global climate change was the best I could have hoped for.

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Abstract

Global annual average temperature has increased since the industrial revolution and is predicted to continue to increase in the future resulting in altered species distributions. Alpine ecosystems are particularly vulnerable to long-term changes in climate because warmer temperatures may facilitate species migration from lower elevations that may outcompete the current species distribution.

 I used time-lapse cameras to investigate how flower visiting insects at Finse, Norway, respond to changes in temperature using an elevation gradient. I recorded number, duration, and taxa of insects visiting *Silene acaulis*. I measured floral traits to see if these changed with elevation, and if they could explain patterns in insect visits. I also collected capsules and looked for evidence of seed predation.

 I found that flower visiting insects were more abundant and had longer visits at higher elevations, while there was a more diverse flower visiting insect community at lower elevations. Flies represented the greatest proportion of insect visits at both elevations, with the flowers at high elevation being almost exclusively visited by flies. Butterflies were more common at lower elevations. There were no significant differences in plant traits of *S. acaulis* between the two elevations, and plant traits were unable to explain the pattern of insect visits. No predation of capsules or seeds was observed. There was, however, a large difference in production of capsules, with the low elevation site producing more capsules despite receiving fewer insect visits. Taken together, this suggests *S. acaulis* may act as an important refuge for insects in the extreme environment of high elevation alpine ecosystems.

Table of contents

Introduction:

Anthropogenic climate change is expected to impact ecosystems worldwide by altering species interactions through changes in temperature and precipitation. Since the industrial revolution, global annual average temperature has increased by approximately 1°C, and is projected to continue to increase in the coming decades (IPCC, 2019). Temperature change is happening particularly fast at higher altitudes and latitudes (IPCC, 2018). Alpine ecosystems cover around 15% of the land surface area (Bliss, 1971), and are among the ecosystems that are most affected by climate change and climate variability (Inouye, 2020). Temperature is an important driver in biological processes, such as productivity (Ernakovich et al., 2014) and decomposition (Kirschbaum, 1995). Since alpine ecosystems are limited by temperature, changes to temperature will therefore affect the seasonal patterns that characterize these systems (Ernakovich et al., 2014). Temperature is an important driver in biological processes, such as productivity (Ernakovich et al., 2014) and decomposition (Kirschbaum, 1995) Elevated temperature can also lead to changes in the phenological traits of plants, such as flowering and leaf budding (Arft et al., 1999), as well as insect activity (Roy & Sparks, 2000).

There are three primary ways of investigating the effect of temperature change on alpine ecosystems. Open top chambers (OTC) are used to raise temperatures in a small area (Klanderud, 2005). Elevation gradients represent a change in temperature through their elevation difference, and lastly, time series studies of the same area over time can be used with natural temperature change. All methods have advantages and disadvantages. For instance, OTCs affect other factors such as humidity and wind. Elevation gradients need more than one elevation, and by choosing at least two sites, factors like species composition of the community might change. Time series require regular monitoring over long periods of time, especially in alpine ecosystems where climatic factors can vary between years.

Climate and biotic interactions are the main drivers of alpine plant diversity (Ohler et al., 2020), which in turn affects the insect diversity. Since insects have important roles as pollinators and herbivores on plants, the activity and distribution of insects can also affect plant diversity. Both insect development (Wu et al., 2015) and flight (Taylor, 1963) are linked to temperature. An increase in temperature can therefore lead to a rapid loss of both plant and insect diversity in alpine ecosystems, at least in the short term (Walker et al., 2006). Alpine ecosystems contain plants that endure stressful conditions in exchange for being poor competitors (Grime, 2006). This makes them vulnerable to climate change, as warmer climate introduces new, more competitive, plant species from lower elevations into the community by prolonging the growth season (Ernakovich et al., 2014). When new plant species migrate to higher elevations, insect species that are dependent on the migrating plants can also establish at new elevations. Insects are an important part of this community, and their interactions with plants are vital for an ecosystem. In addition to responding to community changes, insects also respond to the traits of the plants, and pollinators have

4

been shown to respond positively to flower size (Thompson, 2001) and flower density (Thomson, 1981). With new plant species, factors like these are expected to change, and any changes in this community are likely to affect both plants and insects.

Totland (1994) found that abiotic factors such as wind, light, and temperature are important determinants of insect activity in alpine ecosystems. Therefore, changes to abiotic factors can alter the development, distribution and behavior of alpine insects. Due to challenging abiotic conditions, insect diversity and abundance decreases with increasing elevation and latitudes (Gillespie et al., 2020). This suggests that lower temperatures negatively affect insect diversity. Pollinator diversity also decreases with increasing elevation. Despite this, some species of flies, bumblebees, moths, and butterflies survive at high elevations (Inouye, 2020). At lower elevations, insects perform important ecosystems services, and arthropods have recently been recognized as far more important in arctic and alpine ecosystems than previously thought (Hodkinson & Coulson, 2004), fulfilling important roles as pollinators, decomposers, and serve as a food source for other animals.

Flies are the most numerous insect and are likely key pollinators in alpine ecosystems, however bumblebees and butterflies are also present (Bergman et al., 1996; Totland, 1993). The role of bumblebees and butterflies as pollinators appears to be highly dependent on favorable conditions, as increased activity has been shown to positively correlate with increasing air temperature and solar radiation (Bergman et al., 1996). Importantly, a pollinator community dominated by one insect order is less functionally diverse and more vulnerable to change than more diverse communities. Species migrating to higher altitudes could therefore theoretically lead to a more diverse and robust community.

There are examples of how species of butterflies have migrated to higher elevations as temperatures in alpine ecosystems have increased (Konvicka et al., 2003), and it is expected that more taxa will migrate upslope in the future. This creates a potential for insect species that currently occupy alpine zones to be outcompeted from their historical distributions and either be forced upslope or driven to extinction. This will alter insect communities and shift species distributions in space and time (Shah et al., 2020), leading to new insect communities that have different adaptations to temperature and other abiotic factors. Such changes could have ripple effects throughout the ecosystems (Sorte et al., 2010), as plants may lose important pollinators or gain new herbivores. (Kenis et al., 2009). Changes in insect distribution can also introduce more complex and specialized plant-insect interactions between species, making generalist species less common, negatively affecting both insects and plants.

In addition to introducing new insect species, temperature can also have an effect on plant traits via plasticity or the formation of local ecotypes (Billings, 1973). For example, plant size

typically decreases as elevation increases (Halbritter et al., 2018; Maad et al., 2013), while flower size tends to increase (Herrera, 2004; Kudo & Molau, 1999). However, Fabbro & Körner (2004) found no difference in flower area or flower biomass along an elevation gradient, although they did note that plants at higher elevations put relatively more resources into flowers than plants at lower elevations. One reason plants may put relatively more resources into flowers at high elevation is that there are less overall resources available (Hemborg & Karlsson, 1998) and fewer pollinators (Lara-Romero et al., 2016; Maad et al., 2013). Studies have shown that insects prefer larger flowers (Maad et al., 2013; Ohara & Higashi, 1994; Thompson, 2001), and that plants that offer more floral resources are more likely to be visited by an insect (Carvalheiro et al., 2014). Flowers are also a way for plants to select for different pollinators, as they can act as either barriers or attractors (Junker et al., 2015) through their shape, size and/or color. Large and complex flowers can select for larger and long-tonged pollinators, such as certain bumblebees (Maad et al., 2013). In alpine communities however, most pollinators are small and not specialized (Totland, 1993), as reflected by the small and open flowers dominating these areas.

The short flowering time of alpine plants results in a large overlap (Kudo & Suzuki, 1999) between species and is indicative of a generalist pollinator dominated community. However, phenology is advancing in alpine ecosystems due to earlier snowmelt. Hegland et al. (2009) found that insect pollinated plants advanced their phenology more than wind pollinated plants in response to warming. Rafferty & Ives (2011) suggested that the flowering time of insect pollinated plants is more sensitive to warming because it correlates with insect responses to warming. This forms an evolutionary push and pull mechanism, where plants and insects influence each other. It is unclear if this mechanism between pollinators and plants is happening in alpine ecosystems, and whether new species migrations may place existing species-specific interactions at risk of being disturbed by climate change (Inouye, 2020). For example, generalist pollinators might be displaced by new pollinators. However, since alpine ecosystems are typically dominated by generalist life history strategies, pollinator community turnover may not be harmful for alpine plants.

Mismatches between plants and their pollinators can also emerge as a result of warming temperatures and have negative effects on plant reproduction (Hall et al., 2018). Additionally, changes in snowmelt (Inouye et al., 2003), precipitation (Peñuelas et al., 2004), or more frequent frost events (Inouye, 2008) can also have strong effects on plant reproductive success, and are more likely under new global climate scenarios, resulting in negative consequences for long-term population survival.

One alpine plant affected by changing climate is *Silene acaulis*. Alatalo & Totland (1997) showed by use of OTCs that *S. acaulis* had earlier flowering, faster development of male and female flowers, as well as ovules maturing faster with more seeds under warming experiments, which is consistent with changes in other species of plants (König et al., 2018; Thackeray et al., 2016). Changes in flower and plant traits, as well as development, may also affect plant-herbivore interactions. Thackeray et al. (2016) found that sensitivity to changes

in climate decreased with increasing trophic level, with insects and plants among the most affected groups overall.

S. acaulis is an important species in alpine ecosystems that increases biodiversity by acting as a nurse plant (Antonsson et al., 2009). Molenda et al. (2012) found that *S. acaulis* also increases arthropod diversity, which suggest that *S. acaulis* acts as a foundation species for alpine ecosystem functioning with effects across several trophic levels. Therefore, a shift in *S. acaulis* distribution, abundance, or phenology may have large impacts on alpine communities as many species depend on it for survival.

The reproductive output of *S. acaulis* is partially dependent upon the interaction between *S. acaulis* and flower visiting insects. The relationship between number of insect visits and seed production has been studied in several plants (Jennersten & Nilsson, 1993), and found to have a positive correlation (Stanghellini et al., 1998). When insects visit flowers to feed on nectar, they tend to collect pollen as well. This transfer of pollen to other individual plants of the same species is what makes pollination so crucial for some plants. More visits should lead to more pollen being transferred, resulting in more seeds, up until a threshold. To my knowledge, this relationship has not previously been studied in *S. acaulis*.

