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From seed to survival: how biotic interactions shape boreal plant establishment in alpine habitats

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Ecology

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Abstract

Global warming has been shown to drive range shifts of lowland plant species towards the colder alpine zone. However, the knowledge of the effects of biotic interactions on the colonizers' establishment success and survival in the alpine, and how biotic interaction effects vary across alpine habitats, is limited. To investigate these effects, a seed sowing experiment of three lowland species was conducted in the four dominant habitat types at Finse, an alpine area in Southern Norway. Seeds were sown in control plots with intact vegetation and in experimentally created gaps where vegetation was removed prior to sowing to eliminate aboveground competition by extant plants. Throughout the following growing season, germination and survival was recorded for all emerged seedlings in the plots. The seedling's height, number of leaves and leaf length were measured to detect differences in growth and resource allocation. Vegetation analyses were performed to investigate relationships between neighbouring species and the seedlings' germination, survival and growth traits. Both seed germination and seedling survival were lower in control plots than in gaps. Seed germination followed a gradient in soil-moisture, with highest germination at the wettest end, the snowbed, and lowest at the driest, the leeside. Seedling survival was also highest in the snowbed but lowest on the ridge. No significant differences were detected for leaf lengths, but seedlings were the tallest in meadow, and taller in control plots than in gaps. Seedlings had significantly more leaves in gaps than in intact vegetation. The effect of treatment was reduced in the snowbed for both seedling height and number of leaves. The results indicate that competition is the dominating plant-plant interaction between boreal seedlings establishing in the alpine and the extant alpine species. My findings suggest that alpine plant communities can hinder, or at least slow down, range shifts of boreal species towards higher elevations under current climate by limiting seed germination and survival. Today, the wettest alpine habitats seem more susceptible to invasion, and if climate change leads to increased rainfall, all alpine habitats could become increasingly vulnerable to lowland plant invasions.

Samandrag

Global oppvarming har vist seg å føre til at låglandsartar flyttar utbreiinga si mot kjøligare, alpine strøk. Kunnskapen om korleis biotiske interaksjonar påverkar dei koloniserande artane si etablering og overleving i alpine område, og korleis dette varierer mellom alpine habitat, er likevel avgrensa. For å undersøkje desse effektane vart eit såforsøk med tre låglandsartar gjennomført i dei fire mest dominerande naturtypane på Finse, eit fjellområde i Sør-Noreg. Frøa vart sådde i kontrollplot med intakt vegetasjon og i 'gap'-plot der vegetasjonen vart fjerna i forkant av såing for å eliminere overjordisk konkurranse frå dei eksisterande fjellplantane. Gjennom den komande vekstsesongen vart spiring og overleving registrert for alle frøplantar i plotta. Vekstvariablane høgd, antal blad og bladlengd vart også målt for alle frøplantane for å avdekke skilnader i vekst og ressursfordeling. For å undersøkje samanhengar mellom det eksisterande plantesamfunnet og dei sådde plantane si spiring, overleving og vekst vart det gjort vegetasjonsanalysar. Både frøspiring og overleving var lågast i kontrollplot, samanlikna med i gap-plotta. Spiringa av dei sådde frøa følgde ein gradient for jordfukt, som resulterte i høgast spiring i snøleiet og lågast i lesida. Frøplantane si overleving var også størst i snøleiet men lågast på rabben. Ingen signifikante skilnader i bladlengd kom fram i resultata, men frøplantane var høgast i enga og høgare i kontrollplot enn i 'gaps'. Frøplantane hadde også signifikant fleire blad i dei vegetasjonslause plotta enn i kontrollplot. Effekten av fjerna vegetasjon var redusert i snøleiet både for frøplante-høgd og antal blad. Resultata tyder på at konkurranse er den dominerande plante-plante-interaksjonen mellom boreale frøplantar som etablerer seg i fjellet og dei eksisterande alpine plantane. Funna indikerer at alpine plantesamfunn kan hindre, eller i det minste bremse boreale plantar sin invasjon av fjellet ved noverande klima ved å redusere spiring og overleving. I dag verkar dei fuktigaste habitata i fjellet mest utsette for å bli invaderte, men om klimaendringar fører til meir regn i fjellet i framtida kan alle alpine naturtypar verte meir sårbare for invasjonar av låglandsplantar

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Introduction

Global warming is altering the world's ecosystems, and warming of mountains and tundra regions is happening faster than in lowland areas (IPBES, 2018; Nogués-Bravo et al., 2007; Rangwala et al., 2013). Predicted temperature increases for these areas are of 3-5 ˚C by the end of the century, having stronger effects in northern latitude mountains than in other montane areas across the globe (IPBES, 2018; Nogués-Bravo et al., 2007). In addition to temperature changes, precipitation patterns are changing across the globe and show increased precipitation falling as rain in Arctic and alpine regions, causing reduced snow cover during winter (Hock et al., 2019). These changes are projected to intensify further in the future (IPCC, 2019), augmenting the effects of climate change on Arctic and alpine ecosystems (Bjorkman et al., 2020; Elmendorf et al., 2012; Engler et al., 2011).

Climatic changes are already driving biological responses in mountain ecosystems and are expected to have severe impacts on biodiversity (IPBES, 2018; Pereira et al., 2010). One of the most prominent consequences is shifts in species ranges from lower elevations into the alpine, which reduces the extent of habitats suitable for alpine plant species (Alexander et al., 2016; Hansson et al., 2021; Körner, 2012; Körner & Hiltbrunner, 2021) and increases competition for resources and space (Gottfried et al., 2012; IPBES, 2019; Liang et al., 2018; Pauli et al., 2012). This range shift is especially affecting alpine plants at their lower range-limits, where the treeline ecotone expands (Dirnböck et al., 2003; Körner, 2012; Pellissier et al., 2013), resulting in species migrations further up the mountain or contractions of their ranges (Dullinger et al., 2012; Engler et al., 2011; Hock et al., 2019; Thuiller et al., 2014). More warm-adapted species are already observed to increase in abundance above the current treeline, and cold-adapted alpine species are declining (Cuesta et al., 2023; Hock et al., 2019; Rumpf et al., 2018), causing what is refered to as a 'thermophilization' of the alpine (Gottfried et al., 2012). Due to lagged responses in species range dynamics, where colonizations and extinctions currently fail to keep pace with climate change, species composition changes may initially lead to increases in species richnes and plant abundance at high elevations and thus 'mask' future biodiversity loss and regional homogenization of alpine plant species pools (Block et al., 2022; Dullinger et al., 2012; Engler et al., 2009; Goodwin et al., 2025). Climate-driven range losses thus poses severe threats to the extent of cold alpine plant habitats and species, now, and even more in the future (Dirnböck et al., 2011; IPBES, 2018; Thuiller et al., 2005; Wehn et al., 2014).

Recruitment from seeds at higher elevations is the main mechanism driving boreal plants' range shifts into the alpine, involving the steps of seed dispersal, germination, seedling growth and survival (Clark et al., 1998; Nathan & Muller-Landau, 2000). In this process, seedling emergence is considered the main bottleneck (Graae et al., 2011). For both seed germination and seedling survival in the alpine, temperature is an important controlling mechanism (Fenner, 2000; Grace et al., 2002), and warming will consequently affect both extant plant communities in the alpine, and invaders. Warming of the alpine has led to earlier snowmelt, resulting in a prolonged growing season (Espinosa del Alba et al., 2025; Milbau et al., 2009; Zhang et al., 2025). Cold-adapted alpine species will be greatly affected by such environmental alterations, e.g. by earlier flowering disrupting the synchronization with pollinators, potentially causing reduced reproductive success and weakening the plants' resistance to invasions (Espinosa del Alba et al., 2025; Zhang et al., 2025). Even though seedling emergence and survival responses to warming are species-specific (Lett & Dorrepaal, 2018), warmer conditions are also found to increase reproduction and growth of shrubs and tall stature plants (Fazlioglu & Wan, 2021; Klanderud, 2008). These are traits common in alpine invaders, and increase invaders' chances of seedling survival through the prolonged growing season (Ali et al., 2022; Milbau et al., 2009; Munier et al., 2010). Warming of the alpine could thus facilitate new species' recruitment and establishment in alpine regions and weaken alpine species persistence.

In addition to temperature, other abiotic factors like water, snow, nutrients and light affect seed germination and seedling establishment in the alpine (Lett & Dorrepaal, 2018). Particularly small-seeded plants depend on light and temperature cues for germination (Bu et al., 2017; Ma et al., 2023; Pons, 2000), making them sensitive to environmental changes. Increased temperatures could lead to reduced snowpack during winter and to precipitation falling as rain rather than snow, which could increase the risk of frost damage to plants and lead to early germinating, vulnerable seedlings (Davis & Gedalof, 2018; Hansson et al., 2021). Sufficient moisture levels in the soil is also crucial for seedlings in alpine environments (Forbis, 2003; Lazarus et al., 2018; Shevtsova et al., 2009), and acts as a cue for germination in many species (Lett & Dorrepaal, 2018). Soil moisture can be affected by temperature as well, as higher temperatures in the alpine could result in higher evaporation

(Dahle et al., 2024; Gya et al., 2023) and cause summer drought. The drier conditions could reduce germination and, due to seedlings shallow roots and lack of a periderm, contribute to decreased seedling growth and increased seedling mortality (Gya et al., 2023; Hankin et al., 2025; Lazarus et al., 2018; Orsenigo et al., 2015). The soil chemistry and structure at high elevation alpine sites vary from soil at lower elevations, which can also reduce seedling germination and survival of boreal plants in the alpine (Davis et al., 2018). All these environmental factors vary greatly across the mosaic alpine landscape (Körner & Hiltbrunner, 2021), and seedling responses in different alpine habitats could vary accordingly. Therefore, studying seedling emergence and establishment across a variety of alpine habitats would add to the total understanding of how range shifts will occur, and could aid in understanding what alpine habitat types are the most susceptible to invasion.

Biotic interactions play important roles in the success of individual species in plant communities, and as new species assemblages occur due to shifting ranges these interactions will be altered (Alexander et al., 2015; Chardon et al., 2023; Chen et al., 2011). Plants in the harsh alpine environments have developed resource conservative life strategies and are typically found in facilitative and neutral plant-plant interactions (Olsen et al., 2016). At the other end of the stress-gradient, less stressful lowland environments allow for both resource acquisitive and conservative plants, and competition (for light, nutrients, etc) is the dominating plant-plant interaction (Callaway et al., 2002). This is the basis for the ‘stress gradient hypothesis’ (SGH) posed by Bertness and Callaway (1994), which has been tested and supported by a variety of studies and reviews (Cavieres, 2021; He et al., 2013; Klanderud et al., 2015; Klanderud et al., 2017). This shift in the nature of plant-plant interactions along the stress gradient, as proposed in the SGH, suggests that warming will increase the interspecific competition in alpine habitats, especially at the warmer edge of species’ ranges where co-existence is more likely (IPBES, 2018; Lurgi et al., 2012; Olsen et al., 2016). Notably, the facilitative plant-plant interactions in alpine environments could accelerate the boreal plants’ germination and establishment in the alpine under current climates. However, as temperature stress is reduced with continued warming, a shift towards more competitive interactions between plants in the alpine could potentially hinder future range shifts into the alpine (Dahle et al., 2024). Seedling recruitment in new areas is thus controlled not only by abiotic conditions but also affected by biotic conditions through interactions with surrounding vegetation (Lett & Dorrepaal, 2018; Olsen & Klanderud, 2014), with important implications for alpine species’ persistence. Yet, our understanding of how biotic interactions affect species range shifts under varying, site-specific habitat conditions remains limited and calls for further research.

