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The effects of experimental warming on seedling recruitment within an alpine biodiversity hotspot

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Abstract

In 2000, an *in situ* experiment using open-top chambers was established to assess the effects of increased temperature on a biodiverse *Dryas* heath community located along a wind-exposed ridge at Mount Sanddalsnuten (ca. 1550 m. a.s.l.), Finse, in southwest Norway. In 2003, a similar experiment was established further down the heath, located in a more protected leeside near the foot of the mountain (ca. 1450 m. a.s.l.). A study published in 2024 revealed that long-term experimental warming at the high-elevation site resulted in increased cover of litter and dead *Dryas,* potentially linked to previous extreme weather events like heatwaves or droughts; thereby posing an interesting question about the legacy effects this may have on seedling recruitment within the heath. To investigate if experimental warming affected seedling recruitment and whether this effect varied with elevation, I recorded the naturally occurring seedlings at both sites. In order to identify potential factors impacting the recruitment process, I estimated the percent cover of *Dryas*, different functional groups, litter, and dead *Dryas*, as well as measuring the vegetation height, soil moisture, and normalised difference vegetation index (NDVI). I also surveyed the plant community in-depth at the high-elevation site by recording species of vascular plants, bryophytes, and lichens, and by estimating the local vascular plant species pool and dark diversity within the *Dryas* heath.

Long-term experimental warming resulted in reduced seedling recruitment at both elevations. The effect of warming did not differ between the two sites for any of the variables tested, suggesting a uniform response to warming at the ridge and leeside. Warmed plots at both elevations were characterised by increased cover of litter and taller vegetation, with trends of increased cover of dead *Dryas* and taller *Dryas* where it persisted. Shading effects of taller vegetation and litter, the majority of which were recalcitrant *Dryas* leaves, may have contributed to the decrease in seedling recruitment with warming. Furthermore, the effect of elevation was greater than that of warming, with fewer seedlings being recorded at the high-elevation site. This could likely be attributed to the much lower soil moisture levels at the ridge compared to the leeside, though other elevational differences including higher cover of the dominant *Dryas* at the ridge could also have inhibited seedlings through competition. Finally, the relatively low dark diversity estimates suggest that local dispersal limitations are not strongly limiting species richness and recruitment within the heath. My findings suggest that wetter areas are more open to seedling recruitment, whereas indirect effects of warming can make areas less open to new individuals by driving changes in the vegetation.

Sammendrag

For å vurdere effektene av økt temperatur på en artsrik reinrosehei ble det i år 2000 etablert et eksperiment med bruk av oppvarmingskamre (open-top chambers) lokalisert langs en vindutsatt rabbe på Sanddalsnuten (ca. 1550 moh.) ved Finse, i sørvestlige Norge. I 2003 ble et tilsvarende eksperiment etablert lenger ned i heien, i en mer beskyttet leside nær foten av fjellet (ca. 1450 moh.). En studie publisert i 2024 avdekket at eksperimentell oppvarming over lang tid på rabben førte til økt dekke av strø og død reinrose, mulig knyttet til tidligere ekstreme værhendelser som hetebølger eller tørke. Dette reiste et interessant spørsmål om de videre effektene dette kan ha på etableringen av frøplanter innenfor reinroseheien. For å undersøke om oppvarming påvirket etableringen av frøplanter og hvorvidt denne effekten varierte med høyde, registrerte jeg de naturlig forekommende frøplantene på begge lokalitetene. For å identifisere mulige faktorer som påvirker etableringsprosessen, estimerte jeg prosent dekningen av reinrose, ulike funksjonelle grupper, strø og død reinrose, samt målte vegetasjonshøyde, jordfuktighet og normalisert differanse vegetasjonsindeks (NDVI). Jeg undersøkte også plantesamfunnet på rabben i mer detalj ved å registrere arter av karplanter, moser og lav, samt ved å estimere den lokale ‘species pool’ og ‘dark diversitet’ innenfor reinroseheien.