Seeds are a common food source and seed predation occurs via several different groups of animals, from rodents and birds to insects (Westerman et al., 2003). *S. acaulis* is a common plant in alpine ecosystems with a circumboreal distribution around the northern hemisphere (Gussarova et al., 2015). It can produce a large number of capsules each year and therefore may serve as a food source for animals living in alpine ecosystems, especially since the capsules can stay on the plant throughout the winter and into the next summer. However, little is known about the seed predator community for *S. acaulis*.

Research statement

To better understand how alpine ecosystems might respond to global warming, I tested how changes in temperature affects the distribution of flower visiting insects in an alpine ecosystem by using an elevation gradient. I also investigated how the floral traits of *S. acaulis* change along an elevation gradient, and if these differences, if any, could explain flower visiting insect distributions. In addition, I tested if a difference in flower visits correlated with reproductive output for *S. acaulis*. Lastly, I investigated which insects or animals, if any, predate on *S. acaulis* seed capsules.

Based on the literature, I predict that insect activity and diversity will decrease with increasing elevation and that *S. acaulis* will be smaller, but will put more resources into reproduction at higher elevation by increasing flower size. I also predict that an increase in

insect flower visits will yield an increase in reproductive output in the form of seeds for *S. acaulis*. Lastly, I predict that capsules and seeds of *S. acaulis* will act as a food source for organisms living in alpine ecosystems.

Materials and methods

Study site

This study was carried out at Sanddalsnuten near Finse (60°37'N, 7°32'E), from 20.07.2020 until 15.09.2020 (Figure 1). The sites were located in an alpine landscape, near the summit of Sanddalsnuten. The vegetation consisted of shrub like vegetation , with *Dryas octopetala* covering about 35% of the ground (Klanderud, 2005). In addition to *S. acaulis,* other species included *Thalictrum alpinum, Potentilla crantzii, Bistorta vivipara L. and Cerastium alpinum,* the dwarf shrub *Salix reticulata,* grasses like *Festuca vivipara* and *Poa alpine* and sedges *Carex vaginata, C. atrofusca, C. rupestris* and *Luzula* spp. as described by Klanderud (2005). There were also some lichens and bryophytes growing at the site (Klanderud, 2005). The winter at Finse is usually long with snow cover for 8-10 months, and the growing season typically lasts 90-120 days (Sjursen & Sømme, 2000). I established two main study sites at Sanddalsnuten, one low elevation site, at approximately 1480m, and a high elevation site at approximately 1530m. The high site is more exposed to the wind, and there is less buildup of snow. As a result, the growing season is about three weeks longer at the top of Sanddalsnuten (Birkemoe et al., 2016).
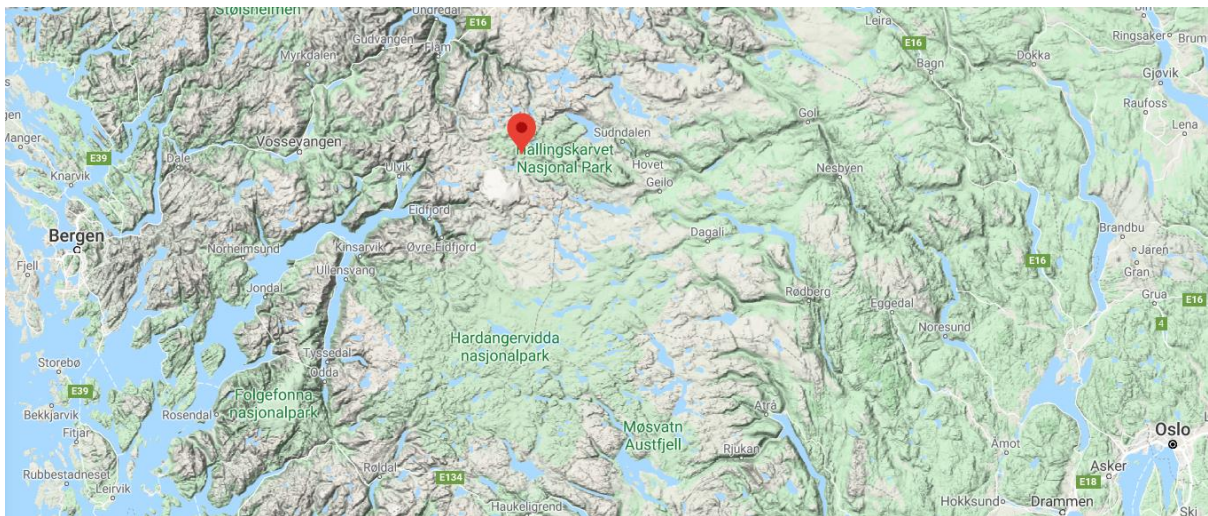
Figure 1: Shows the location of Sanddalsnuten, which is located in the southern part of Hallingskarvet national park. This summit is just over 1550 meters above sea level. Source: Google maps and Norgeskart (2021).

Sanddalsnuten has a long history of temperature manipulation studies. As a result, there are several OTCs in the area at different elevations. I decided to use an elevational difference, with one high site and one low site. This avoids the problems associated with classical methods for observing the effects of temperature change, such as OTCs. Physical objects, like OTCs, can be challenging to use when studying insects and their behavior. An OTC affects more than just temperature and could help shelter insects from wind. They also affect the moisture levels inside the OTC compared to outside. In addition, the OTC itself can act as an obstacle for insects, where they struggle to get out or in. My personal observations from this fieldwork season confirms that insects sometimes fly straight into the OTC or takes shelter within them. By using an elevation difference, I was able to avoid all of these interactions the insects possibly could have with the OTC itself. The temperature difference between the two sites was 1,1°C in air temperature, and is comparable to reports from previous studies using OTCs (Bokhorst et al., 2013). This temperature difference is also in line with the global average increase since the industrial revolution, which is 1,2°C (Sridhar et al., 2020), giving a realistic temperature difference.

Study species
Silene acaulis
S. acaulis is a well-studied cushion plant in the alpine landscape. They are found across the northern part of the world, from USA (Gehring & Delph, 1999) to Europe, and live to be up to 300 years (Roy et al., 2018). *Silene* forms light green, moss-like cushions with pink

flowers (Alatalo & Totland, 1997). Most of the individuals at Finse are female and hermaphrodites (Alatalo & Totland, 1997), and male plants are rare. *Silene* has an important role in alpine ecosystems, as it can facilitate other plants (Molenda et al., 2012), leading to more diverse communities. *S. acaulis* is insect pollinated, with visiting flies, bumblebees and butterflies (Alatalo & Totland, 1997).

Pollinators
A study from Totland (1993) found that flies are the most frequently visiting pollinator in alpine ecosystems in Norway. Bumblebees and butterflies were less frequent in alpine Norwegian areas. A study from Sweden investigated pollinators' effect on reproduction and concluded that insect pollination was crucial for many alpine species (Bergman et al., 1996), and that flies and bumblebees were substantially more important than butterflies.

Seed predators/insect community
Larvae and adults insects (Molau et al., 1989; Munoz & CAVIERES, 2006), as well as birds and mammals feed on seeds. Seed predation can be an important factor in plant reproduction (Krushelnycky, 2014), with high seed predation rates influencing community composition in plant communities. As *S. acaulis* can produce a lot of capsules per individual, it could theoretically be an important food source for insects and small mammals. The capsules also stay on the plant throughout the winter and into spring and summer, making it easily accessible.

Experimental setup Cameras were used to monitor plants and to collect pictures of insect visits during the summer season. The cameras used were
10 Wingscapes TimelapseCam Pro® WCT-00126. They were mounted on a rig of steel pipes that consisted of two A- frames as support and one pipe going across horizontally. The camera was mounted on the cross section and faced downwards (Figure 2). The camera lens was between 45-55 cm away from the ground, which gave good resolution to easily identify insects (Figure 3). In order to maximize the potential for successful images of flower visiting insects while optimizing the lifetime of the batteries, the cameras were programmed to take one picture every minute from 05:00 in the morning until 21:59 in the evening. For further settings of the cameras, see Appendix 1. Due to delays, cameras were rigged after the first flowering. This is unlikely to be a major issue, as insect visits of *S. acaulis* have been shown to peak in the middle of the season (Hall et al., 2018). Starting August 16th, the cameras were programmed to take one picture every fifth minute (Table 1), as the focus was on capsules instead of flowers, and I decided that I didn't need the same frequency of pictures to observe predation as I did flower visits.

Figure 2: The cameras were mounted to a wooden plate and protected by an improvised housing of aluminum foil. The cameras were then mounted to a horizontal bar between a double A-frame. Five of these were placed at each site.

Figure 3: Example of how pictures taken by the cameras appear. A lepidopteran is visiting *S. acaulis.*

Table 1: The dates for when cameras were maintained, and when they were active. Each period is marked by me switching batteries and memory cards.

Period	From	Until
1	06.07.2020	19.07.2020
2	19.07.2020	01.08.2020
3	01.08.2020	16.08.2020
4	16.08.2020	15.09.2020

Field observations

Parallel to the camera observations, field observations of flower visiting insects were conducted. The field observations were performed next to the cameras on the same plants. Thus, each plant was observed both manually and by camera. The field observations were done at distances where all the insects could be observed but not disturbed, approximately one meter away from the plant (Figure 4). Each plant was observed for 15 minutes while taxa of visiting insects were recorded, along their activity and length of visit. Field observations were conducted on the 22nd, 23rd, 24th, 25th and 31st of July. Each individual plant had 130 minutes of observations. This gives a total of 1300 observation minutes, and 1430 total minutes of observed individuals, as plot seven contained two individual plants.

Figure 4: Lepidopterans observed visiting *S. acaulis* during my field observations.

Temperature measurements

Tiny tag temperature loggers were used for temperature measurements, and one was placed at each camera (see Appendix 2 for which camera had soil and air measurements). An additional 14 loggers were placed at other spots at the two sites, for a total of 24 temperature loggers. The loggers recorded the temperature every 30th minute for the whole field season. I had ten loggers at the low site, and 14 on the high site. Nine of the loggers had a probe that measured ground temperature (Figure 5), while the remaining 15 measured air temperature. Four of the ground temperature loggers were at the low site. All loggers were placed by *S. acaulis* individuals, and the probes were put into the ground immediately adjacent to the individuals. The cameras also recorded temperature on each picture taken, but it was decided that these data were not as accurate as the loggers, and therefore not used. One of the loggers placed with a camera malfunctioned during the field season and was excluded from statistical analyses.