The role of biotic interactions in plant establishment is not fixed but can vary across different stages of plant development. At early stages, neighbouring plants can facilitate germination by retaining ground moisture and providing protection (Chen et al., 2011), but they may also hinder seeds from reaching the soil and reduce light availability (Graae et al., 2011). Abiotic factors such as temperature and moisture often play an important role early on, while biotic interactions become increasingly important at later stages of plant establishment and growth (Klanderud et al., 2021; Olsen & Klanderud, 2014). Alpine species may be particularly vulnerable to competition at these later stages. They often lack competitive traits required for resisting seedling emergence and establishment, due to lower above-ground plant-biomass, smaller leaf areas and shorter stature than their lowland counterparts (Meineri et al., 2020). This could make them more open to invasion. Consequently, the effects of biotic interactions on seed germination and survival are likely to vary between species, environmental conditions, and throughout plant ontogeny. This complexity makes it difficult to predict how establishment, growth and survival of boreal species in the alpine will be affected by biotic interactions, both under current and future climates, and in different alpine habitats. Disentangling this complexity calls for more research spanning all phases of plant establishment, from germination to seedling growth and survival and ultimately flowering and reproduction, and how all these stages are shaped by biotic interactions.

Aim and hypotheses of the study

The aim of this study is to explore how germination, growth and seedling survival of boreal species is affected by biotic interactions in an alpine environment. I also aim to explore how these effects vary between alpine habitats with different environmental conditions, and between lab conditions and alpine sites. Lastly, I aim to explore how neighbouring species composition relates to the germination, survival and seedling traits. This will be tested through a seed sowing experiment of three common sub-alpine native plant species, *Betula pubescens, Potentilla erecta* and *Chamaepericlymenum suecicum*, in the lab, and in extant vegetation vs in experimentally created gaps in four major alpine habitat types at Finse in Southern Norway, with the goal of answering the following research questions:

I. How was germination (%) in the lab compared to at the alpine sites? How did the total alpine germination (%) and survival (%) vary between the treatments (control and removal) and habitat types (leeside, meadow, ridge and snowbed) ?
II. How did seedling height, number of leaves and length of longest leaf vary between treatments and habitat types?
III. How do surrounding plant community composition and environmental conditions (vegetation cover and height, and soil moisture) relate to seed germination, seedling survival and seedling traits (height, number of leaves, leaf length)?

Due to plants' sensitivity for environmental conditions, I expect higher germination in the lab than in the field. At the alpine site, I hypothesize that germination will be highest in removal plots due to reduced competition, but that survival rates will be highest in control plots due to facilitation from the existing vegetation. Germination and survival are expected to be lowest on the exposed and dry ridge. I also expect seedlings to grow taller and grow more, and longer, leaves in control plots and in the more productive habitats, meadow and leeside, due to facilitation. I expect soil moisture to be a key factor shaping species composition in the neighbouring plant communities and to be positively associated with germination, survival and seedling traits. Lastly, I hypothesize that cover of vascular plants will be positively associated with germination, survival and seedling traits due to facilitation.

Method

Study site

The study was conducted close to the Finse Alpine Research Centre, in Ulvik municipality in south-western Norway (Figure 1). Finse is located at approximately 1222 m.a.s.l. in the low-alpine zone. Bryn and Horvath (2020) found the nature types, in this thesis referred to as ‘habitat types’, ridge, leeside, semi-natural meadow and snowbed to be dominant in the area, using the NiN 2 system (Bryn et al., 2018; Bryn & Ullerud, 2018). Granite is the dominant bedrock in the area around Finse Alpine Research Centre (Askvik, 2008), resulting in nutrient poor soils. This results in plant communities composed of cold-adapted species with low nutrient demands, such as *Vaccinum myrtillus, Empetrum nigrum, Salix herbacea* and *Carex bigelowii*.

The growing season at Finse is short, usually with a snow-free period from late June to the end of September (Seklima.no, 2024). The annual precipitation is about 750 mm, with the heaviest precipitation in late summer to early autumn (Seklima.no, 2024; Senorge.no, 2024). Over the last five growing seasons the average temperature has been 7.3˚C, while the annual average has been -0.7˚C (Seklima.no, 2024).

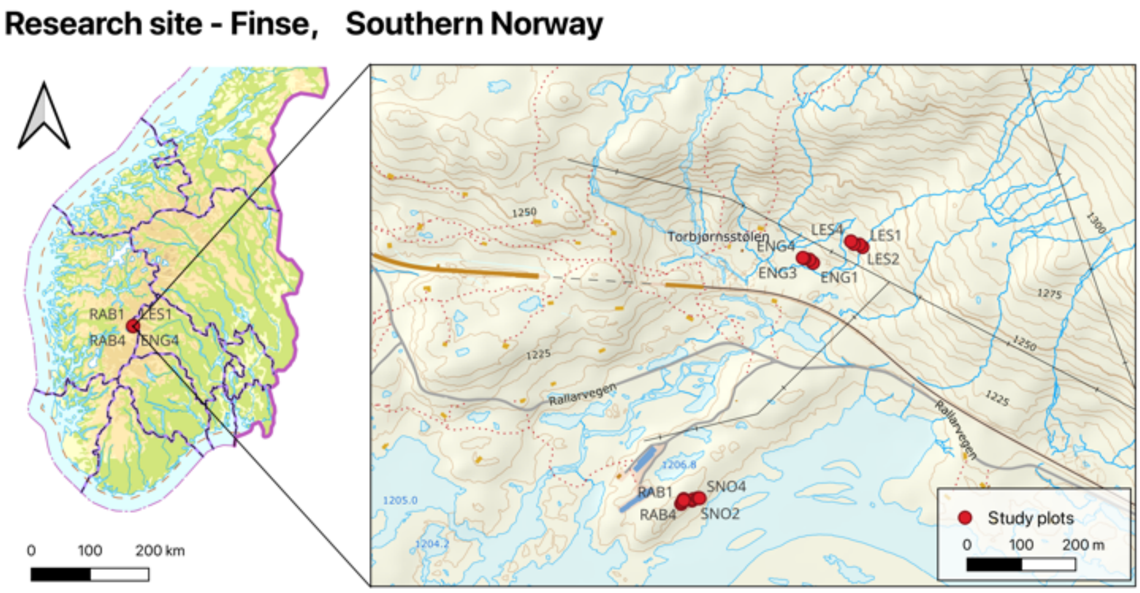

Figure 1. Location of the study site at Finse, Southern Norway. Red dots mark the locations of the plots, labelled with habitat type and replicate number. Ridge (RAB) and snowbed (SNO) plots were situated close to the main buildings of the Finse Alpine Research Centre, south of the railway tracks (brown line). The meadow (ENG) and leeside (LES) plots were situated close to Torbjørnsstølen,

north of the railway tracks. Figure made with QGIS version 3.40 (QGIS.org, 2024). Background map: Topographical map of Norway (Kartverket, 2024).

Experimental design

Seed sampling and plot establishment

Three common plant species found in the sub-alpine area Geilo (790 m.a.s.l.), close to Finse and easily accessible, were selected as target species: the tree species *Betula pubescens* and the forbs *Potentilla erecta* and *Chamaepericlymenum suecicum*. These species were chosen because they represent distinct growth forms (tree vs forbs) and have different seed traits (large; *C. suecicum,* vs small seeds; *B. pubescens* and *P. erecta*) and may exhibit dissimilar developments in the different vegetation types. Approximately 1000 ripe seeds of each species were collected at the end of August 2023, at Geilo, Norway.

Experimental plots of 10 cm × 10 cm were established in the four dominant habitat types at Finse (ridge, leeside, semi-natural meadow and snowbed). Half of the plots consisted of intact alpine vegetation (treatment: control) while in the other half vegetation gaps were created, by cutting loose vegetation using scissors and then removed (treatment: removal) (Figure 2). One plot of each treatment was established close to each other, as paired plots. In each vegetation type four replicates of plot pairs were established, resulting in eight plots in each of the four vegetation types, for a total of 32 experimental plots (Figure 1). In mid-September 2023, 30 seeds of each of the collected species were randomly mixed and sown in the experimental plots.

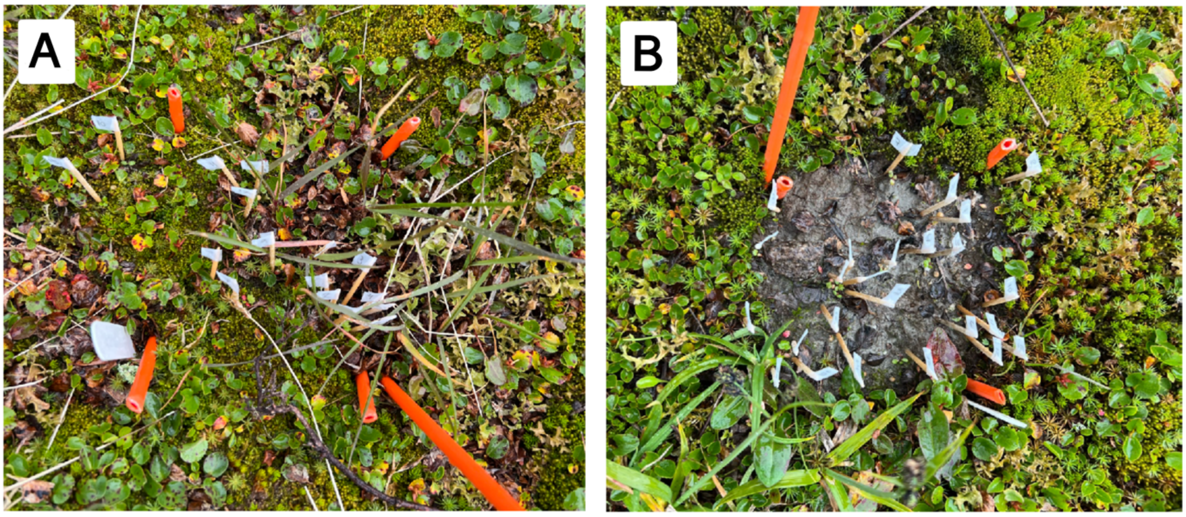

Figure 2. Paired research plots at Finse. Control plot (A) and removal plot (B) in snowbed. Seedlings marked by flags, and plots marked by plastic tubes in the ground.