Langtidsoppvarming førte til at færre frøplanter etablerte seg ved begge høyder. Effekten av oppvarming var ikke forskjellig mellom de to lokalitetene for noen av variablene jeg så på, noe som antyder en homogen respons på oppvarming både ved rabben og lesiden. Plottene med oppvarmingskamre var på begge lokaliteter preget av økt dekke av strø og høyere vegetasjon, med en tendens mot økt dekke av død reinrose og høyere reinrose der den vedvarte. Høyere vegetasjon og økt strødekke, hvorav mesteparten var tungnedbrytbare reinroseblader, kan ha bidratt til nedgangen i etablering av frøplanter ved oppvarming. Dessuten var effekten av høyde større enn den av oppvarming, med færre frøplanter registrert på rabben som var høyere opp på fjellet. Dette kan trolig skyldes betydelig lavere jordfuktighetsnivå ved rabben sammenlignet med lesiden, selv om andre høydemessige forskjeller også kan ha hemmet frøplanter, f.eks. større dekke av reinrosen på rabben som kan medføre økt konkurranse. Jeg fant relativt lavt antall ‘dark diversity’ arter, noe som indikerer at spredningsbarrierer ikke har en sterkt begrensende effekt på etablering av arter innad reinroseheien. Mine funn tyder på at fuktigere områder er mer åpne for etablering av frøplanter, mens indirekte effekter av oppvarming kan gjøre områder mindre åpne for nye individer ved å drive endringer i vegetasjonen som negativt påvirker frøplanterekruttering.

Table of Contents

1. Introduction

Climate change is one of the top five drivers identified as contributing to a loss of biodiversity worldwide (Balvanera et al., 2019). Anthropogenic greenhouse gas emissions are leading to increased global warming, with projected estimates reaching 1.5 °C above pre-industrial levels by 2040 (IPCC, 2023). Alpine regions often experience accelerated warming when compared to neighbouring lowland areas (IPCC, 2023; Pepin et al., 2022), and these ecosystems can support high biodiversity despite its relatively small surface area (Körner, 2004). This high biodiversity is in part due to the heterogeneous landscape with a great diversity of microhabitats, often engineered by the local patches of vegetation itself (Körner, 2021; Körner & Hiltbrunner, 2021). In light of continuous anthropogenic climate change, examining how alpine vegetation responds to climate change is of great importance.

Alpine plants are in many aspects robust against climatic changes, due to their inherent adaptability to rapid and unpredictable shifts in environmental conditions, their clonal life strategies that stabilise plant communities over long periods, and their proximity to a mosaic of potentially suitable microhabitats (Körner & Hiltbrunner, 2021). Despite this, trends of how climate change has begun to affect alpine ecosystems include a loss of alpine habitats across the globe due to a gradual upslope elevational shift of the treeline (Cazzolla Gatti et al., 2019; Kullman, 2007) and an increase in plant species richness on mountain summits in Europe, where lowland species establish at higher elevations (Steinbauer et al., 2018). Both of these migratory processes hinges on species successfully dispersing into new areas. Additionally, reports of vegetation 'greening' and 'browning' in both Arctic and alpine regions, often detected at large scales through remote sensing using the Normalised Difference Vegetation Index (NDVI), indicate that the vegetation has responded to warming with either increased or decreased productivity and biomass (Myers-Smith et al., 2020; Phoenix & Treharne, 2022). While vegetation greening can be linked to overall warmer growing seasons (Elmendorf et al., 2012), extreme weather events and winter warming are suggested as the driving forces behind vegetation browning (Bjerke et al., 2017; Myers-Smith et al., 2020; Phoenix & Bjerke, 2016). Extreme weather events are projected to increase in frequency with climate change and may be more detrimental to ecosystems than the gradual increase in mean temperatures (Walsh et al., 2020).

Classical ecological theory dictates a trade-off between investing resources in vegetative and sexual reproduction (Harper, 1967). Due to the harsh environmental conditions in alpine ecosystems, most alpine plant species display long-lived, clonal growth – which would in theory be associated with low seed production. Indeed, it was previously postulated that alpine plant species generally invest little into sexual reproduction (Grime, 1977). Studies have since found seedling recruitment rates of alpine species to be similar to that of perennial plants in other ecosystems (Forbis, 2003; Forbis & Doak, 2004), and researchers report abundant observations of seedlings at alpine study sites (Körner, 2021; Venn & Morgan, 2009; Welling & Laine, 2000). Sexual reproduction is important to maintain genetic diversity (Pluess & Stöcklin, 2004) and for shifting distribution ranges in response to environmental change (Walck et al., 2011). Thus, understanding how early life-stages of plants can be affected by warming is critical also in alpine ecosystems.