Figure 5: Tiny tag logger with a probe for soil temperature measurements placed next a *S. acaulis* cushion.

Plant measurements

In order to investigate if there are any connections between plant characteristics and insect visits, different plant traits were measured. The surface area of each plant was calculated by measuring the longest axis and the one orthogonal to the longest axis. Then the percentage of missing area for each plant was calculated. This was then used to calculate the surface area of each individual plant, and was done for all eleven individuals with camera monitoring. The number of flowers was also estimated once during the growing season for all eleven plants with camera monitoring. This was used to estimate flower density and to investigate if there were any differences between the sites. Different floral traits like petal width and length and total flower diameter were also recorded by randomly measuring ten flowers from each individual plant with a camera. At the end of the season all of the capsules were collected and counted to investigate if there was a relationship between the number of insect visits and capsule formation. The capsules were picked by hand and placed in a paper bag marked with individual plant identity for storage. The capsules were counted in the laboratory.

Data handling and statistics

Image handling
At the end of the field season the cameras had captured roughly 400 000 pictures. Of these, about 300 000 were included in the statistical analysis. Each picture was inspected manually using a software called VGG image annotator (Dutta & Zisserman, 2019) and pictures capturing insects visiting the flowers of *S. acaulis* were annotated. When an insect visited a plant, the group it belonged to (e.g. butterfly, bumblebee or fly), and how long it stayed was recorded.

Statistical analysis
The temperature at the high and the low site was compared with a t-test. I did this for both air temperature and ground temperature. The data was grouped into high and low site and then air or soil for both the sites. I then averaged the values for all the groups, so that all the loggers for air temperature at the high site ended up as one value and so on for all groups. I then used these averages when comparing and doing the t-test.

An anova was used to investigate if elevation had an effect on insect visits. The insect visits were grouped into total visits at high and low, and controlled for differences in flowers and size of the different individual *S. acaulis* by dividing the total number of visits of a plant on the size or flowers respectively (see Appendix 3 for the data used in these analysis). All these were then tested using an anova and controlling for flowers turned out to be the best alternative. All insect observations were included in most of the test. Only when testing relative proportion were bumblebees not calculated due to their low observation count.

In order to check if traits of *S. acaulis* changed with the elevation difference, anovas were used. All traits were grouped into high and low and tested individually. The different plant traits were then put into a generalized linear model (GLM) and tested if they could explain insect visits when combined. The first model did not give any significant effects when all traits were included. Therefore, an Akaike information criterion (AIC) was used to investigate if fewer explanatory variables could explain the difference. The best model from the AIC still had no significant traits that could explain the insect visits.

Lastly, I investigated the effect elevation would have on reproductive output in the form of capsules for *S. acaulis*, by using an anova to test the two elevations against each other. Insect visits were then used to explain this difference in capsules, but when insect visits were used as an explanatory factor in a GLM neither fly visits or butterfly visits could explain the difference in capsules for *S. acaulis.*

All statistical analysis were done in RStudio, version 1.1.456.

14

Results

1. Temperature at the two elevations

The average soil temperature was 8.1 °C at the low site vs 7.6 °C at the high site and the air temperature was 8.8 °C vs 7.6 °C at the two sites respectively. The temperature difference was tested with a t-test, and the result was p<0.001 for both air and soil.

2. Insects at the two elevations

There was a total of 452 visits at the high site, while there was a total of 322 at the low site (Table 2). The mean number of visits per flower at the high site was twice as high as the low site (Figure 6). An anova was used to test if elevation had an effect, and elevation had a significant effect with a p-value of 0.03, where low elevation had a negative effect on insect visits per flower.

Number of visits per flower
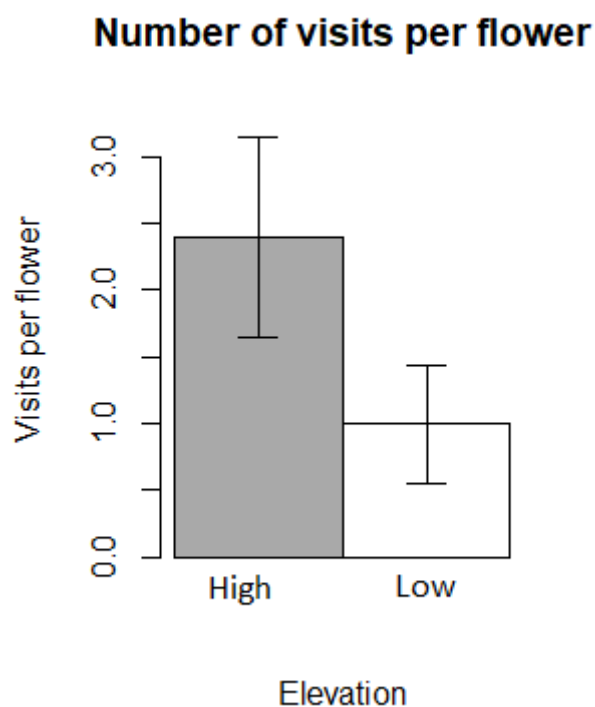
Figure 6: Bar graph showing the number of insect visits observed per flower at Sandalsnuten, Finse, with 95% confidence intervals. These observations are based on analyzing photos taken by ten time lapse cameras, taking one picture every minute during daytime (05:00 until 21:59), in the period 19.07.2020 until 01.08.2020. the average elevation in meters above sea level at the high and low site were 1534 and 1478 respectively.

Splitting the insect visits into order made it clear that, flies dominated at both sites, while butterflies were more abundant at the low site (Figure 7). The estimated proportions of flies at the high site are 0.93, and an anova was used to test the effect of elevation on the proportions. For flies the anova gave a negative effect of low elevation of -0.25 and a p-

15

value of 0.002. For butterflies, the expected value at the high site was 0.057, and elevation low had a positive effect of 0.25, with a p-value of 0.001. Elevation was therefore important for the flower visiting insect community, which included more butterflies at lower elevations.

Table 2: The total visits observed by the cameras, split into the different orders. Plants 1 to 5 are at the high site, while 6 to 10 are at the low site. Insects not identified at order are categorized as no ID.

Plant ID	Number of visits	Fly	Bumblebee	Butterfly	No ID
1	134	124	1	9	0
2	81	73	0	4	4
3	74	72	0	2	0
4	98	85	1	11	1
5	65	63	0	2	0
6	109	65	0	43	1
7a	49	36	0	13	0
7b	61	55	0	6	0
8	29	18	0	11	0
9	36	22	0	14	0
10	38	22	3	13	0
total	774	635	5	128	6
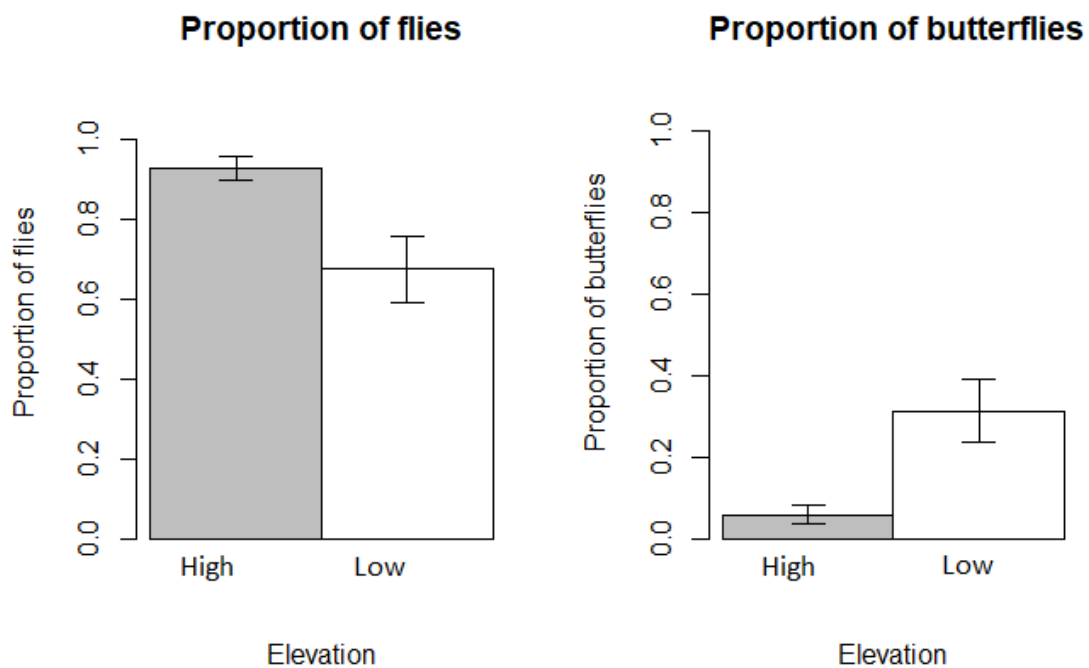
Figure 7: Bar graph showing the proportions of different taxa which visited flowers of *S. acaulis* at each site on Sandalsnuten, Finse, with 95% confidence intervals.

The average duration of the visit was longer at the high elevation by just over one minute, from 3.08 to 4.2 minutes (Figure 8). The anova resulted in a significant effect of elevation on length of visit. Elevation had a positive effect on the length of flower visits (p=0.02).
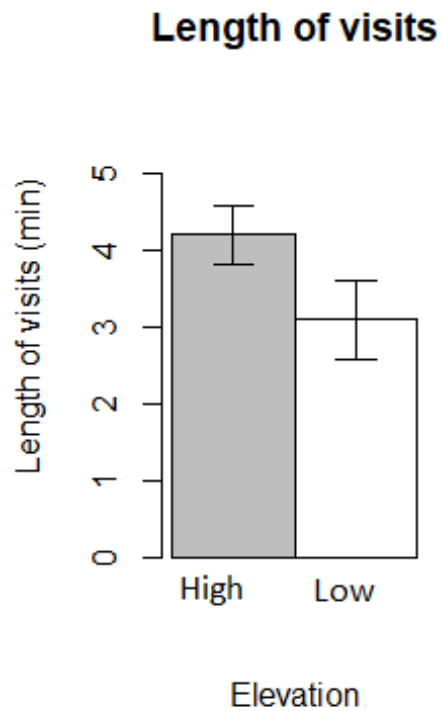
Length of visits

Figure 8: Bar graph showing the length of insect visits observed per flower at the two sites on Sandalsnuten, Finse, with 95% confidence intervals.