Germination rate experiment

The left-over seeds of *B. pubescens* and *P. erecta* were used for an indoor germination experiment conducted in the lab, to determine the seeds germination rates. After collection, the seeds were stored in dry bags in the fridge (4˚C) until December, then vernalized outdoors in a closed box under ambient temperature until February. At that point, twenty seeds of each species were randomly selected and stratified on damp paper towels and placed in plastic bags in the fridge (4˚C) for 4-6 weeks. After stratification they were sown in moist soil in germination trays and left under growth lights (approx. 20˚C) and watered every day for approximately one month. The seedlings were counted and marked daily, and their germination and survival recorded (Figure 3).

Figure 3. Laboratory germination rate experiment. Seedlings were marked with the date of emergence.

Seedling surveys and vegetation analyses

From the end of June to the end of September 2024 the experimental plots at Finse were visited about every two weeks to record seedling germination, survival and growth. At all visits new seedlings were marked, and the traits (number of leaves, seedling height and length of longest leaf) of all seedlings were measured (in mm, using a ruler). In addition, soil moisture was measured on all four sides of the plots using a Delta-T SM150 moisture meter (Delta-T Devices Ltd., England). At the end of the growing season, when seedlings had developed sufficiently, the species identity was recorded for all seedlings.

Vegetation analyses were conducted in early August, at peak growing season. The analyses were done in 25 cm × 25 cm plots, divided into 25 5 cm × 5 cm sub-plots, which were placed midway between the paired control/removal plots (Figure 4). This was done for all the 16 plot pairs. In each sub-plot, presence of all vascular plant species and lichens was recorded, and fertile individuals noted. In the plot as a whole, vegetation cover (in %) of each vascular species was estimated visually, as well as the total cover of vascular plants, unidentified seedlings, lichens, bryophytes, bare soil, rock and litter. NDVI was measured from all four sides of the plots using a handheld Greenseeker (Trimble Inc., USA). Vegetation height (mm) was measured in four sub-plots (7, 9, 17 and 19) in all vegetation plots (Figure 4).

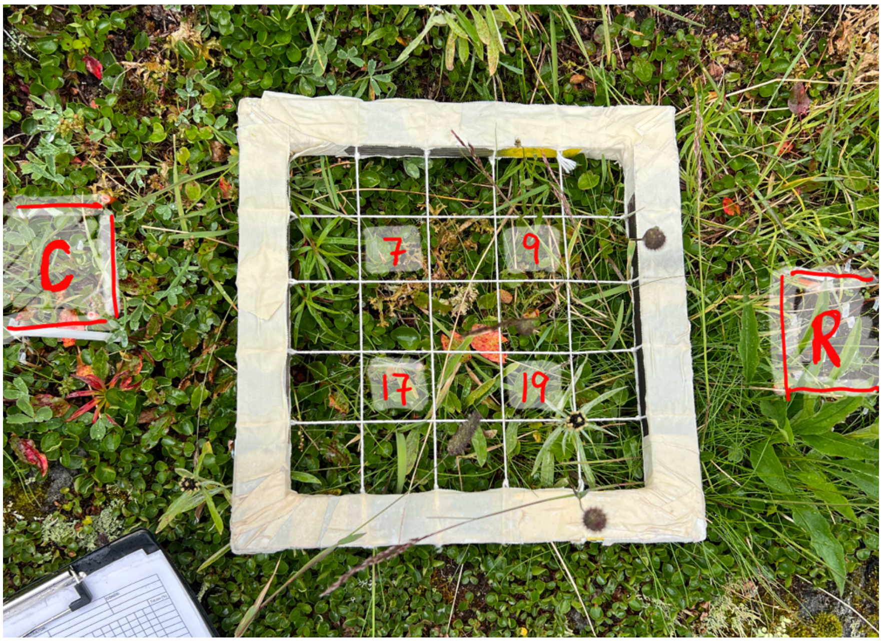

Figure 4. Vegetation plot divided into 25 sub-plots, placed between adjacent control (C) and removal (R) seed sowing plots. Sub-plot 7, 9, 17 and 19, where vegetation heigh was measured, are marked.

Data analysis and statistics

Software and packages

Statistical analyses were conducted in R version 4.4.2 (R Core Team, 2024) using R Studio version 2024.9.1.394 (Posit team, 2024). The R-package ‘readxl’ (Wickham & Bryan, 2023) was used for loading data, and the packages ‘ggplot2’, ‘tidyr’ and ‘dplyr’ from ‘tidyverse’ were used to organize data and create figures (Wickham et al., 2019). For extracting raw data tables the package ‘writexl’ (Ooms, 2024) was used, and the packages ‘sjPlot’ (Lüdecke, 2024) and ‘kableExtra’ (Zhu, 2024) were used to create output tables from regression analyses and post-hoc tests. For solving errors and for coding assistance, and for academic language improvement throughout the writing phase, the OpenAI language model ChatGPT was used (OpenAI, 2025).

Soil moisture analysis

To test for differences in soil moisture between the habitat types, I did a one-way ANOVA of average soil moisture per habitat type after verifying that the assumptions for ANOVA were met. This was done by conducting a Shapiro-Wilk normality test with the base R ‘shapiro.test’ function, and a Levene’s test for homogeneity of variances by using the ‘leveneTest’ function from the ‘car’ package (Fox & Weisberg, 2019). Soil moisture values were log-transformed for the analysis. The ANOVA was performed using the ‘aov’ function, followed by a Tukey’s post-hoc test to identify soil moisture levels, using the ‘TukeyHSD’ function. This gradient was then used to establish the order of habitat types in subsequent analyses.

Mixed-effect regression model selection

To test for differences in germination rate, survival rate and seedling growth (seedling height, number of leaves and length of longest leaf) between treatments and habitat types, I conducted mixed-model regression analyses using the distribution that best fitted the data (for more details about the individual models, see below). I started out with the most complex appropriate mixed regression model and then removed non-significant interactions (backwards selection). Models were further evaluated by performing residual diagnostics using the ‘DHARMa’ package (Hartig, 2024). If multiple models fit the data, and residual diagnostics were good, I used Akaike’s Information Criterion (AIC) and selected the model with the lowest AIC-value (Akaike, 1974).

Germination and survival rate analyses

To statistically test for differences in germination rates between the treatments and habitat types I fitted a binomial distributed GLMM with a logit-link function, using the ‘glmmTMB’ package (Brooks et al., 2017). Germination rate (germinated seeds/total sown) was used as response variable in the model. Treatment and habitat type were used as fixed effects, and the interaction between these was removed due to its non-significant effect. The random effects included in the model were paired plots (adjacent control and removal plots) and species. A pairwise post-hoc test was performed using the ‘emmeans’ package (Lenth, 2024).

In further analyses of survival rates and seedling traits, the leeside and ridge habitats were excluded, as no seedlings of the studied species emerged in control plots in these habitats. To test for differences in survival rates between the treatments and the two remaining habitat types, a beta GLMM with a logit-link function from the package ‘glmmTMB’ was used (Brooks et al., 2017). The model type handles continuous proportions between 0 and 1, and I thus added/subtracted a small value from zeros and ones ($* 0.999 + 0.0005$) to fit within the interval. The transformed survival rate was used as response variable, treatment and habitat type and their interaction were used as fixed effects, and plot pair and species as random effects. The interaction between the fixed effects was not significant and therefore removed.

Seedling trait analyses

To account for variation in morphology between the sown species, they were analysed separately when comparing seedling height, number of leaves and leaf length between the habitat types and treatments (see details below). Due to a very low germination rate in *C. suecicum,* this species was excluded from the analyses. The maximum value of each trait per seedling was used for the analyses.

To compare seedling height of *B. pubescens* seedlings between treatments and the two remaining habitat types, an LMM with maximum seedling height as response variable was fitted by REML, using the 'lme4' package (Bates et al., 2015). Paired plots were included as random effects, and treatment, habitat type and their interactions were used as fixed effects. The model returned a warning for singular fit and was therefore reduced to a linear model without random effects, which returned the exact same result as the mixed model but without the warning. Despite the singular fit warning, the LMM was retained due to the importance of accounting for random effects and for consistency with other models. The same mixed model structure was used to analyse *P. erecta* seedling height. The interaction between treatment and habitat type was retained in this model despite not being significant, due to a near-significant effect.

Differences in number of leaves of *B. pubescens* seedlings were tested through a Conway-Maxwell Poisson regression model (compois family), using the 'glmmTMB' package (Brooks et al., 2017). This kind of Poisson model handles under-dispersed data and small sample sizes while still allowing for random effects (Shmueli et al., 2005). Number of leaves was used as response variable, paired plots added as random effects, and treatment and habitat type as fixed effects. The interaction between the fixed effects was non-significant and therefore removed. A model with the same structure was used to analyse number of leaves of *P. erecta* seedlings. The interaction between treatment and habitat type was significant in this model and thus included.

A Conway-Maxwell Poisson regression model was fitted to test differences in *B. pubescens* leaf length between treatments and habitat types, with leaf length as response variable, plot pair as a random effect and treatment and habitat type as fixed effects. This model was chosen due to a Poisson-like distribution and under-dispersion of the data. The interaction between treatment and habitat type was not significant and therefore excluded. To analyse leaf length of *P. erecta* seedlings the same model structure was used. The interaction between the fixed effects was non-significant in this case too and thus removed.

Ordination of plant community and environmental data

To visualize the relationship between germination, survival and seedling traits, and environmental factors and species composition in the neighbouring vegetation, a non-metric multidimensional scaling (NMDS) ordination with two dimensions and Bray-Curtis dissimilarity measures was performed. The ‘metaMDS’ function from the ‘vegan’ package (Oksanen et al., 2024) was used to conduct the ordination, and the ‘scores’ function from the same package was used to extract axis scores for species and sites. An environmental fitting analysis (envfit) was performed to assess how the recorded environmental variables (vegetation height, soil moisture, NDVI, cover of different functional groups, total vascular plant cover and seedling height, number of leaves and leaf length) correlated with the ordination axes. The results were extracted as vectors for visualisation.

Results

Soil moisture gradient

The ANOVA of soil moisture revealed significant differences in soil moisture between the habitat types, and post-hoc results suggested the following soil-moisture gradient from the dryest to wettest habitat: Leeside < Meadow < Ridge < Snowbed (see Appendix Table 1 for details). This order was used in the proceeding regression analyses.

Germination and survival

The rates of germination in the indoor germination experiment were higher than at the alpine research site for both *Betula pubescens* and *Potentilla erecta,* the two species tested in the lab (Table 1). *B. pubescens* germinated at a rate of 7.8% in the alpine sites, while indoors the rate was at 26.4%. *P. erecta* had a higher germination rate, at 12.3% at the alpine research sites and 42.9% in the lab. The ratio between lab germination and alpine germination was ≈ 3.4:1 for both species. *Chamaepericlymenum suecicum* also germinated at the alpine sites, but at a very low rate (Table 1).