Most research has focused on responses of adult plants to warming in alpine regions, with more attention being dedicated to earlier life-stages of plants mainly in later years (Briceño et al., 2015; Vázquez-Ramírez & Venn, 2021). Seedling recruitment refers to the process wherein new plant individuals are recruited into a population, as developing seedlings emerge from germinated seeds (Eriksson & Ehrlén, 2008). This represents one of the most vulnerable stages in a plant's life cycle and are expected to be sensitive to climatic changes (Walck et al., 2011). Increased temperatures have generally been reported to have positive effects on early life-stages of plants (e.g. Vázquez-Ramírez & Venn, 2021), though negative or neutral effects of higher temperature have also been observed (Lett & Dorrepaal, 2018; Shevtsova et al., 2009; Vázquez-Ramírez & Venn, 2021). Warming can also indirectly affect seedling recruitment by driving changes in various community properties over time. Competition has been reported to reduce seedling recruitment (Forbis, 2009; Klanderud, 2010; Margreiter et al., 2021; Tingstad et al., 2015) and this effect might increase as a result of vegetation greening leading to denser and taller vegetation. Conversely, increased litter as a result of vegetation browning could function as a mechanical barrier that also inhibits seedling recruitment (Facelli & Pickett, 1991). These factors may also promote seedling recruitment, as facilitation from resident vegetation (Nystuen et al., 2019) and litter (Venn & Morgan, 2009) shading the soil has been proposed as an important process for early seedling survival in the alpine. Furthermore, soil moisture has been noted to play an important role in the spatial distribution of naturally occurring seedling (Forbis, 2003; Venn & Morgan, 2009), and climate change predicts changes in precipitation along with increased temperatures (IPCC, 2023)

The International Tundra Experiment (ITEX) was established in the 1990s to assess the response of cold-adapted plant species and tundra ecosystems to a warming climate using open-top chambers (Henry et al., 2022). An ITEX site was established in 2000 at a wind-exposed ridge of Mount Sanddalsnuten (ca. 1550 m. a.s.l.), Finse, in southwest Norway. In 2003, a similar warming experiment was established further down the *Dryas* heath, located in a more protected leeside near the foot of the mountain (ca. 1450 m. a.s.l.). The calcareous bedrock in the area allows for a species-rich community dominated by the semi-evergreen dwarf shrub *Dryas octopetala* (hereafter *Dryas*) (Roos et al., 2023). While the *Dryas* heath at Sanddalsnuten has shown resistance to warming (e.g. Roos et al., 2023), increased *Dryas* die-off as well as overall vegetation browning and taller vegetation was reported at the high-elevation site after 23 years of warming (Eiterjord, 2024); thus, raising an interesting question about the potential legacy effects on seedling recruitment.

Further insight into recruitment dynamics can be gained from examining plant species composition inside and outside the established plots. Previous studies have identified a positive relationship between species richness and naturally occurring seedlings (Klanderud, 2010), and suggested that the absence within plots of locally present species could indicate various dispersal limitations (Riibak et al., 2015). Dark diversity is a biodiversity metric defined as the number of species that are ecologically suitable and present in the regional species pool yet are currently absent from a specific habitat (Pärtel et al., 2011). There are different methods for assessing dark diversity, with species co-occurrence and niche-based being most common (Lewis et al., 2016), but dark diversity can also identified more directly at smaller scales by recording which species are present outside of already established plots where the species composition is known (Rixen et al., 2019). On average, around 30 species are regionally present but have never been detected inside plots across various ITEX sites (Daskalova et al. in prep). Dark diversity is useful for understanding ongoing and future biodiversity changes as it can be used to estimate community completeness; a biodiversity metric representing the proportion of regionally suitable species actually present at a site (Pärtel et al., 2013). Since community completeness assesses the degree to which the biodiversity potential at a site is realised, it is comparable across ecosystems that may have large regional variations in their biodiversity potentials (Pärtel et al., 2025). This has revealed global patterns of lower plant diversity in response to anthropogenic activity that are not apparent when using other biodiversity metrics (Pärtel et al., 2025).