3. Plant traits at the two elevations
Size of the Silene-cushions varied between the two sites, but there was no significant difference between the two elevations (Figure 9). An anova gave an estimated value for the high site as 1039 cm^2, with a positive effect of 348 cm^2 with decreasing elevation (p=0.68).
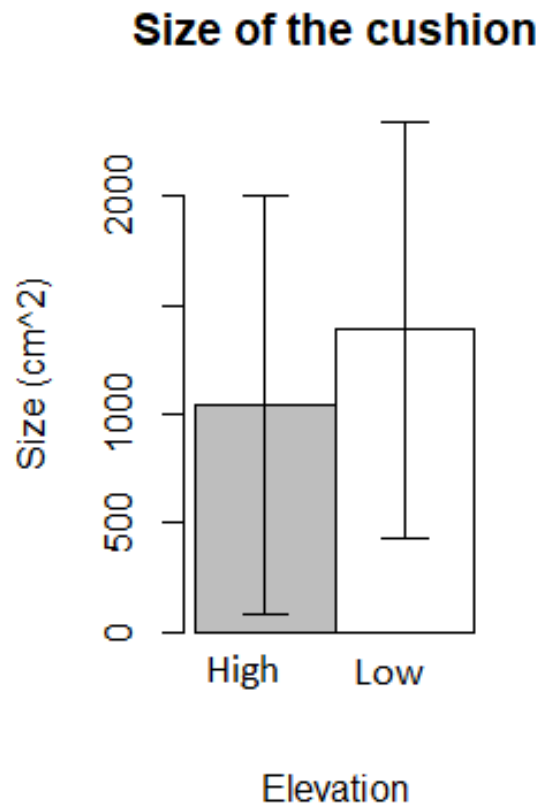
Size of the cushion

Figure 9: Bar graph showing the size of the cushions at Sandalsnuten, Finse, with 95% confidence intervals. These observations are based on analyzing measurements done in the field.

Total number of flowers and flower density were also tested. There was a large but nonsignificant difference in total number of flowers in the *Silene* cushions (Figure 10). An anova was used to investigate the relationship between total number of flowers and elevation and resulted in a nonsignificant p-value of 0.19 and when this was combined with the cushion size, I found that there was no difference in flower density between the two sites. The means in both groups were the same, and a simple anova test confirmed that there was no practical difference between the two elevations with a p-value of 0.93.
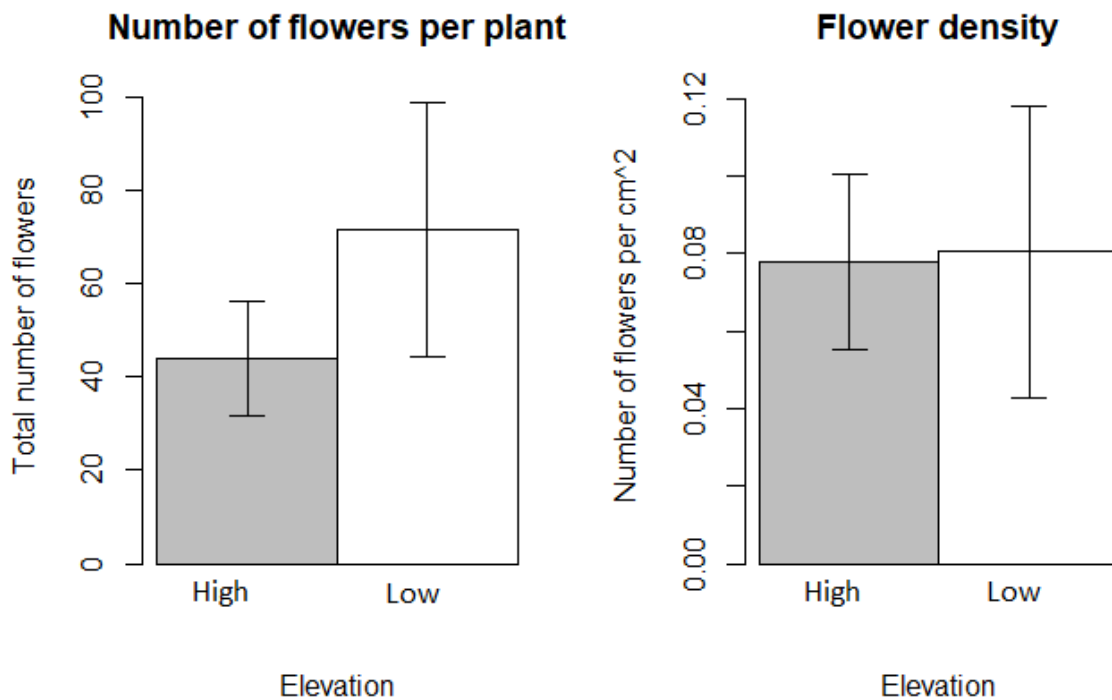
Figure 10: Bar graph showing the total number of flowers (left side) and flower density (right side) at the two sites on Sandalsnuten, Finse, with 95% confidence intervals.

Petal length, petal width, and total flower diameter was measured and used as an indication of flower quality (Figure 11). Petal length had an average length of 4.18 mm at the high site, and an estimated value of 3.57mm at the low site. An anova was used to test this relationship, and there was a nonsignificant trend with a p-value of 0.15. Petal width was almost identical for the high and low elevation, with expected values of 3.02mm and 3.08mm respectively, although the lower site had a much higher degree of variance. An anova test gave a non-significant relationship between petal width and elevation, with a p-value of 0.84. Total flower diameter gave a similar trend to petal length, where the high site was expected to have total diameter of 10.3mm, while the lower have an expected value of 9.47mm. The same type of anova test was used here to test if this relationship between elevation and total flower diameter was significant, and the resulting p-value was 0.13.
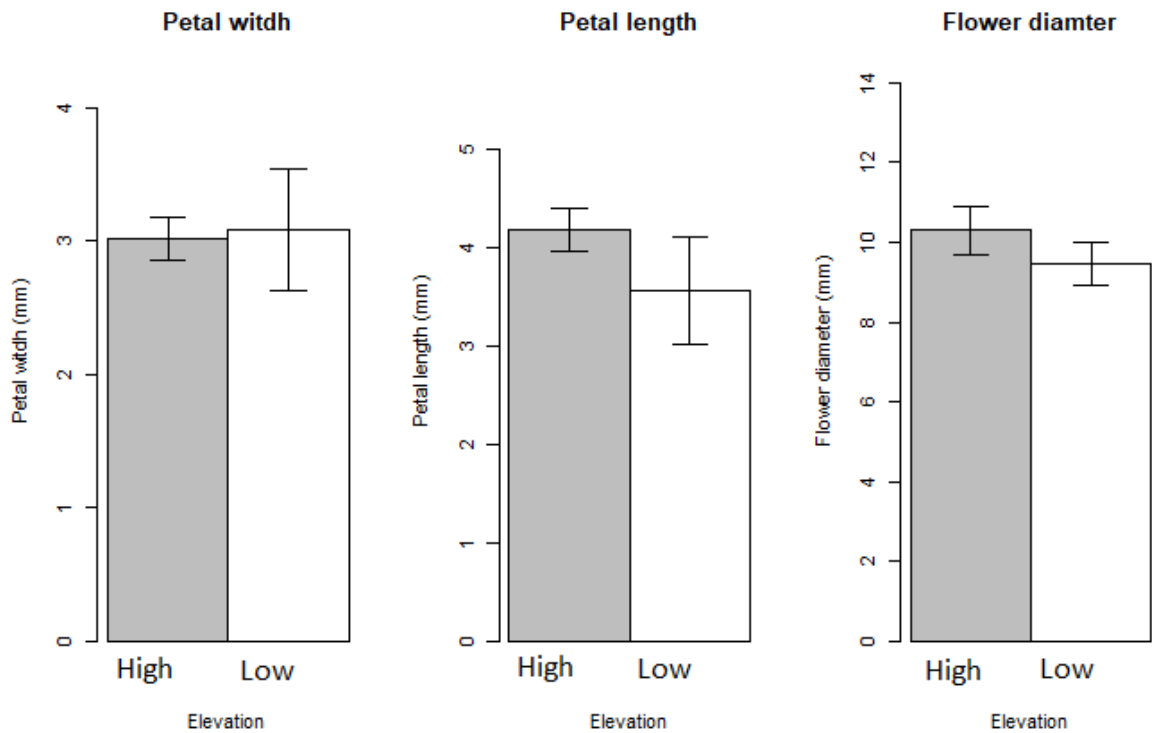
Figure 11: Bar graph showing the different floral traits at the two sites on Sandalsnuten, Finse, with 95% confidence intervals.

4. Can plant traits explain insect visitations?

In order to test if any of these flower traits could explain the insect visits, I used a GLM with insect visits as response variable, and size, total number of flowers, flower density, flower diameter, petal length and petal width as predictor variables. At first, the model yielded no significant results (Table 3), therefore I ran the GLM through a step AIC function, removing all the explanatory factors. Thus, none of the plant traits I measured could explain why the insect visits differed between the two sites.

Table 3: the output from the glm model trying to predict insect visits based on plant traits.

	Estimate	Std. error	t-value	p-value
Intercept	60.666	158.853	0.382	0.772
Size	-0.003	0.028	-0.139	0.896
Total flowers	-0.470	0.915	-0.514	0.634
Flower density	107.906	777.229	0.139	0.896
Diameter	-22.527	56.303	-0.400	0.710
Petal length	30.937	77.529	0.399	0.710
Petal width	44.734	65.194	0.686	0.530

5. Insect visits and their effect on reproductive output?

There was a large difference in reproductive output between the two elevations, with the high site estimated at 1.8 capsules per plant, while the low site has an estimate of 67

capsules per plant (Figure 12). An anova test shows that there is a clear, near significant trend of more capsules at the lower site with a p-value of 0.053. In order to investigate if insect visits could explain the difference in capsules, I used a GLM. The GLM included number of capsules as response variable, and the taxonomic groups flies and butterflies as explanatory variables. The results were not significant, meaning that insect visits alone did not explain the difference in reproductive output (Table 4). When tested with a GLM, neither butterflies nor flies could explain this difference in reproductive output by themselves.