*Table 1. Number of sown seeds, number of germinated seeds and germination rates (%) of the studied species (*B. pubescens, C. suecicum *and* P. erecta*) in the lab experiment vs at the alpine site.*

Species	# Sown lab	# Germin. lab	Germination rate lab (%)	# Sown field	# Germin. alpine	Germ. rate alpine (%)
B. pubescens	148	39	26.4	960	75	7.8
C. suecicum	0	-	-	960	10	1.0
P. erecta	84	36	42.9	960	118	12.3

Germination occurred under both removal treatment and in control plots (Table 2), but the GLMM analysis showed significantly higher germination under removal treatment (Table 3). The overall highest germination rates occurred in removal plots in the snowbed and removal plots in the meadow (Figure 5). No seeds germinated in control plots in the leeside, nor in control plots in the ridge (Figure 5). Seeds germinated in all four studied habitat types, at the highest rate in the snowbed and lowest rates in the leeside (Table 2). The GLMM analysis showed that germination rates were significantly higher in the snowbed and near-significantly higher in meadow plots compared to in the leeside (Table 3). Post-hoc testing did not show the same significant differences but supported a trend of higher germination rates in snowbed than leeside (see Appendix Table 2).

Survival of seedlings was high across both treatments (Figure 5), with significantly higher rates in removal plots (Table 3). Survival of the seedlings was also high across all four habitat types, with the highest rate in the snowbed and lowest on the ridge (Table 2). The GLMM analysis showed no significant differences in survival rate between meadow and snowbed plots (Table 3).

Table 2. Seedling germination, survival and deaths, both in numbers of seedlings and rates (%), across all studied species. Numbers and rates are given per treatment (control and removal) and habitat type (leeside, ridge, meadow and snowbed).

		Germinated (# total)	**Germination rate (%)**	**Survived (# total)**	**Survival rate (%)**	**Dead (# total)**	**Death rate (%)**
Habitat type	Leeside	25	3.5	23	92.0	2	8.0
	Meadow	58	8.1	54	93.1	4	6.9
	Ridge	44	6.1	37	84.1	7	15.9
	Snowbed	76	10.6	73	96.1	3	3.9
Treatment							
	Control	23	1.6	21	91.3	2	8.7
	Removal	180	12.5	166	92.2	14	7.8

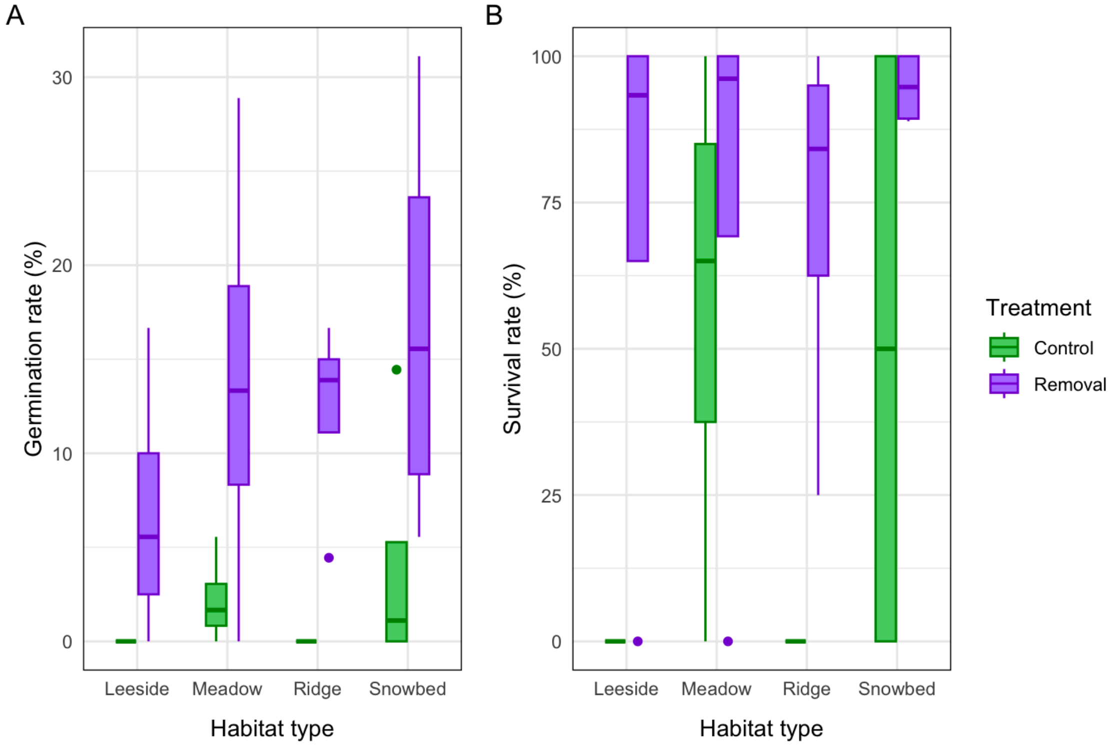

Figure 5. Germination (%) (A) and survival rates (%) (B) of seedlings across plots in the alpine research site at Finse. Rates are visualized per treatment: control (green) and removal (purple), within four habitat types, following the soil-moisture gradient (leeside, meadow, ridge and snowbed).

Table 3. Results from a binomial GLMM test for total germination rate under the different treatments (control and removal), and in the different habitat types (leeside (intercept), meadow, ridge and snowbed), and from a beta GLMM test for total survival rate, under the different treatments (control and removal) and habitat types (meadow (intercept) and snowbed). Estimated differences in germination and survival rates are given on the log-odds (logit) scale, and are followed by standard errors (SE), 95% confidence intervals (CI) and p-values. Significant p-values (< 0.05) are in bold.

	Estimate	SE	CI	p
Germination rate				
Intercept	-6.01	0.60	-7.18 – -4.83	**<0.001**
Treatment: removal	2.37	0.23	1.92 – 2.83	**<0.001**
Habitat type: meadow	1.22	0.71	-0.18 – 2.61	0.088
Habitat type: ridge	0.90	0.72	-0.50 – 2.31	0.207
Habitat type: snowbed	1.68	0.71	0.29 – 3.06	**0.018**
Survival rate				
(Intercept)	-0.67	0.35	-1.36 – 0.02	**0.057**
Treatment: removal	0.98	0.41	0.17 – 1.79	**0.017**
Habitat type: snowbed	0.24	0.39	-0.52 – 1.01	0.532

Seedling growth

The seedlings of both species were significantly shorter in removal plots than in the control plots (Table 4, Figure 6). A significant interaction in the *B. pubescens* model, and a near significant interaction in the *P. erecta* model revealed that the effect of removal treatment on seedling height was smaller in snowbed plots than in the meadow (Table 4). Both *B. pubescens* and *P. erecta* seedlings were tallest in meadow plots (Figure 6), and significantly shorter in the snowbed compared to the meadow (Table 4).

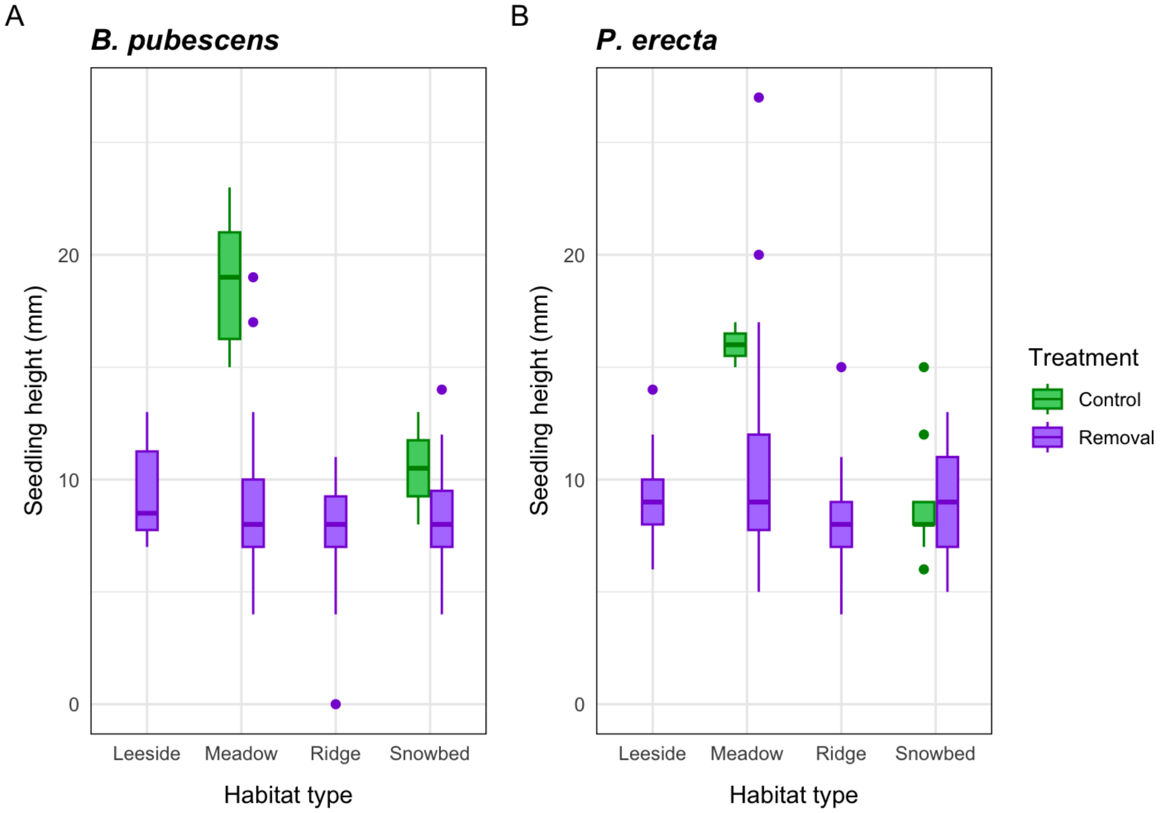

Figure 6. Seedling height (mm) for B. pubescens *(A) and* P. erecta *(B) across plots at Finse. Heights are visualized per treatment: control (green) and removal (purple), within four habitat types (leeside, meadow, ridge and snowbed).*

Table 4. Results from LMM tests for seedling height of B. pubescens *and* P. erecta *seedlings across the treatments (control (intercept) and removal) and between the different habitat types (meadow (intercept) and snowbed). Estimates are given with standard errors (SE), 95% confidence intervals (CI) and p-values. Significant p-values (< 0.05) are in bold.*

	Estimates	SE	CI	p
B. pubescens				
(Intercept)	18.83	1.27	16.27 – 21.40	**<0.001**
Treatment: removal	-9.98	1.44	-12.88 – -7.07	**<0.001**
Habitat type: snowbed	-8.33	2.55	-13.46 – -3.20	**0.002**
Treatment: removal × Habitat type: snowbed	7.87	2.72	2.40 – 13.34	**0.006**
P. erecta				
(Intercept)	16.02	2.50	11.04 – 21.01	**<0.001**
Treatment: removal	-5.98	2.51	-11.00 – -0.97	**0.020**
Habitat type: snowbed	-6.21	2.94	-12.09 – -0.34	**0.039**
Treatment: removal × Habitat type: snowbed	4.91	2.77	-0.61 – 10.44	0.080

Overall, fewer leaves were recorded on *B. pubescens* seedlings than on *P. erecta* seedlings (Figure 7). Seedlings of both species had significantly more leaves in removal plots than in control plots, but for *P. erecta* a significant interaction between snowbed and removal revealed that this effect was reduced in the meadow (Figure 7, Table 5). There were no significant differences in leaf number of *B. pubescens* between the habitat types, while *P. erecta* seedlings had significantly more leaves per seedling in the snowbed than in the meadow (Figure 7, Table 5).