The aim of this study was to assess the effects of long-term experimental warming on seedling recruitment within a *Dryas octopetala* heath at two different elevational sites, i.e. ridge and leeside, as well as accounting for species composition and dark diversity at the high-elevation site. The two elevational sites have different temperatures, soil moisture availability, and length of growing season, allowing for a comparison of the effects of warming at differing levels of environmental stress. By presenting a detailed survey of the plant community, I seek to answer the following research questions:

1. Does the number of naturally occurring seedlings differ significantly with elevation and warming?
2. Do factors that may influence the number of seedlings – i.e. soil moisture, NDVI, vegetation and *Dryas* height, the cover of different functional groups, bare soil, litter, and living and dead *Dryas* – differ significantly with elevation and warming?
3. How does the number of seedlings relate to species composition, soil moisture, NDVI, vegetation and *Dryas* height, the cover of different functional groups, bare soil, litter, living and dead *Dryas*, and the number of flowering species at the high-elevation site?
4. How many of the vascular plant species recorded outside the established high-elevation plots could potentially inhabit the *Dryas* heath, i.e. constitute dark diversity, and how does this relate proportionally to the community as a whole, i.e. the community completeness index?

I hypothesise that there will be fewer seedlings in warmed plots at both elevations, and that there will be fewer seedlings at the drier, high-elevation site. I expect warmed plots to have higher cover of overall litter and dead *Dryas*, taller vegetation, including taller *Dryas*, and that further analysis based on species composition will show negative associations between these variables and the number of seedlings. I hypothesise that the effects of warming on the cover of litter and dead *Dryas* might be more severe at the high-elevation site due to lower soil moisture than at the low-elevation site, whereas the effect of warming on vegetation height might be higher at the low-elevation site due to higher productivity. Lastly, I expect the number of species constituting dark diversity to be similar to that of other ITEX sites, though competition from *Dryas* may lead to higher dark diversity due to better recruitment success outside the plots, resulting in a fairly average estimates of community completeness.

2. Materials and methods

2.1 Study area

My study was conducted during the summer of 2024 at Mount Sanddalsnuten, Finse, located in the alpine region of southwest Norway (Figure 1), where long-term experimental warming studies have been ongoing for over 20 years (Roos et al., 2023). To assess the effect of experimental warming and elevational differences on naturally occurring seedlings, I examined plots at two different elevational sites within a *Dryas octopetala*-dominated heath (Figure 1). The high-elevation site was a wind-exposed ridge on the south-facing slope of the summit (ca. 1550 m a.s.l.), whereas the low-elevation site was a leeside further down the slope near the foot of the mountain (ca. 1450 m a.s.l.).