Table 4: the output from the glm with insect groups to explain the reproductive output.

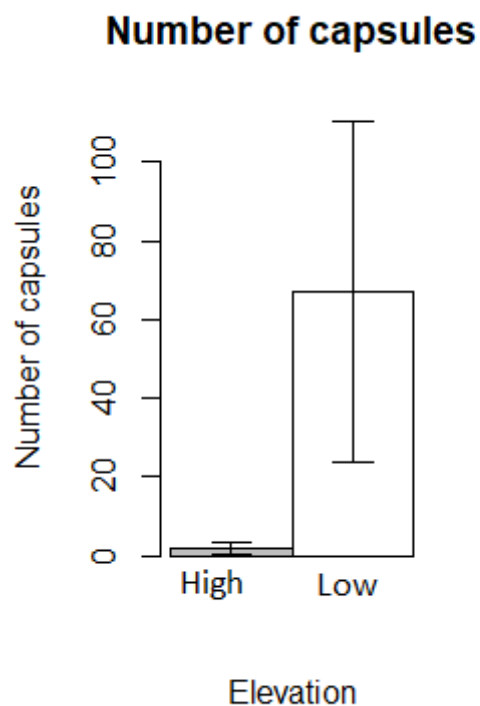|	Estimate	Std error	t-value	p-value
intercept	76.427	39.054	1.957	0.086
fly	-0.910	0.514	-1.768	0.115
butterfly	1.158	1.459	0.794	0.450

Figure 12: Bar graph showing the number of capsules at the two sites on Sandalsnuten, Finse, with a 95% confidence interval.

6. Are there any animals that feed on the capsules of *Silene acaulis*

No insects or vertebrates that feed on capsules of *S. acaulis* were observed on the images. A couple of snails were however observed at the capsules for a longer than normal period of time at the low site.

Discussion

Do insects respond to elevation?

Here, I explored the potential effects of global climate change on plant-insect interactions in alpine ecosystems through the use of an elevational gradient. The mean summer air and soil temperatures at my low elevation site were significantly warmer than the high elevation site (1.1°C; 0.5°C). In contrast to my predictions, there were significantly more insect visits to flowers at the high elevation site. Flies were the most abundant insect visitor at both sites; however, the relative proportion of butterflies was greater at the low elevation site. The duration of insect visit was significantly longer (1min and 7sec) at the high site than the low site.

There were twice as many insect visits per flower at the high site, compared to the low site, and 40% more visits in total, despite the fact that the high site had lower temperature and is more exposed to wind than the low site. Since insects are ectotherms and therefore maintain body temperature from their environment, their activity and metabolism are greatly linked to their surroundings (Mellanby, 1939). Flying behavior is also sensitive to wind (Møller, 2019), with higher wind speeds resulting in lower insect activity. Considering that the abiotic factors are more favorable at lower elevations, and that insect therefore should have a higher activity at the lower site, these results are unexpected.

Although there were more total insect visits at the high site, not all taxa were equally represented. Gillespie et al. (2020) found that diversity of insects should decrease with increasing elevation. This is supported by my results, which show a relatively more diverse community at the low site, due to a greater number of butterfly visits to *S. acaulis*. Although some butterflies depend on and use wind for migration and dispersal (Robbins & Small Jr, 1981), the butterflies found at Finse are not wind dispersed and therefore should not favor wind exposure. In addition, I found flies to be more abundant at the high elevation site, despite the warmer and more favorable conditions lower down the mountain slope.

My results do not agree with previous insect visitation studies completed at Finse. Totland (1993) studied two south facing mountains 2,5 km apart with an elevation difference of

22

about 200m, including Sandalsnuten, the same general area as my high elevation site. In contrast to my results, he found that *S. acaulis* had more total insect visits at the low elevation site. Totland (1993) also noted that the insect community at Finse is less diverse than other alpine areas, because Finse lacks bees, except for *Bombus spp*. The *Bombus spp*. that are present, together with syrphids, are in low abundance. Nonetheless, there is still a large difference in composition between high elevation and low elevation insect communities.

Similar to my results, Totland (1993) also found that flies were the most dominant flower visiting insect, regardless of elevation. However, an additional difference between Totland's results and mine is a lack of Lepidopteran visits overall in his study. While I did not observe many Lepidopteran at my high elevation site, there were significantly more Lepidoptera at my low elevation site. One explanation for this difference could be methodological. Totland collected data using field observations, while I used time interval cameras. However, I also observed several butterflies during my field observations, at both the high and low elevation site. On the other hand, given that Totland carried out his study almost 30 years ago, it could also be that climate change has already affected these ecosystems, by allowing new flower visiting insects like Lepidopteran to move upwards. If so, then new species and interactions are already establishing in these alpine ecosystems. However, alpine ecosystems experience large fluctuations in insect population sizes between years, and more research is needed to conclude exactly which mechanisms are driving the increase in Lepidoptera distribution.

Do plants respond to elevation?
There were no significant differences in plant traits between the high and low elevation sites. The prediction that traits of *S. acaulis* would change with increasing elevation was not met. Flower traits were not significantly different between the two sites, although this may be due to the relatively small elevation difference between my sites. Future investigations should consider investigating flower traits across a broader elevational gradient. The total number of flowers was greatest at the low site, and plants were larger in size, but average flower density was the same for both sites. Thus, none of the plant traits explain the difference in insect visits between the two elevations.

Current literature suggests that relative resource allocation to reproduction increases with elevation for alpine plants (Herrera, 2004; Kawano & Masuda, 1980). Zygomorphic flowers are rare, as pollinators are a less common resource for plants as elevation increases. Just 10% of flowers at Finse are categorized as zygomorphic, and mostly pollinated by bumblebees (Totland, 1993). Most flowers in alpine regions are simple, as they have to be able to be pollinated by the diversity of pollinators available. Flower size is important, as this is one of the main ways for plants to attract pollinators, and larger flowers signals more potential rewards for the pollinators. However, if temperature increases and insects

become more available at higher elevations, plants may not need to allocate as many resources to flowers at higher elevations. This could lead to increased energy for growth and competition.

The plants at the high site had a small but non-significant increase in some floral traits. This increase was expected and could also partly explain the difference in insect visits. As the higher site had slightly larger flowers, it could be expected that these plants would also attract and receive more visits from insects (Ohara & Higashi, 1994). Although I did not find a significant correlation between floral traits and the number of insect visits, this may be a result of the low number of plants investigated.

In addition, alpine plants are generally smaller at higher elevations (Maad et al., 2013) because growing seasons are short and resources less abundant. Thus, a greater proportion of available plant resources are put into reproduction, compared to low elevation plants. A warmed climate in the future may alter these allocation ratios resulting in a shift in plant reproduction.

Can community change with elevation?
Plants and insects both respond directly to temperature, and the insect community at low elevation was more diverse. In addition, changes to the plant community can further affect insects. As temperature increases, it is possible that both plant and insect species from lower elevations will migrate upwards. New pollinators from lower elevations can then establish and outcompete the existing pollinator community. This does not necessarily affect the plants negatively, as most alpine flowers are adapted to generalist pollinators (Totland, 1993). Therefore, the new pollinators may still be able to function as successful pollinators for the present plants. This also applies to *S. acaulis,* which has round and open flowers. However, pollinating insects may spend some portion of their life cycle as herbivores, directly damaging plants. This can lead to other important plant-insect or insect-insect interactions like herbivory (Rasmann et al., 2014) or predator/parasitoid-prey (Durant et al., 2007; Harrington et al., 1999) being shifted and has the potential to be harmful for the ecosystem.

The current diversity of alpine ecosystems is likely to be lost due to climate warming (Randin et al., 2009). One of the possible ways this can happen is when trees and shrubs move upwards, shrinking the habitat, and potentially leading to fewer pollinating insects (Inouye, 2020). Another way this might happen is through a change in plant or insect community via upslope migration. Inouye (2020) suggest that 50% of current European alpine species might lose 80% of their habitat by 2070. Differences in pollinator communities can be an important driver of plant-pollinator relationships. A diverse pollinator community likely has species that differ in their contribution when pollinating plants, and a diverse pollinator community could therefore be important for plant reproduction (Albrecht et al., 2012; Woodcock et al., 2019). This suggests that a higher diversity of pollinators may lead to higher plant reproductive success. It may also be that diverse communities of flowers better

sustain the pollinators (Blüthgen & Klein, 2011). If the diversity of pollinators is lost, then plant reproduction might also be negatively affected. An increase in temperature might allow species from lower elevations to establish and compete with current alpine communities. This can potentially be harmful for the current community, if species important for their survival are outcompeted.

The migration of species to higher elevations may have already happened at Finse, with butterflies more abundant in my study than in previous studies. There are other examples of species migrating upslope as well. Steinbauer et al. (2018) revisited old sites of alpine studies to examine the change in the plant communities over the last hundred years and found that many of the areas had shown an increase in biodiversity, rather than a decrease. They called this an extinction debt, which means that the species that were historically present at these areas are long lived enough that they persist for some time before they are outcompeted. When I compare my results with Totland (1993), it suggests that butterflies have moved upwards, and that historically native species are now competing with new species. The review by Steinbauer et al. (2018) shows that long time series studies are required to determine what impact this will have on the alpine ecosystem, although further research is needed in order to conclude what the effects of the new interactions are.

In addition to the extinction debt, species interacting in a plant-pollinator relationship have vastly different life history and dispersal abilities. While plants can live for hundreds of years (Morris & Doak, 1998) and are sessile, insects are short-lived, and mobile. This can lead to asynchronous range shifts (Richman et al., 2020), which can make important species-specific interactions disappear or end up out of sync. In a long-term perspective, alpine plants and insects both face the risk of extinction, unless they are able to adapt to and interact with new species.