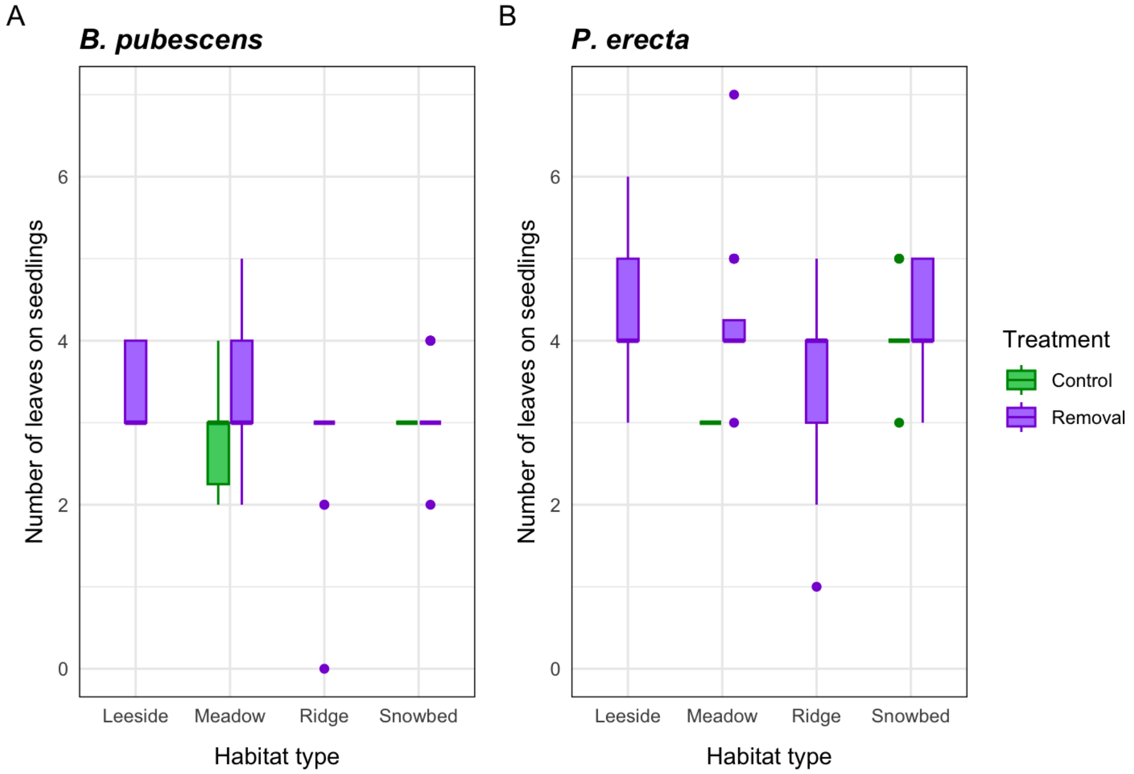

Figure 7. Number of leaves on B. pubescens *(A) and* P. erecta *seedlings (B) across plots at Finse. Number of leaves are visualized per treatment: control plots (green) and removal plots (purple), within four habitat types (leeside, meadow, ridge and snowbed).*

Table 5. Results from Conway-Maxwell Poisson model tests of number of leaves of B. pubescens *and* P. erecta *seedlings across the treatments (control (intercept) and removal) and habitat types (meadow (intercept) and snowbed). The table presents estimates followed by standard errors (SE), 95% confidence intervals (CI) and p-values. Significant p-values (< 0.05) are in bold.*

Predictors	Estimates	SE	CI	p
B. pubescens				
(Intercept)	1.08	0.07	0.93 – 1.22	**<0.001**
Treatment: removal	0.16	0.08	0.01 – 0.32	**0.043**
Habitat type: snowbed	-0.09	0.06	-0.21 – 0.02	0.114
P. erecta				
(Intercept)	1.05	0.12	0.81 – 1.29	**<0.001**
Treatment: removal	0.41	0.12	0.16 – 0.65	**0.001**
Habitat type: snowbed	0.43	0.14	0.16 – 0.71	**0.002**
Treatment: removal × Habitat type: snowbed	-0.46	0.14	-0.73 – -0.19	**0.001**

Seedlings of *P. erecta* generally had longer leaves than *B. pubescens* seedlings (Figure 8). There were no significant differences in leaf length between the treatments, nor between the habitats, for any of the species (Table 6).

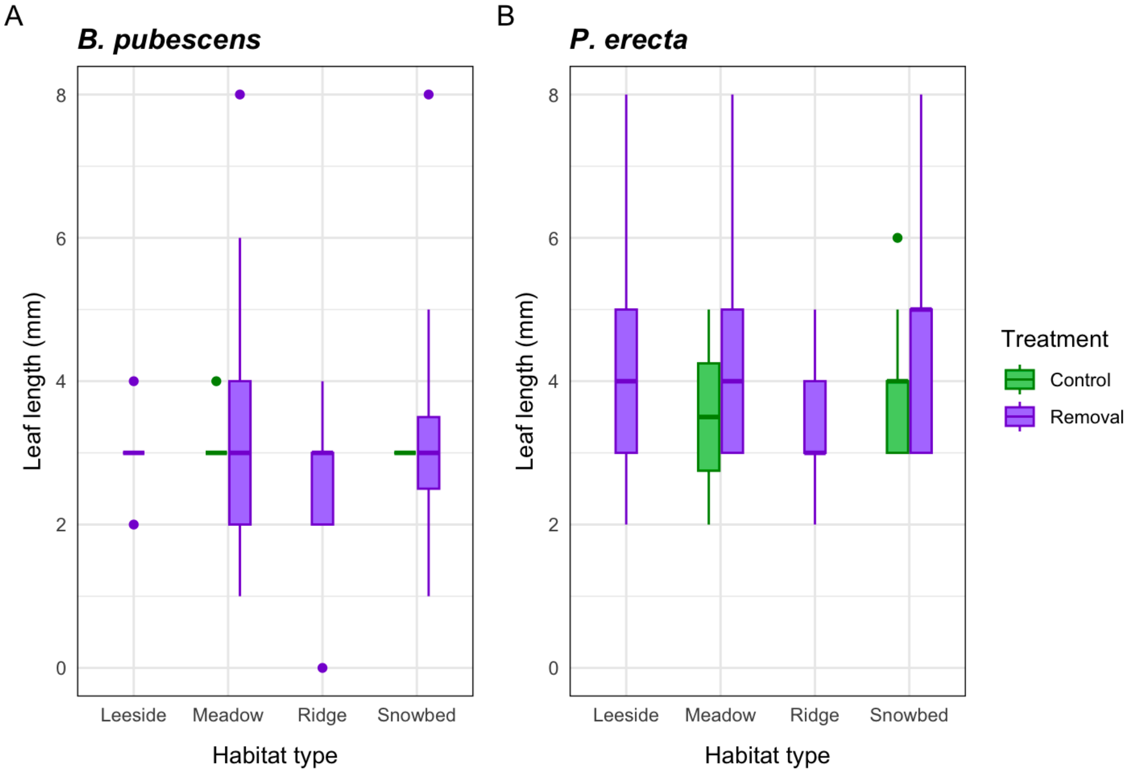

Figure 8. Length of the longest leaf of B. pubescens *(A) and* P. erecta *(B) seedlings across plots at Finse. Leaf lengths are visualized per treatment: control plots (green) and removal plots (purple), within four habitats (leeside, meadow, ridge and snowbed).*

Table 6. Results from Conway-Maxwell Poisson regression models on length of longest leaf of B. pubescens *and* P. erecta *seedlings across the treatments (control (intercept) and removal) and habitat types (meadow (intercept) and snowbed). Estimates are followed by standard errors (SE), 95% confidence intervals (CI) and p-values. Significant p-values (< 0.05) are in bold.*

	Estimates	SE	CI	p
B. pubescens				
(Intercept)	3.19	0.56	2.27 – 4.49	**<0.001**
Treatment: removal	1.05	0.18	0.76 – 1.47	0.758
Habitat type: snowbed	0.84	0.16	0.58 – 1.22	0.353
P. erecta				
(Intercept)	1.40	0.12	1.16 – 1.63	**<0.001**
Treatment: removal	0.07	0.09	-0.11 – 0.25	0.457
Habitat type: snowbed	0.03	0.12	-0.21 – 0.26	0.835

Neighbour community and environmental effects on the sown species

The NMDS ordination showed clear variation in species composition between the habitat types (Figure 9). Ridge plots were grouped tightly, indicating high similarity in species composition dominated by mainly lichen and shrub species, and lichen cover (significant) (Figure 9, Table 7). The other habitats were also grouped but showed larger variation in species composition. One snowbed plot diverged from the others, positioned between the leeside plots and the meadow plots. A few forbs and graminoids, and the dwarf shrub *Vaccinium myrtillus*, clustered around the leeside plots, which aligned with vegetation height and bryophyte cover (significant in envfit analysis; Table 7, Figure 9). Meadow plots were associated with greater forb and graminoid diversity and the shrub *Salix herbacea,* and aligned with total graminoid cover (significant in envfit analysis; Table 7, Figure 9). Graminoid and forb species clustered around the three grouped snowbed plots, and cover of un-identified, naturally recruited seedlings (significant in envfit) pointed in their direction (Figure 9, Table 7). Total forb and vascular plant cover, as well as NDVI (all significant in envfit analysis, Table 7) pointed towards the outlier snowbed plot (Figure 9). Soil moisture, a significant explanatory variable for the species composition in the envfit-analysis (Table 7), aligned with the grouped snowbed plots (Figure 9).

The seed germination and seedling survival variables aligned with the snowbed plots, almost pointing the same direction as soil moisture and away from leeside plots (Figure 9). Seedling height and number of leaves pointed towards the outlier snowbed plot, and away from the lichen species and cover, and ridge plots (Figure 9). Leaf length pointed between meadow and snowbed plots, aligning with cover of seedlings, and away from the leeside plots (Figure 9).