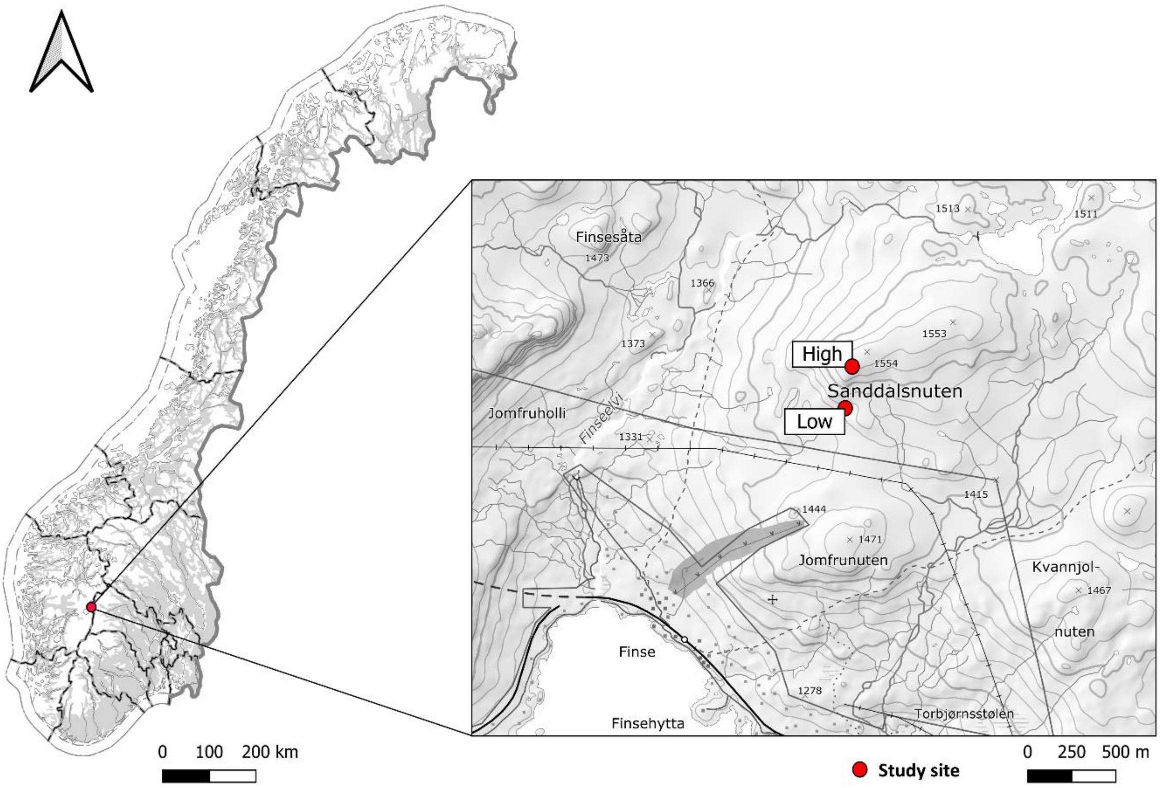

Figure 1. *Map showing the location of the study sites at Sanddalsnuten. Red dot marked as "High" is the ridge site at ca. 1550 m. a.s.l., whereas the red dot marked as "Low" is the leeside site at ca. 1450 m. a.s.l. Sanddalsnuten is north of Finse and located in Ulvik municipality in southwest Norway. The map was created using QGIS version 3.42.2 (QGIS.org, 2025). Background map: topographical map of Norway (Kartverket, 2025).*

The ridge site at higher elevation has a thinner snow cover during the winter and earlier snow melt than at the leeside, resulting in a ca. 3 week longer growing season (Nybakken et al., 2011) that typically spans from early May or June through August. The ridge remains quite dry throughout the growing season (Roos et al., 2023), whereas the leeside at lower elevation has much higher soil moisture, due to a combination of water drainage above, higher snow accumulation, and better water retention in the soil (Nybakken et al., 2011).

The average annual temperature at Finse between 1970-1990 was -2.0 ˚C, and temperatures increased by 0.36 ˚C per decade between 1970-2020 (Roos et al., 2023). In a report commissioned by the Norwegian Environmental Agency, expected average annual temperature increases by 2071-2100 for this region is somewhere between 1.2 ˚C and 3.9 ˚C higher than 1971-2000 temperatures (Hanssen-Bauer et al., 2017). In 2024, average monthly temperature during June, July, and August were 7.4 °C and average monthly precipitation over these months were 136.5 mm at the weather station located 1200 m a.s.l. at Finse (The Norwegian Meteorological Institute, 2025). The average differences in air temperature between the two elevational sites in July-August has been measured to be ca. 0.8 ˚C warmer at the leeside (Nybakken et al., 2011).

The calcareous bedrock, phyllite, allows for a species-rich flora at and around Sanddalsnuten (Roos et al., 2023). The dominant semi-evergreen dwarf shrub *Dryas octopetala* (henceforth *Dryas*) grows in dense mats with a variety of other species interspersed (Klanderud & Totland, 2005). Common species previously reported in the area include dwarf shrubs *Salix herbacea* and *Salix reticulata*; forbs *Bistorta vivipara*, *Potentilla crantzii*, *Saussurea alpina*, *Silene acaulis*, and *Thalictrum alpinum;* graminoids *Carex rupestris*, *Carex vaginata*, *Festuca ovina*, and *Festuca vivipara*; lichens *Cetraria ericetorum*, *Cetraria islandica*, *Cladonia arbuscula*, *Cladonia gracilis, Flavocetraria cucullata, Flavocetraria nivalis,* and *Thamnolia vermicularis*; and bryophytes *Hylocomium splendens*, *Ptilidium ciliare*, *Sanonia uncinata*, and the genera *Dicranum*, *Polytrichum*, and *Racomitrium* (Eiterjord, 2024).