Another important limitation in alpine communities is the length of the growing season. While plants that flower early risk the flowers freezing at night, late flowering on the other hand is associated with the risk of not being able to mature seeds and capsules before winter. Ongoing climate change might shift the start and end of the seasons. In addition to increasing the risk of early flowers freezing, it can also lead to a trophic mismatch between insects and plants. *S. acaulis's* flowers last for about 6-7 days (Fabbro & Körner, 2004), which is a short period for insects to visit. A mismatch here between pollinators and flowering could have large consequences for the reproductive output of *S. acaulis*.

Do insect visits explain reproductive output in the form of capsules?
There was a large, significant difference in the number of seed capsules produced by plants between the two sites. However, in contrast with my predictions, plants receiving fewer insect visits produced more seed capsules.

It is important to note that I did not measure successful pollination, only visitation rate. Visitation rate can be a good indicator of successful pollination (Vázquez et al., 2005) when combined with estimates of seed production. Based on the assumption that the individual plants at both the high and low elevation sites have the same threshold of visits needed to reproduce, plants at the high elevation site should have produced at least equal numbers of seed capsules as the low elevation site, since they received more visits. Instead, plants at the low elevation site produced on average 37 times more seed capsules than plants at the high elevation site. Although there was a more diverse flower visiting insect community at the low elevation site, and more diverse insect communities have been shown to positively affect reproductive output in plants (Senapathi et al., 2021; Woodcock et al., 2019), this was not supported by my analysis. None of the individual taxa and their visits could explain the difference in capsules between the two sites.

Limited resources may explain the difference in plant reproductive output. It is possible that plants at the high elevation sites had fewer overall resources and that abiotic factors such as temperature and precipitation affected reproduction (Bisi et al., 2016). However, my sites were located relatively close to each other on the same mountain slope with about 1°C difference in air temperature, making it less likely that differences in resource availability would lead to such a large difference in reproductive output. I did not take soil samples from my sites to compare the resources and nutrients available, but Hågvar & Klanderud (2009) found that the soil at Finse is generally nutrient poor. Even though seed production can be limited by low temperatures in alpine ecosystems (Totland, 2001), other factors like pollen limitation (García-Camacho & Totland, 2009) are important for seed production as well. Some cushion plants even increase their seed production with increasing elevation (Chen et al., 2017), although this was not the case for my study.

S. acaulis can have both male, female and hermaphrodite individuals, where females are reported to produce more seed capsules than hermaphrodites, with about 4,4 times higher lifetime reproductive output than hermaphrodites (Morris & Doak, 1998). Most of the individuals at Finse are also reported to be females and hermaphrodites, with males being rare (Alatalo & Totland, 1997). Therefore, it is possible that I selected female individuals at the low site, and hermaphrodites or males at the high site. Although this is unlikely, since nearly all individuals observed at the high site also produced a limited number of capsules (personal observations), and the difference in reproductive output between the two sites was about eight times higher than what Morris & Doak (1998) found. A study by Hermanutz & Innes (1994) found that six of their seven study populations of *S. acaulis* had between 72-80% female plants, indicating that females generally dominate in a population, making it even less likely that I selected no females at the high site.

None of the factors above offer a good explanation for the difference in reproductive output. The higher visitation rate, longer visit duration, coupled with lower reproduction

suggests that *S. acaulis* may be acting as a refuge for insects at the high elevation site. Alpine ecosystems are highly stressful for insect's survival, and it has been suggested that less stressful microclimatic conditions could be important for insect survival and development (Molina-Montenegro et al., 2006). The concept of plants offering insects more suitable environments is not uncommon, as ants and trees can have close mutualistic relationships (Janzen, 1966). Molina-Montenegro et al. (2006) found that cushion plants in the Andes mountains provided less stressful environments for insects, and that insects greatly favored cushions over the surrounding environments. Dietrich & Körner (2014) showed by using thermal imaging that the flowers of several alpine plants are warmer than the air temperature, including *S. acaulis*. In addition to the flowers being warmer than the air, the cushions themselves also physically offer insects shelter from the wind and rain. When I did field observations, I noted several insects taking shelter on the cushions, especially early in the morning and in cold and windy conditions. Reid & Lortie (2012) also showed that cushion plants in general attract and interact with more arthropods than surrounding vegetation. At Finse, if insects gain shelter in *S. acaulis* cushions, that may explain the difference in the number and length of insect visits, and the difference in reproductive output between the high and low elevation sites. This could also mean that cushion plants like *S. acaulis* are important for insect survival in alpine areas and may even help insects from lower elevations establish.

Are there any seed predators that feed on the capsules of *S. acaulis*?
Lastly, I investigated the potential seed predator community of *S. acaulis* capsules. I found that there are few to no insects or small vertebrates that are utilizing *S. acaulis* seed capsules as a food source. I observed two snails that may have been feeding on capsules, although this is hard to verify through camera images. *Nysius groenlandicus*, a seed sucking insect, is known to feed on seeds of *S. acaulis* and has previously been reported at Finse, but I did not detect it in any of my images. It could be that *N. groenlandicus* has a small population at Finse, and the observations are from 1960s and 70s (Artsdatabanken, 2021), making it uncertain if it is still found at Finse today. It could also be that *N. groenlandicus* is nocturnal, in which case my cameras were unable to detect it, as they did not capture pictures between 21:59 and 05:00. But experiments from Böcher & Nachman (2001) showed that *N. groenlandicus* preferred temperatures around 30°C, suggesting it is active and feeding during summer days. Lundbye et al. (2012) documented that *N. groenlandicus,* which fed on seeds of *S. acaulis,* reduced the mass of the seed by 3%. Although they did mention that the feeding time was short, and that *N. groenlandicus* could have been starved for longer before the experiment started. Importantly, they found that feeding had no effect on germination rate, and actually decreased the time to germination for seeds that were fed upon, possibly because the hole left by *N. groenlandicus* increased water uptake in the seeds. This suggests that *S. acaulis-N. groenlandicus* interactions may be important for *S. acaulis* population persistence.

Conclusion

My study suggests that flower visiting insects in alpine areas are using flowering cushion plants for shelter, as well as food. This supports the idea that *S. acaulis* facilitates species across trophic levels in alpine ecosystems. This resulted in higher visitation rates and longer visit durations at the high elevation site, but did not result in improved pollination and *S. acaulis* reproductive success.

Future research

Seasons in alpine areas can vary between years making it important to have studies over more than one season to understand how variation affects species interactions. As climate is expected to continue warming, it is important to have long time series to observe how plants and insects respond to these changes. My study serves as an important starting point for future work to build on to better understand how changes and variation in climate affects alpine ecosystems. My study also shows that *S. acaulis* can act as a refuge for insects, and future research on this is needed to understand how these interactions work and may change with climate.

References

Alatalo, J. & Totland, Ø. (1997). Response to simulated climatic change in an alpine and subarctic pollen-risk strategist, Silene acaulis. *Global Change Biology*, 3 (S1): 74-79.

Albrecht, M., Schmid, B., Hautier, Y. & Müller, C. B. (2012). Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, 279 (1748): 4845-4852. doi: doi:10.1098/rspb.2012.1621.

Antonsson, H., Björk, R. G. & Molau, U. (2009). Nurse plant effect of the cushion plant Silene acaulis (L.) Jacq. in an alpine environment in the subarctic Scandes, Sweden. *Plant Ecology & Diversity*, 2 (1): 17-25. doi: 10.1080/17550870902926504.

Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., et al. (1999). RESPONSES OF TUNDRA PLANTS TO EXPERIMENTAL WARMING:META-ANALYSIS OF THE INTERNATIONAL TUNDRA EXPERIMENT. *Ecological Monographs*, 69 (4): 491-511. doi: https://doi.org/10.1890/0012-9615(1999)069[0491:ROTPTE]2.0.CO;2.

Artsdatabanken. (2021). Tilgjengelig fra: https://artskart.artsdatabanken.no/app/#map/107779,6740076/7/background/greyMap/filter/%7B%22TaxonIds%22%3A%5B79861%5D%2C%22IncludeSubTaxonIds%22%3Atrue%2C%22Found%22%3A%5B2%5D%2C%22NotRecovered%22%3A%5B2%5D%2C%22Style%22%3A1%7D (lest 30.04).

Bergman, P., Molau, U. & Holmgren, B. (1996). Micrometeorological Impacts on Insect Activity and Plant Reproductive Success in an Alpine Environment, Swedish Lapland. *Arctic and Alpine Research*, 28 (2): 196-202. doi: 10.1080/00040851.1996.12003166.

Billings, W. (1973). Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience*, 23 (12): 697-704.

Birkemoe, T., Bergmann, S., Hasle, T. E. & Klanderud, K. (2016). Experimental warming increases herbivory by leaf-chewing insects in an alpine plant community. *Ecology and evolution*, 6 (19): 6955-6962.

Bisi, F., von Hardenberg, J., Bertolino, S., Wauters, L. A., Imperio, S., Preatoni, D. G., Provenzale, A., Mazzamuto, M. V. & Martinoli, A. (2016). Current and future conifer seed production in the Alps: testing weather factors as cues behind masting. *European Journal of Forest Research*, 135 (4): 743-754. doi: 10.1007/s10342-016-0969-4.

Bliss, L. C. (1971). Arctic and alpine plant life cycles. *Annual review of ecology and systematics*, 2 (1): 405-438.

Bokhorst, S., Huiskes, A., Aerts, R., Convey, P., Cooper, E. J., Dalen, L., Erschbamer, B., Gudmundsson, J., Hofgaard, A., Hollister, R. D., et al. (2013). Variable temperature effects of Open Top Chambers at polar and alpine sites explained by irradiance and snow depth. *Global Change Biology*, 19 (1): 64-74. doi: https://doi.org/10.1111/gcb.12028.

Böcher, J. & Nachman, G. (2001). Temperature and humidity responses of the arctic-alpine seed bug Nysius groenlandicus. *Entomologia Experimentalis et Applicata*, 99 (3): 319-330. doi: https://doi.org/10.1046/j.1570-7458.2001.00831.x.

Carvalheiro, L. G., Biesmeijer, J. C., Benadi, G., Fründ, J., Stang, M., Bartomeus, I., Kaiser-Bunbury, C. N., Baude, M., Gomes, S. I. F., Merckx, V., et al. (2014). The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecology Letters*, 17 (11): 1389-1399. doi: https://doi.org/10.1111/ele.12342.