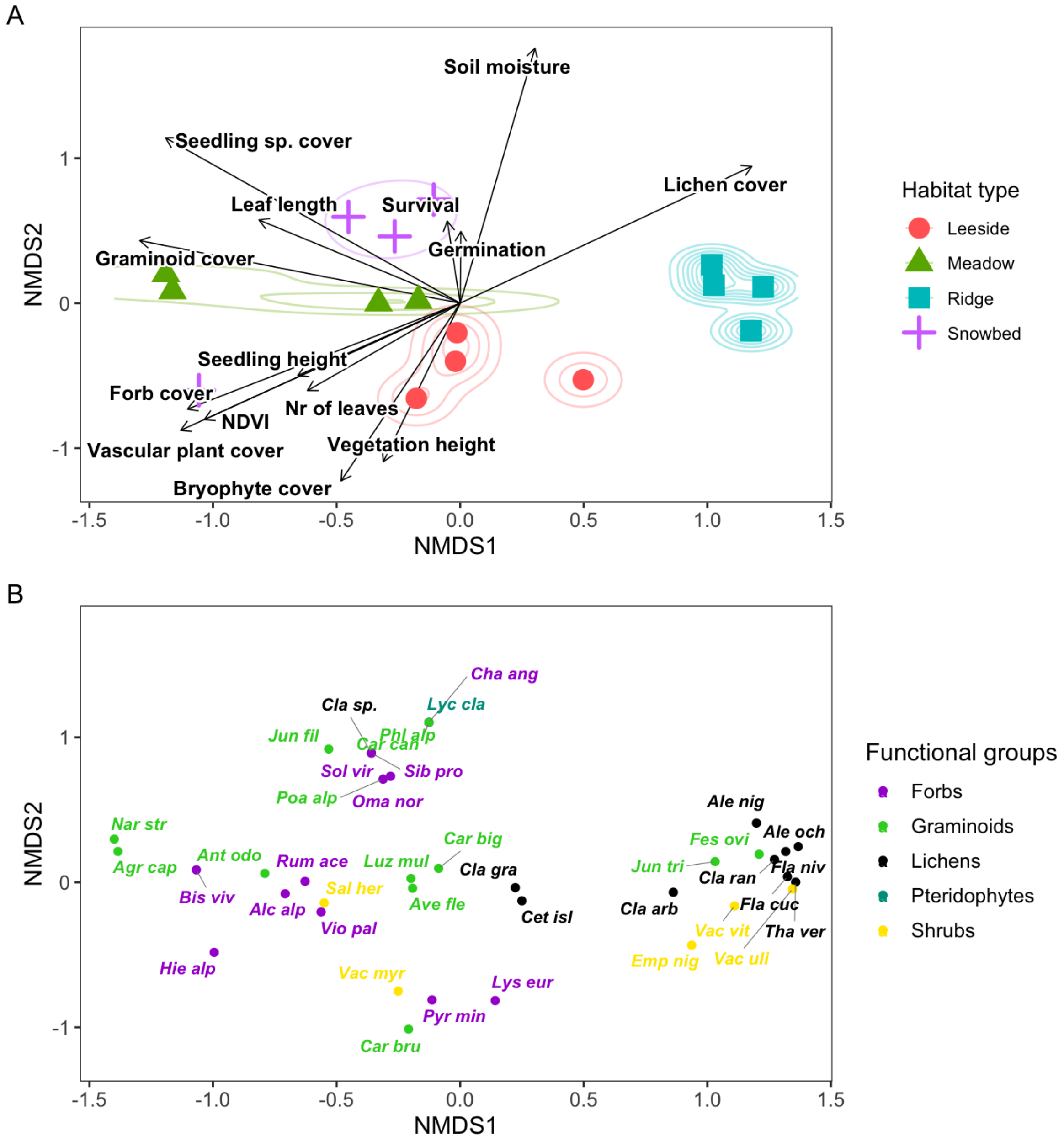

Figure 9. Non-metric multidimensional scaling (NMDS) environmental/vegetation variables and species composition. Plots for this analysis were located between control and removal plots. A) Distribution of vegetation plots along the two NMDS-axes. Symbols represent the individual vegetation plots, coloured per habitat type (leeside, meadow, ridge, snowbed), with 2D kernel-density contours indicating clustering patterns. Arrows represent significant environmental variables from the envfit analysis, and include soil moisture, NDVI, vegetation height, cover of functional groups, as well as total cover of vascular plants and naturally recruited seedlings (sp.). Seedling variables (number germinated, number survived, average seedling height, average number of leaves and average leaf length of the longest leaf) are also shown with arrows and included regardless of significance. Arrow direction indicate association with species (B), arrow length indicates strength of the association. B) Species composition and distribution along the two NMDS-axes. Species are coloured according to functional group and labelled with abbreviated names (full list in Appendix Table 3).

Table 7. Envfit analysis results from the NMDS ordination showing Pearson correlation coefficients for NMDS1 and NMDS2 of each environmental/vegetation variable. Correlation coefficients are followed by the squared correlation coefficients (r^2), indicating the proportion of species composition variation that can be explained by the variable. P-values indicate the statistical significance of the correlation. Significant p-values (< 0.05) are in bold and included as vectors in the NMDS plot. Germination and survival of seedlings, and seedling height, number of leaves and leaf length are included as vectors in the ordination plot despite not being significant.

	NMDS1 Correlation	NMDS2 Correlation	r^2	p
Bare soil cover	-0.0685034	0.3400932	0.1203561	0.561
Bryophyte cover	-0.2409232	-0.6126315	0.4333614	**0.042**
Forb cover	-0.5517006	-0.3652411	0.4377746	**0.011**
Germination	0.0013171	0.2474924	0.0612542	0.707
Graminoid cover	-0.6483721	0.2159445	0.4670184	**0.006**
Lichen cover	0.5900030	0.4722611	0.5711341	**0.002**
Litter cover	-0.3061144	0.2817193	0.1730718	0.353
NDVI	-0.5176740	-0.4013420	0.4290618	**0.030**
Rock cover	0.0062807	0.3346755	0.1120471	0.529
Seedling height	-0.3284200	-0.2492297	0.1699751	0.360
Seedling leaf length	-0.4071236	0.2871416	0.2481999	0.207
Seedling nr of leaves	-0.3089826	-0.3014049	0.1863152	0.323
Seedling sp. cover	-0.5960837	0.5702025	0.6804467	**0.002**
Shrub cover	0.2767864	-0.2662254	0.1474867	0.383
Soil moisture	0.1512511	0.8792371	0.7959348	**0.001**
Survival	-0.0260659	0.2829161	0.0807209	0.648
Vascular plant cover	-0.5653754	-0.4382472	0.5117100	**0.011**
Vegetation height	-0.1555270	-0.5466059	0.3229667	0.119

Discussion

This study showed highest germination in removal plots and in the wetter habitat types. Seedling survival was significantly higher in removal plots than in controls but did not vary significantly between habitat types. Seedlings were tallest in control plots for both species, but with a reduced effect of treatment in snowbed plots, and taller in meadow than in snowbed. Both species had more leaves in removal plots and *P. erecta* seedlings had more leaves in snowbed plots than in the meadow. No significant differences in leaf length were detected for any of the species. Soil moisture explained much of the variation in species composition and was positively linked to germination and survival. Seedling traits seemed to positively correlate with forb and vascular plant cover and negatively correlate with lichens and shrubs.

Competition controls both seed germination and seedling survival

Germination was significantly higher in plots where vegetation was removed, as hypothesized, indicating that competition is the dominating plant-plant interaction acting at this stage of plant life-history. Results from similar studies in Southwestern Norway have demonstrated the same, e.g. Tingstad et al. (2015) found higher emergence of boreal conifer tree seedlings in gap plots compared to intact alpine vegetation. Klanderud et al. (2021) conducted a removal experiment in grasslands across environmental gradients in south-western Norway, sowing seeds from the local plant communities, and found, like my results also show, increased seedling emergence in gap plots. In another removal study from the same geographic area, Dahle et al. (2024) transplanted seeds of six sub-alpine species into alpine locations and found seedling emergence to be limited by competition. All these results, along with mine, imply that under extant alpine climates in the south of Norway, even the earliest stage of plant life-history is controlled by competition rather than facilitation.

Contrary to my hypothesis, seedling survival was also significantly higher in removal plots compared to in controls. Similarly, Marsman et al. (2021) performed a pine seed sowing experiment across alpine tundra plant communities at Dovrefjell, Norway, and found that 6.4 times more seedlings survived in plots where vegetation was removed compared to in intact vegetation. Removal of mosses also enhanced survival of *Betula pubescens* and *Pinus sylvestris* seedlings at the subarctic-alpine treeline in northern Sweden due to the release from competition (Lett et al., 2020). These findings are in line with my results and indicates that competition is the main plant-plant interaction acting on the early seedling survival too, not just on seed germination, even in alpine environments where neutral or facilitative interactions could be expected.

However, the role of biotic interactions on plant survival can vary across species, plant's life stages and local environmental context. While most studies examining seedling survival have had results similar to mine, by showing competition to dominate alpine seedling survival, some have yielded different results, suggesting facilitation to be more important. E.g., Jabis et al. (2020) found neighbouring plants to facilitate seedling survival of one species of *Pinus* in the alpine zone in the Colorado Rocky Mountains, indicating that the nature of biotic interactions depend on species or local environmental conditions. In southern Norway, Olsen et al. (2016) found that adult lowland generalist plants had higher population growth rates in plots where graminoids were removed across temperature and precipitation gradients, due to higher survival compared to control plots. The results of these studies supports my findings of competition dominating in the alpine, while a meta-analysis of the net-outcome of plant-plant interactions conducted by He et al. (2013) revealed that in cold climates, interactions measured as plant survival ranged from neutral to facilitative depending on the level of environmental stress. While Jabis et al. (2020) looked at seedling survival, like I did, Olsen et al. (2016) looked at adult plants and He et al. (2013) included all life stages. The contrasting results highlight that biotic interaction effects on plant survival vary across life-stages, and that it may depend on both local environments and on species.

The importance of soil moisture

Seed germination was higher under the controlled laboratory conditions than in the field, as hypothesized and found in other studies (Graae et al., 2011; Vandvik et al., 2017). At the alpine sites germination was highest in the snowbed, being the wettest habitat, intermediate in ridge and meadow (intermediate soil moisture), and lowest in the leeside, having the dryest soils of the study's habitats. The clear relationship between germination and soil moisture indicates that germination may be controlled by environmental variables like soil moisture, as also suggested by other studies (Bailey et al., 2021; Forbis, 2003; Graae et al., 2011; Welling & Laine, 2002). I did expect soil moisture to be important, and thus the germination to be lowest in the dryest habitat type, which resulted in my hypothesis partially being met.

In the NMDS, the alignment of germination, survival and soil moisture indicated soil moisture to be important for those variables, as supported by the germination results discussed above. Soil moisture also had the strongest correlation with species composition of all the tested variables in the NMDS, and thus significantly explained the variation in species composition in my vegetation plots, as I hypothesized. These findings are in line with results from a study in western Norway by Klanderud et al. (2015), where they found the impacts of the abiotic environment, such as precipitation, which greatly affects the soil moisture content, and temperature, to be determinant variables for species composition in the alpine. A global review by Seastedt and Oldfather (2021) also highlighted soil moisture and growing season duration to be of the most important structuring factors for plant community assemblages at high-elevation sites. Strong moisture gradients are created in the mosaic alpine landscapes, even at small spatial scale, hosting a wide variety of habitats, allowing higher biodiversity in small areas (Körner & Hiltbrunner, 2021). My findings highlight the sensitivity of alpine vegetation to soil moisture conditions, and the important role it plays in shaping the plant community. Altered soil moisture regimes, resulting from e.g. higher evaporation due to warming and from altered precipitation patterns, can consequently have large impacts on alpine biodiversity and facilitate boreal invasions of alpine habitats.