Chen, J., Li, Y., Yang, Y. & Sun, H. (2017). How cushion communities are maintained in alpine ecosystems: A review and case study on alpine cushion plant reproduction. *Plant Diversity*, 39 (4): 221-228. doi: https://doi.org/10.1016/j.pld.2017.07.002.

Dietrich, L. & Körner, C. (2014). Thermal imaging reveals massive heat accumulation in flowers across a broad spectrum of alpine taxa. *Alpine Botany*, 124 (1): 27-35. doi: 10.1007/s00035-014-0123-1.

Durant, J. M., Hjermann, D. Ø., Ottersen, G. & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate research*, 33 (3): 271-283.

Dutta, A. & Zisserman, A. (2019). *The VIA Annotation Software for Images, Audio and Video*. Proceedings of the 27th ACM International Conference on Multimedia, Nice, France, s. 2276–2279: Association for Computing Machinery.

Ernakovich, J. G., Hopping, K. A., Berdanier, A. B., Simpson, R. T., Kachergis, E. J., Steltzer, H. & Wallenstein, M. D. (2014). Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology*, 20 (10): 3256-3269. doi: https://doi.org/10.1111/gcb.12568.

Fabbro, T. & Körner, C. (2004). Altitudinal differences in flower traits and reproductive allocation. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 199 (1): 70-81.

García-Camacho, R. & Totland, Ø. (2009). Pollen limitation in the alpine: a meta-analysis. *Arctic, Antarctic, and Alpine Research*, 41 (1): 103-111.

Gehring, J. L. & Delph, L. F. (1999). Fine-scale genetic structure and clinal variation in Silene acaulis despite high gene flow. *Heredity*, 82 (6): 628-637.

Gillespie, M. A. K., Alfredsson, M., Barrio, I. C., Bowden, J. J., Convey, P., Culler, L. E., Coulson, S. J., Krogh, P. H., Koltz, A. M., Koponen, S., et al. (2020). Status and trends of terrestrial arthropod abundance and diversity in the North Atlantic region of the Arctic. *Ambio*, 49 (3): 718-731. doi: 10.1007/s13280-019-01162-5.

Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties*: John Wiley & Sons.

Gussarova, G., Allen, G. A., Mikhaylova, Y., McCormick, L. J., Mirré, V., Marr, K. L., Hebda, R. J. & Brochmann, C. (2015). Vicariance, long-distance dispersal, and regional extinction–recolonization dynamics explain the disjunct circumpolar distribution of the arctic-alpine plant Silene acaulis. *American Journal of Botany*, 102 (10): 1703-1720. doi: https://doi.org/10.3732/ajb.1500072.

Halbritter, A. H., Fior, S., Keller, I., Billeter, R., Edwards, P. J., Holderegger, R., Karrenberg, S., Pluess, A. R., Widmer, A. & Alexander, J. M. (2018). Trait differentiation and adaptation of plants along elevation gradients. *Journal of Evolutionary Biology*, 31 (6): 784-800. doi: https://doi.org/10.1111/jeb.13262.

Hall, E. S., Piedrahita, L. R., Kendziorski, G., Waddle, E., Doak, D. F. & Peterson, M. L. (2018). Climate and synchrony with conspecifics determine the effects of flowering phenology on reproductive success in Silene acaulis. *Arctic, Antarctic, and Alpine Research*, 50 (1): e1548866.

Harrington, R., Woiwod, I. & Sparks, T. (1999). Climate change and trophic interactions. *Trends in Ecology & Evolution*, 14 (4): 146-150. doi: https://doi.org/10.1016/S0169-5347(99)01604-3.

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, 12 (2): 184-195. doi: https://doi.org/10.1111/j.1461-0248.2008.01269.x.

Hemborg, Å. M. & Karlsson, P. S. (1998). Altitudinal variation in size effects on plant reproductive effort and somatic costs of reproduction. *Écoscience*, 5 (4): 517-525. doi: 10.1080/11956860.1998.11682495.

Hermanutz, L. A. & Innes, D. J. (1994). Gender variation in Silene acaulis (Caryophyllaceae). *Plant Systematics and Evolution*, 191 (1): 69-81.

Herrera, J. (2004). Flower Size Variation in Rosmarinus officinalis: Individuals, Populations and Habitats. *Annals of Botany*, 95 (3): 431-437. doi: 10.1093/aob/mci041.

Hodkinson, I. & Coulson, S. (2004). Are high Arctic terrestrial food chains really that simple? – The Bear Island food web revisited. *Oikos*, 106 (2): 427-431. doi: https://doi.org/10.1111/j.0030-1299.2004.13091.x.

Hågvar, S. & Klanderud, K. (2009). Effect of simulated environmental change on alpine soil arthropods. *Global Change Biology*, 15 (12): 2972-2980. doi: https://doi.org/10.1111/j.1365-2486.2009.01926.x.

Inouye, D. W., Saavedra, F. & Lee-Yang, W. (2003). Environmental influences on the phenology and abundance of flowering by Androsace septentrionalis (Primulaceae). *American Journal of Botany*, 90 (6): 905-910.

Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, 89 (2): 353-362.

Inouye, D. W. (2020). Effects of climate change on alpine plants and their pollinators. *Annals of the New York Academy of Sciences*, 1469 (1): 26-37. doi: https://doi.org/10.1111/nyas.14104.

IPCC. (2018). *Summary for Policymakers. In: Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*.

IPCC. (2019). *Summary for Policymakers. In: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*.

Janzen, D. H. (1966). Coevolution of Mutualism Between Ants and Acacias in Central America. *Evolution*, 20 (3): 249-275. doi: 10.2307/2406628.

Jennersten, O. & Nilsson, S. G. (1993). Insect flower visitation frequency and seed production in relation to patch size of Viscaria vulgaris (Caryophyllaceae). *Oikos*: 283-292.

Junker, R. R., Blüthgen, N. & Keller, A. (2015). Functional and phylogenetic diversity of plant communities differently affect the structure of flower-visitor interactions and reveal

convergences in floral traits. *Evolutionary Ecology*, 29 (3): 437-450. doi: 10.1007/s10682-014-9747-2.

Kawano, S. & Masuda, J. (1980). The productive and reproductive biology of flowering plants. *Oecologia*, 45 (3): 307-317.

Kenis, M., Auger-Rozenberg, M.-A., Roques, A., Timms, L., Péré, C., Cock, M. J. W., Settele, J., Augustin, S. & Lopez-Vaamonde, C. (2009). Ecological effects of invasive alien insects. *Biological Invasions*, 11 (1): 21-45. doi: 10.1007/s10530-008-9318-y.

Kirschbaum, M. U. (1995). The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology and biochemistry*, 27 (6): 753-760.

Klanderud, K. (2005). Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, 93 (1): 127-137. doi: https://doi.org/10.1111/j.1365-2745.2004.00944.x.

Konvicka, M., Maradova, M., Benes, J., Fric, Z. & Kepka, P. (2003). Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecology and Biogeography*, 12 (5): 403-410. doi: https://doi.org/10.1046/j.1466-822X.2003.00053.x.

Krushelnycky, P. D. (2014). Evaluating the interacting influences of pollination, seed predation, invasive species and isolation on reproductive success in a threatened alpine plant. *PloS one*, 9 (2): e88948.

Kudo, G. & Molau, U. (1999). Variations in reproductive traits at inflorescence and flower levels of an arctic legume, Astragalus alpinus L.: Comparisons between a subalpine and an alpine population. *Plant Species Biology*, 14 (3): 181-191. doi: https://doi.org/10.1046/j.1442-1984.1999.00012.x.

Kudo, G. & Suzuki, S. (1999). Flowering phenology of alpine plant communities along a gradient of snowmelt timing.

König, P., Tautenhahn, S., Cornelissen, J. H. C., Kattge, J., Bönisch, G. & Römermann, C. (2018). Advances in flowering phenology across the Northern Hemisphere are explained by functional traits. *Global Ecology and Biogeography*, 27 (3): 310-321. doi: https://doi.org/10.1111/geb.12696.

Lara-Romero, C., García, C., Morente-López, J. & Iriondo, J. M. (2016). Direct and indirect effects of shrub encroachment on alpine grasslands mediated by plant–flower visitor interactions. *Functional Ecology*, 30 (9): 1521-1530.

Lundbye, H., Johansson, D. K., Andersen, M. R. & Philipp, M. (2012). The effect of a seed-sucking bug on seed germination of an arctic cushion plant. *Ecoscience*, 19 (3): 209-212.

Mellanby, K. (1939). Low temperature and insect activity. *Proceedings of the Royal Society of London. Series B-Biological Sciences*, 127 (849): 473-487.

Molau, U., Eriksen, B. & Knudsen, J. T. (1989). Predispersal seed predation in Bartsia alpina. *Oecologia*, 81 (2): 181-185. doi: 10.1007/BF00379803.

Molenda, O., Reid, A. & Lortie, C. J. (2012). The Alpine Cushion Plant Silene acaulis as Foundation Species: A Bug's-Eye View to Facilitation and Microclimate. *PLOS ONE*, 7 (5): e37223. doi: 10.1371/journal.pone.0037223.

Molina-Montenegro, M. A., Badano, E. I. & Cavieres, L. A. (2006). Cushion plants as microclimatic shelters for two ladybird beetles species in alpine zone of central Chile. *Arctic, Antarctic, and Alpine Research*, 38 (2): 224-227.

Morris, W. F. & Doak, D. F. (1998). Life history of the long-lived gynodioecious cushion plant Silene acaulis (Caryophyllaceae), inferred from size-based population projection matrices. *American Journal of Botany*, 85 (6): 784-793. doi: https://doi.org/10.2307/2446413.

Munoz, A. A. & CAVIERES, L. A. (2006). A Multi-species Assessment of Post-dispersal Seed Predation in the Central Chilean Andes. *Annals of Botany*, 98 (1): 193-201. doi: 10.1093/aob/mcl087.

Møller, A. P. (2019). Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution*, 9 (11): 6581-6587. doi: https://doi.org/10.1002/ece3.5236.

Maad, J., Armbruster, W. S. & Fenster, C. B. (2013). Floral size variation in Campanula rotundifolia (Campanulaceae) along altitudinal gradients: patterns and possible selective mechanisms. *Nordic Journal of Botany*, 31 (3): 361-371. doi: https://doi.org/10.1111/j.1756-1051.2013.01766.x.

Ohara, M. & Higashi, S. (1994). Effects of inflorescence size on visits from pollinators and seed set of Corydalis ambigua (Papaveraceae). *Oecologia*, 98 (1): 25-30.

Ohler, L.-M., Lechleitner, M. & Junker, R. R. (2020). Microclimatic effects on alpine plant communities and flower-visitor interactions. *Scientific Reports*, 10 (1): 1366. doi: 10.1038/s41598-020-58388-7.

Peñuelas, J., Gordon, C., Llorens, L., Nielsen, T., Tietema, A., Beier, C., Bruna, P., Emmett, B., Estiarte, M. & Gorissen, A. (2004). Nonintrusive Field Experiments Show Different Plant Responses to Warming and Drought Among Sites, Seasons, and Species in a North–South European Gradient. *Ecosystems*, 7 (6): 598-612. doi: 10.1007/s10021-004-0179-7.

Rafferty, N. E. & Ives, A. R. (2011). Effects of experimental shifts in flowering phenology on plant–pollinator interactions. *Ecology Letters*, 14 (1): 69-74. doi: https://doi.org/10.1111/j.1461-0248.2010.01557.x.

Randin, C. F., ENGLER, R., NORMAND, S., ZAPPA, M., ZIMMERMANN, N. E., PEARMAN, P. B., VITTOZ, P., THUILLER, W. & GUISAN, A. (2009). Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, 15 (6): 1557-1569. doi: https://doi.org/10.1111/j.1365-2486.2008.01766.x.

Rasmann, S., Pellissier, L., Defossez, E., Jactel, H. & Kunstler, G. (2014). Climate-driven change in plant–insect interactions along elevation gradients. *Functional Ecology*, 28 (1): 46-54. doi: https://doi.org/10.1111/1365-2435.12135.

Reid, A. M. & Lortie, C. J. (2012). Cushion plants are foundation species with positive effects extending to higher trophic levels. *Ecosphere*, 3 (11): art96. doi: https://doi.org/10.1890/ES12-00106.1.

Richman, S. K., Levine, J. M., Stefan, L. & Johnson, C. A. (2020). Asynchronous range shifts drive alpine plant–pollinator interactions and reduce plant fitness. *Global change biology*, 26 (5): 3052-3064.

Robbins, R. K. & Small Jr, G. B. (1981). Wind dispersal of Panamanian hairstreak butterflies (Lepidoptera: Lycaenidae) and its evolutionary significance. *Biotropica*: 308-315.

Roy, D. & Sparks, T. (2000). Phenology of British butterflies and climate change. *Global change biology*, 6 (4): 407-416.

Roy, J., Bonneville, J. M., Saccone, P., Ibanez, S., Albert, C. H., Boleda, M., Gueguen, M., Ohlmann, M., Rioux, D. & Clément, J. C. (2018). Differences in the fungal communities nursed by two genetic groups of the alpine cushion plant, Silene acaulis. *Ecology and Evolution*, 8 (23): 11568-11581.

Senapathi, D., Fründ, J., Albrecht, M., Garratt, M. P. D., Kleijn, D., Pickles, B. J., Potts, S. G., An, J., Andersson, G. K. S., Bänsch, S., et al. (2021). Wild insect diversity increases inter-annual stability in global crop pollinator communities. *Proceedings of the Royal Society B: Biological Sciences*, 288 (1947): 20210212. doi: doi:10.1098/rspb.2021.0212.

Shah, A. A., Dillon, M. E., Hotaling, S. & Woods, H. A. (2020). High elevation insect communities face shifting ecological and evolutionary landscapes. *Current Opinion in Insect Science*, 41: 1-6. doi: https://doi.org/10.1016/j.cois.2020.04.002.

Sjursen, H. & Sømme, L. (2000). Seasonal changes in tolerance to cold and desiccation in Phauloppia sp.(Acari, Oribatida) from Finse, Norway. *Journal of Insect Physiology*, 46 (10): 1387-1396.

Sorte, C. J. B., Williams, S. L. & Carlton, J. T. (2010). Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, 19 (3): 303-316. doi: https://doi.org/10.1111/j.1466-8238.2009.00519.x.

Sridhar, J., Kumar, K. K., Murali-Baskaran, R., Senthil-Nathan, S., Sharma, S., Nagesh, M., Kaushal, P. & Kumar, J. (2020). Impact of Climate Change on Communities, Response and Migration of Insects, Nematodes, Vectors and Natural Enemies in Diverse Ecosystems. I: *Global Climate Change: Resilient and Smart Agriculture*, s. 69-93: Springer.

Stanghellini, M., Ambrose, J. & Schultheis, J. (1998). Seed production in watermelon: a comparison between two commercially available pollinators. *HortScience*, 33 (1): 28-30.

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

Taylor, L. (1963). Analysis of the effect of temperature on insects in flight. *The Journal of Animal Ecology*: 99-117.

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D. & Leech, D. I. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535 (7611): 241-245.

Thompson, J. D. (2001). How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? *Oecologia*, 126 (3): 386-394. doi: 10.1007/s004420000531.

Thomson, J. D. (1981). Spatial and temporal components of resource assessment by flower-feeding insects. *The Journal of Animal Ecology*: 49-59.

Totland, Ø. (1993). Pollination in alpine Norway: flowering phenology, insect visitors, and visitation rates in two plant communities. *Canadian Journal of Botany*, 71 (8): 1072-1079.

Totland, Ø. (1994). Influence of Climate, Time of Day and Season, and Flower Density on Insect Flower Visitation in Alpine Norway. *Arctic and Alpine Research*, 26 (1): 66-71. doi: 10.1080/00040851.1994.12003041.

Totland, Ø. (2001). ENVIRONMENT-DEPENDENT POLLEN LIMITATION AND SELECTION ON FLORAL TRAITS IN AN ALPINE SPECIES. *Ecology*, 82 (8): 2233-2244. doi: https://doi.org/10.1890/0012-9658(2001)082[2233:EDPLAS]2.0.CO;2.

Vázquez, D. P., Morris, W. F. & Jordano, P. (2005). Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters*, 8 (10): 1088-1094. doi: https://doi.org/10.1111/j.1461-0248.2005.00810.x.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., et al. (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, 103 (5): 1342-1346. doi: 10.1073/pnas.0503198103.

Westerman, P. R., Hofman, A., Vet, L. E. M. & van der Werf, W. (2003). Relative importance of vertebrates and invertebrates in epigeaic weed seed predation in organic cereal fields. *Agriculture, Ecosystems & Environment*, 95 (2): 417-425. doi: https://doi.org/10.1016/S0167-8809(02)00224-4.

Woodcock, B. A., Garratt, M. P. D., Powney, G. D., Shaw, R. F., Osborne, J. L., Soroka, J., Lindström, S. A. M., Stanley, D., Ouvrard, P., Edwards, M. E., et al. (2019). Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nature Communications*, 10 (1): 1481. doi: 10.1038/s41467-019-09393-6.

Wu, T.-H., Shiao, S.-F. & Okuyama, T. (2015). Development of insects under fluctuating temperature: a review and case study. *Journal of Applied Entomology*, 139 (8): 592-599. doi: https://doi.org/10.1111/jen.12196.

Appendix 1

The cameras had several different options for settings. First, I set the date and time to match the actual date and time. I then selected for photo instead of video, and the desired interval between the images. After that I selected one time lapse program per day and set the start and stop time for this time lapse, which in my case was from 0500-2159. I then said no to upgrade the firmware and did not set a security code. Then I set the temperature units to be Celsius and said no for ac connected and wifi SD card. After that I named my cameras from 1 to 10 and said yes to imprint this info on the pictures. This means that the name, date, time, and temperature show up at the bottom of the picture. I skipped doing anything to the video settings, as I was just using images. I then set the photo quality to high (10MP) and told the camera to not overwrite. Lastly, I selected no when asked to reset to factory settings.

Appendix 2

Table 5: The different plants with their respective logger for either air or soil temperature. The exact coordinates for each plant are also included in WGS 84 format, as well as meters above sea level.

Plant ID	Logger	North coordinates	East coordinates	Meters above sea level
1	Soil	60.36917	07.31278	1530
2	Air	60.36947	07.31232	1532
3	Air	60.36945	07.31261	1542
4	Soil	60.36914	07.31287	1531
5	Air	60.36925	07.31286	1535
6	Air	60.36845	07.31229	1470
7a	Air	60.36873	07.31152	1469
7b	Air	60.36873	07.31152	1469
8	Air	60.36848	07.31218	1471
9	Air	60.38680	07.31219	1492
10	Soil	60.36863	07.31225	1488

Appendix 3

Table 6: the data used for the analysis.

plantid	visits	fly	bumblebee	butterfly	noid	kapsler	Length of visits (min)	size cm^2	flowers	flowerdensity	d (mm)	pl (mm)	pw (mm)	visitsperflower
1	134	124	1	9	0	5	4,6	386,8	40	0,103412616	10,2	4,1	3	3,35
2	81	73	0	4	4	1	4,2	422,8	40	0,094607379	9,9	4,1	3,2	2,025
3	74	72	0	2	0	0	4,9	250,5	20	0,079840319	11,8	4,7	3,3	3,7
4	98	85	1	11	1	0	3,5	542,5	50	0,092165899	9,4	3,8	2,7	1,96
5	65	63	0	2	0	3	3,8	3593	70	0,019482327	10,2	4,2	2,9	0,928571429
6	109	65	0	43	1	49	3,1	1123,3	70	0,062316389	9,5	3,1	4	1,557142857
7a	49	36	0	13	0	173	1,9	661,2	120	0,181488203	10,6	4,4	3,2	0,408333333
7b	61	55	0	6	0	2	4	736,8	50	0,067861021	8,3	3,4	2,1	1,22
8	29	18	0	11	0	98	3,8	4203,6	50	0,011894567	9,2	2,3	3,6	0,58
9	36	22	0	14	0	77	3	1302,4	120	0,092137592	10	4,4	3	0,3
10	38	22	3	13	0	3	2,7	298,3	20	0,067046597	9,2	3,8	2,6	1,9