Germination in the snowbed may have benefitted from the late snowmelt in multiple ways. As my results show, the soil moisture was generally higher in the snowbed than in the other habitats, but the delayed germination of the sown species may also have benefitted from being protected by snow until temperatures were higher and more stable than earlier in spring. In a review of snowbed plant communities, Björk and Molau (2007) concluded the optimal conditions present after snowbed snowmelt, both due to temperature and higher water- and nutrient availability, increased the germination and productivity within the (shortened) growing season compared to in other alpine habitats. These findings contrasted to previous assumptions of unsuitable conditions for germination and plant productivity in snowbed plant communities (Callaghan, 1974; Chambers et al., 1990; Dawson, 1990), but were e.g. supported by the findings of Rosbakh et al. (2022) along a snowmelt gradient in the North Caucasus. The high snowbed germination in my study thus may descend from both high soil moisture and other favourable conditions present in the snowbed and emphasize that snowbed communities are indeed both productive alpine habitats and favourable for earlier plant stages such as seed germination.

I expected ridge plots to have the lowest soil moisture and thus lowest germination in this study, due to conditions typically being harsh and dry, calling for highly adapted species (Edvardsen et al., 2024; Körner & Hiltbrunner, 2021; Nagy & Grabherr, 2009). However, ridge plots had unexpectedly high soil moisture, which may reflect the sheltered location of the ridge of my experiment, in the Finse valley rather than at a mountain top, causing greater germination rates. The seeds of the sown species could also have been more robust than expected, hence tolerating the rough ridge-conditions, and may have benefitted from the high soil moisture availability. Leeside germination was lower than expected. Although alpine leesides are typically moist and productive, favouring germination (Artsdatabanken, 2025b; Billings & Bliss, 1959), the southwest-facing, rocky slope in this study likely experienced high sun exposure and drainage, making it the driest habitat of the study. Similar patterns were found by Welling and Laine (2002) in subarctic Finland, where seeds remained dormant under dry, alpine conditions. The unexpected patterns in germination are therefore likely to be a result of the dry conditions at my leeside plots, where a large portion of the seeds may remain dormant in the soil seed bank.

Very few *C. suecicum* seeds germinated in the field experiment. One explanation of the low germination rate could relate to the fruit type of *C. suecicum*, stone-fruits, which often depend on endozoochory for seed scarification, breaking dormancy, dispersal and fertilization (Taylor, 1999). Taylor (1999) also discovered a potential double-dormancy, where the seeds of *C. suecicum* only germinated after two winters, which could also explain the low germination in my experiment. Another possible explanation is that the growing season at Finse could be too short for it to germinate, as large seed sized species can require more time to germinate (Norden et al., 2009). I think these two factors together may be the main explanation for the low *C. suecicum* germination in my study. As 9 out of the 10 emerged seedlings of this species were located in snowbed plots, I also think soil moisture was important. This could relate to the hard coating of the seeds, and it thus requiring more moist conditions to break dormancy. The coating could make the seeds robust and well-protected against challenging climates, but seemingly breaking dormancy may require multiple winters or endozoochory, in contrast to the other studied species. Results from the following growing season, which will be gathered by another master's student, could thus reveal greater germination rates of this species, or align with my low *C. suecicum* germination, suggesting that the alpine conditions don't support germination of this species.

The results followed my expectation of lowest survival rate in the ridge plots, though results were non-significant. In general, survival rates were high across the habitat types, ranging from 84% in ridge plots to 96% in snowbed, and a large proportion of the germinated seedlings survived throughout the growing season. Seemingly, the harsh ridge-conditions resulted in higher seedling mortality, and the protective snowbed environment, with higher soil moisture, resulted in greater seedling survival. The reduced survival on the ridge indicates that soil moisture is less important for seedling survival than for germination, as shown by the non-significant differences in survival between habitat types, despite soil moisture and survival aligning in the NMDS. Still, moisture could be an important aspect through 'air-moisture stress' (Zhang et al., 2018) caused by frequent and strong wind at the ridge. In contrast, in a study from the Niwot Ridge, Colorado, Forbis (2003) found high survival in fellfield plots compared to other alpine habitat types. They suggested this to result from the fellfield species' traits making them tolerant to the harsh conditions. The boreal species sown in my study are not pre-adapted to harsh alpine conditions but may still have traits allowing them to survive in the alpine, even in the harshest habitat type, explaining their high overall survival rate. Alternatively, this may be explained by the conditions being more benign than expected at the site, as discussed earlier. This indicates that under extant climates at Finse, boreal seedlings can manage to survive in a variety of habitats but also emphasize that local environmental conditions act on survival as well as germination. Including multiple growing seasons in this study could also reveal if winter conditions limit seedling survival, potentially explaining why range shifts are not already occurring at faster rates at Finse.

Competition's effect on seedling traits

Both *B. pubescens* and *P. erecta* seedlings were significantly taller in control plots than removal plots, supporting my hypothesis. Although only snowbed and meadow were included in the analyses of seedling growth traits, the significantly taller seedlings in the meadow met my expectation of taller seedlings in more productive habitats. The findings align with the NMDS ordination results, linking seedling height to plant cover and NDVI. I expected denser extant vegetation to facilitate height growth of the seedlings by providing protection from harsh conditions, but these results may also arise from competition for light and other resources. Insufficient light conditions can trigger etiolated plant growth (Nemhauser & Chory, 2002) and stem elongation in plants (Ballaré et al., 1991; Lu et al., 2021). Due to the high vegetation density in the meadow (own observation) along with the results of lower survival in that habitat type, I believe tall meadow seedlings to be a result of competition for light rather than of facilitation by neighbours. This suggests that meadow species act as strong competitors, shading the seedlings, emphasising a need for the seedlings to grow tall to persist. Based on my results, I speculate that boreal species that can grow tall early in seedling life could have higher competitive advantages when expanding into densely vegetated alpine habitats such as meadows, allowing them to establish even at sites where competition is high.

Potentilla erecta produced significantly more leaves in snowbed plots than in the meadow, while *B. pubescens* showed no significant differences between the habitat types. Both species had significantly more leaves in removal plots than control plots. These results contrast with my hypothesis that productive habitats (meadow and leeside) and intact vegetation would facilitate leaf production. The strong competition in the meadow and control plots in general, may have suppressed leaf production through allocating resources to height growth in the seedlings. Previous removal studies conducted at Finse have found the same when removing the dominant dwarf shrub *Dryas octopetala*: both *Carex vaginata* and *Thalictrum alpinum* grew more leaves (Klanderud, 2005; Klanderud & Totland, 2005). Number of leaves aligned with seedling height in the NMDS ordination, suggesting that similar neighbouring species and variables promote overall seedling growth, weakening the previous argument of resource allocation specifically to height growth. Still, the higher leaf numbers on seedlings in removal and snowbed plots, which had more natural gaps in the vegetation and lower vegetation height (own observation and NMDS results), indicate that reduced competition may promote leaf production. These results indicate that both the effect of biotic interactions and environmental conditions affect leaf production in seedlings in the alpine, but that this study alone doesn’t give clear answers to the nature of these mechanisms.

Leaf length was similar across all habitat types and treatments for both species, rejecting the posed hypothesis. Other studies at Finse have found leaf length of *Thalictrum alpinum, Carex vaginata* and *C. atrofusca* to decrease under removal treatment, potentially due to a lack of facilitative shelter from neighbour vegetation (Klanderud, 2005; Klanderud & Totland, 2005). Similarly, Kjær et al. (2018) found *Bistorta vivipara* to perform better by growing larger leaves when growing in rather than outside *Silene acaulis* cushions at Finse. The species of these studies are well-established at Finse, in contrast to my sown species (Artsdatabanken, 2025a). This may reflect that alpine species have developed facilitative interactions and adaptations that my focal species may not have, or that the conditions at my sites were milder than those at the sites of the previous studies from Finse, resulting in lower needs for facilitative shelter at my sites. In the NMDS analysis seedling leaf length pointed between snowbed and meadow plots, supporting the results of the regression analyses where those two were the only included habitat types. The mechanisms controlling leaf lengths of boreal seedlings emerging in alpine habitats may be too complex to unveil in this study and may be controlled by conditions not controlled for in this study. Or, as the results suggest, leaf lengths may not be controlled by different environmental conditions nor by different biotic interactions. To further disentangle the effects on seedling leaf sizes, measuring specific leaf area (SLA) could be a useful addition in future studies.

Lowland species seedling establishment beyond their range limits

Why did the sown species manage to germinate, grow and survive in the alpine environment outside their altitudinal range? Alexander et al. (2011) found that alien plant invaders of the alpine need a broad environmental tolerance to spread into mountains. Most, at least non-native plants, invading the alpine are therefore typically environmental generalists with high phenotypic and morphologic plasticity (Alexander et al., 2011; Alexander et al., 2016), which could also be the case of the sown lowland species of my study. Plasticity allows plants to alter their morphology or timing of development in response to changed environmental conditions (Schlichting, 1986; West-Eberhard, 1989), which could allow lowland species to adjust when exposed to new environments such as the alpine. Erect species of *Potentilla* have expressed plastic morphology in response to different light conditions (Huber, 1996), and *B. pubescens* have shown plastic morphological leaf responses to altered temperatures (Kramer, 1995). The seedlings grown in my study could have similar plastic abilities, explaining the (somewhat) large germination and survival rates, along with the seedling height and leaf traits I observed. This could give highly competitive lowland species with plastic abilities a double advantage when expanding their ranges into the alpine.

The results of this study suggest competition to be the dominating plant-plant interaction acting on the seedlings at Finse, despite it being a stressful alpine environment, implying that such interactions are influenced by more than just local climate. This is not in line with the suggested outcome by the stress-gradient hypothesis which predicts facilitation to dominate in stressful environments (Bertness & Callaway, 1994; He et al., 2013). The un-predicted outcome could derive from the level of environmental stress at the study site, as earlier mentioned. Although being situated in an alpine environment above the treeline, the climatic conditions at my site at Finse may not have been ‘stressful enough’ to promote facilitative biotic interactions. This in contrast to at e.g. mountain tops, where the environment is harsher and facilitation may be more evident (Callaway et al., 2002). Biotic interactions are also found to depend on species and their resource strategies (Olsen et al., 2016). This was also shown in the study by Dahle et al. (2024), where species with a resource conservative strategy, which is common in alpine species, had higher emergence in extant alpine vegetation than resource acquisitive ones. The resource acquisitive species of Dahle et al.’s study had higher emergence in removal plots, especially under warming, like the seedlings of my study showed even at current temperatures. Additionally, in my study only above-ground biomass was removed in the vegetation gaps. Below-ground plant meristems are important for alpine plants longevity by protecting them from yearly variation in weather conditions (Körner & Hiltbrunner, 2021), indicating that also below ground biomass should have been removed to fully unveil the biotic effect of plant neighbours on seedlings. To better understand how biotic interactions influence the establishment of range-shifting species, it is therefore important to consider species-specific resource strategies and the potentially overlooked role of below-ground interactions.

Biotic interactions could change over time, due to fluctuations in climate. Temperatures recorded at the Finsevatn weather station over the summer of 2024 were in line with the reported average of the last 10 years, while precipitation was higher than usual throughout this growing season (Seklima.no, 2024). The wetter-than-usual conditions could be part of the explanation of the competitive outcome. Lett et al. (2020) found precipitation and moss removal to interact on seedling survival in a transplant experiment in northern Sweden. Under high precipitation, *B. pubescens* survived better where mosses were removed, but worse where mosses remained. This suggests that mosses became stronger competitors under wetter conditions due to enhanced growth (Lett et al., 2020; Stuiver et al., 2014). A similar mechanism may have applied in my study, where increased rainfall and consequently increased soil moisture could have boosted the growth of the extant alpine species, both mosses and vascular plants (Engler et al., 2011; Lett & Dorrepaal, 2018; Vázquez-Ramírez & Venn, 2021). This may then have boosted their competitive effects on the sown species. If this is the case, increased precipitation due to climatic changes could enhance the alpine plant community's resistance to invasion, and it could explain the high competition effect observed in this study.

Analyses of both seedling height and number of leaves revealed significant or close-to-significant interactions between removal treatment and the habitat type snowbed for one or both species. In the snowbed the vegetation was more sparse than in the meadow, and more exposed soil was present, making removal and control plots more similar. It is likely that this reduced the competition experienced by the seedlings in snowbed control plots, which explains the reduced effect of treatment here compared to in the meadow. Other studies have found the competitive effect to be strongest at intermediate precipitation levels (Dahle et al., 2024; Klanderud et al., 2021), indicating that high amounts of water could increase environmental stress. High soil moisture in the snowbed could thus mean it is a more stressful environment to the plants, which should then shift the biotic interactions towards being neutral or facilitative according to the SGH (Bertness & Callaway, 1994; Klanderud et al., 2017). The reduced competitive effect on leaf number and leaf length in the snowbed may therefore actually support the SGH. This highlights that biotic interactions are indeed depending on abiotic conditions, and that their nature is complex. While certain conditions drive competition to act on germination and survival, the same conditions could cause facilitation to act on seedling growth, as the results of Klanderud et al. (2021) also highlight. Predicting how biotic interactions will affect range shifts into the alpine is thus very complex and requires careful but urgent evaluation, as temperatures increase at quicker rates, potentially accelerating alpine invasions.

Future implications for range shifts and alpine biodiversity

My results indicate that competition is the main plant-plant interaction affecting seedling emergence and establishment of the studied boreal species in the alpine. The resident alpine vegetation appears to possess competitive traits sufficient to hinder, or at least slow down, the establishment of lowland species invading these habitats. Temperatures at Finse have increased by 0.36˚C per decade since 1970 (Roos et al., 2022), and climate change is expected to result in further temperature increase and higher precipitation in western Norway (Hanssen-Bauer et al., 2017). Under such novel conditions, competition is expected to play an increasingly bigger role in plant-plant interactions at high elevations (Bertness & Callaway, 1994; Collins et al., 2022; Dahle et al., 2024; Fazlioglu & Wan, 2021; Klanderud, 2008). The altered conditions can lead to increased interspecific competition by the alpine plants (Olsen et al., 2016; Zhang et al., 2025), limiting the loss of alpine plant diversity, but also more suitable growing conditions for boreal species, facilitating range shifts (Fazlioglu & Wan, 2021; Klanderud et al., 2017; Tingstad et al., 2015; Vázquez-Ramírez & Venn, 2021). How plant-plant interactions in the alpine will change in the coming decades may determine the fate of the species I observed at Finse in this study, and of alpine vegetation across the world.

The results from my study indicate that boreal species can establish at Finse already at present temperatures, if conditions are moist enough and competition is limited e.g. in vegetation gaps. Currently this puts the wettest alpine habitats, snowbeds, at highest threat of invasion, but under future climates, with greater precipitation and melting of permanent ice caps at higher elevations increasing moisture availability across lower alpine sites, all alpine habitats may be prone to invasion. Snowbed plant communities are already threatened, as they are often highly specialized and sensitive to changes in annual snowfall patterns (Björk & Molau, 2007). Under changed climates and facing higher invasion rates, snowbed habitats may become smaller and scattered in the alpine landscape, causing losses of snowbed plant diversity and thus overall alpine biodiversity. For alpine herbivores, such as e.g. lemmings, birds, reindeer, and multiple insects, snowbeds provide shelter and feed throughout the snow free season (Björk & Molau, 2007; Moen et al., 1993; Skogland, 1984). Consequently, if snowbed habitats become smaller and snowbed plant diversity and abundance decrease, herbivores may lose important food sources, causing impacts even at higher trophic levels. My findings indicating that boreal plants can establish in wet and sparse alpine habitats, suggest that, beyond impacting snowbed and alpine plant diversity, there may be broader ecological consequences for alpine biodiversity as a whole.

Since seeds of *B. pubescens* managed to germinate and seedlings to survive at alpine sites, this implies that treeline expansions may not only be limited by climate but rather by competition from extant alpine vegetation. In leeside and ridge the competitive effect on seed germination was stronger than in the other habitats, indicating that in these habitat types boreal species may need disturbances to successfully establish from seeds. Man-made disturbances causing gaps and scars in the alpine vegetation could thus promote invasions by lowland range shifters, as also emphasized by other studies (Dahle et al., 2024; Klanderud et al., 2021; Vandvik et al., 2017). Human land-use changes in alpine areas resulting in patches of bare soil could consequently impact the fate of alpine biodiversity, especially when created close to roads where humans already facilitate spread of both native and alien species into alpine ecosystems (Alexander et al., 2016; Pauchard & Alaback, 2004; Pauchard et al., 2009; Rew et al., 2020). Avoiding soil surface alterations and road expansions in mountains could therefore contribute to limiting the spread and by that act as important measures for conserving alpine biodiversity.

Conclusion

Competition limited seed germination and seedling survival of the boreal species sown at Finse, and to a certain degree also growth, while soil moisture increased germination and survival. This suggests that alpine plant communities may limit the spread of range shifting species into their habitats, but that moist, and sparsely vegetated alpine habitats may be more vulnerable to invasions than others. Experiments including lowland species from a wider range of functional groups, establishing sites in more alpine habitats such as more calcareous ones, including below-ground biotic interactions and looking at different stages of plant establishment could widen the understanding of how the nature of biotic interactions fluctuate. The most vulnerable alpine habitats, such as snowbeds, should be carefully monitored and a priority in conservation as climate change and range shifts are accelerating. Human land use practices also facilitate range shifts into the alpine by creating vegetation gaps with reduced competition from alpine plants, emphasizing the negative effects of humans on biodiversity.

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Appendix

Table 1: Tukey's post-hoc results following an ANOVA analysis of differences in soil moisture (log-transformed) between the habitat types (leeside, meadow, ridge and snowbed) to reveal a gradient in soil moisture. Estimated differences are followed by confidence interval (lower and upper), and p-value. Significant p-values (< 0.05) are in bold.

Comparison	Difference	Lower CI	Upper CI	p
Leeside - meadow	-0.271	-0.531	-0.010	**0.040**
Ridge – meadow	0.461	0.200	0.721	**0.000**
Snowbed – meadow	0.825	0.564	1.086	**0.000**
Ridge – leeside	0.731	0.471	0.992	**0.000**
Snowbed – leeside	1.096	0.835	1.356	**0.000**
Snowbed - ridge	0.365	0.104	0.625	**0.004**

Table 2: Pairwise post hoc comparisons of seed germination rates across habitat types (leeside, meadow, ridge and snowbed) following the GLMM analysis. Estimated differences are presented on log-odds scale, including standard errors (SE), degrees of freedom (df), z-ratios and p-values. Significant p-values (< 0.05) are in bold. Infinite degrees of freedom could be a result of small sample size combined with a complex mixed effects structure.

Contrast	Estimate	SE	df	z	p
Leeside - Meadow	-1.215	0.711	Inf	-1.708	0.320
Leeside - Ridge	-0.904	0.717	Inf	-1.261	0.588
Leeside – Snowbed	-1.677	0.707	Inf	-2.371	0.083
Meadow – Ridge	0.311	0.671	Inf	0.464	0.967
Meadow - Snowbed	-0.462	0.654	Inf	-0.707	0.894
Ridge - Snowbed	-0.773	0.661	Inf	-1.170	0.646

Table 3: Complete list of species recorded in the vegetation analysis, which were included in NMDS ordination. Columns present abbreviated species names used in the NMDS ordination, full scientific species name, Norwegian species name and functional group.

Species name abbreviation	Scientific species name	Functional group
Agr cap	*Agrostis capillaris*	Graminoid
Alc alp	*Alchemilla alpina*	Forb
Ale nig	*Alectoria nigricans*	Lichen
Ale och	*Alectoria ochroleuca*	Lichen
Ant odo	*Anthoxanthum odoratum*	Graminoid
Ave fle	*Avenella flexuosa*	Graminoid
Bis viv	*Bistorta vivipara*	Forb
Car big	*Carex bigelowii*	Graminoid
Car bru	*Carex brunnescens*	Graminoid
Car can	*Carex canescens*	Graminoid
Cet isl	*Cetraria islandica*	Lichen
Cha ang	*Chamerion angustifolium*	Forb
Cla arb	*Cladonia arbuscula*	Lichen
Cla gra	*Cladonia gracilis*	Lichen
Cla ran	*Cladonia rangiferina*	Lichen
Cla sp.	*Cladonia sp.*	Lichen
Emp nig	*Empetrum nigrum*	Shrub
Fes ovi	*Festuca ovina*	Graminoid
Fla cuc	*Flavocetraria cucullata*	Lichen
Fla niv	*Flavocetraria nivalis*	Lichen
Hie alp	*Hieracium alpinum*	Forb
Jun fil	*Juncus filiformis*	Graminoid
Jun tri	*Juncus trifidus*	Graminoid
Luz mul	*Luzula multiflora*	Graminoid
Lyc cla	*Lycopodium clavatum*	Pteridophyte
Lys eur	*Lysimachia europaea*	Forb
Nar str	*Nardus stricta*	Graminoid
Oma nor	*Omalotheca norvegica*	Forb
Phl alp	*Phleum alpinum*	Graminoid
Poa alp	*Poa alpina*	Graminoid
Pyr min	*Pyrola minor*	Forb
Rum ace	*Rumex acetosa*	Forb
Sal her	*Salix herbacea*	Shrub
Sib pro	*Sibbaldia procumbens*	Forb
Sol vir	*Solidago virgaurea*	Forb
Tha ver	*Thamnolia vermicularis*	Lichen
Vac myr	*Vaccinium myrtillus*	Shrub
Vac uli	*Vaccinium uliginosum*	Shrub
Vac vit	*Vaccinium vitis-idaea*	Shrub
Vio pal	*Viola palustris*	Forb

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