2.2 Study design

Long-term experimental warming of the *Dryas* heath is achieved using open-top chambers (OTCs). Open-top chambers provide a passive warming effect, with an intensity depending on factors such as cloud cover and weather, making them an appropriate method for simulating future climate change predictions (Hollister et al., 2023). A total of 40 OTC and 40 control plots were established in 2000 at the high-elevation site (Klanderud & Totland, 2007), whereas 20 OTC and 20 control plots were established in 2003 at the low-elevation site (Sandvik & Eide, 2009). At both sites, OTCs were found to increase average air and soil temperatures by 1.5 °C and 1 °C, respectively (Klanderud & Totland, 2005; Sandvik & Eide, 2009).

At the high-elevation site, I surveyed the remaining plots that were not examined in 2023 (Eiterjord, 2024), i.e. 9 OTC and 8 control plots. At the low-elevation site, I chose to survey the five OTC plots that were *Dryas* dominated, as these would be comparable to the high-elevation plots. The established control plots at the low-elevation site could no longer be found due to identifying markers having been removed. I therefore established five new control plots, using the position of each OTC plot as a starting point. I randomly generated a number between 1 and 4 to determine which cardinal direction the control plot would be placed and then generated a number between 1 and 5 to decide how many metres the location would be from the OTC plot. If the location was deemed unsuitable, e.g. too steep topography or little to no *Dryas* present, new numbers were generated.

2.3 Vegetation analysis

I completed my fieldwork during the summer of 2024, from late June to mid-August. The method used for the vegetation analysis largely follows the protocol from Eiterjord (2024).

At the high-elevation site, each plot measured 60 x 60 cm and was sectioned into 36 subplots of 10 x 10 cm. In each subplot, I recorded the presence of every species of vascular plants, bryophytes, and lichens to the best of my ability. Vascular plant species followed the nomenclature in Elven et al. (2022), bryophytes followed Hallingbäck (2021), and lichens followed Holien and Tønsberg (2023). Species I failed to identify to species level were instead recorded to genus. This includes forbs *Ranunculus* and *Taraxacum*; graminoids *Luzula spicata* and *Luzula confusa* if they presented without flowers; bryophytes *Andreaeopsida, Bryum, Dicranella, Dicranum, Hypnum, Lophozia, Plagiomnium, Pohlia, Polytrichum, Racomitrium,* and *Syntricia;* and lichens *Cladonia* (only some specimens), *Collema*, *Peltigera*, *Solorina*, and *Stereocaulon*. I found one lichen species that I could not identify and was recorded in plots as "Lichen sp.".

For vascular flowering plants, I also noted whether the species was fertile based on the presence of flower buds, flowers, or fruits within the subplot. In each plot, I provided a visual estimation of the percent cover for each species and different functional groups, namely dwarf shrubs, forbs, graminoids, bryophytes, and lichens. Estimated cover at less than 1% was registered as 0.1% for the analyses. I also estimated the percent cover bare soil, biological crust, as well as overall litter (including dead *Dryas*) and the percent cover of dead *Dryas* specifically in each plot. Due to difficulties in distinguishing whether dead *Dryas* was still attached to the plant, estimates also include dead leaves still attached.

Finally, I counted the number of seedlings found in each subplot. Individuals were recorded as seedlings if the cotyledons were still attached (Figure 2). Annual plants, whose presence must result from germination within the growing season, were recorded as seedlings even if cotyledons had fallen off. This only applied to *Euphrasia wettsteinii* and *Gentiana nivalis*. Seedling observations represent a snapshot of the naturally occurring dicot seedlings during one field season, which is a part of the long-term recruitment of individuals into the plant community, though I did not differentiate between this year and previous years' seedlings. I use the term "recruitment" when discussing my findings, but it is important to note that studies spanning multiple seasons typically discern between seedling establishment being the initial phase following seed germination and seedling emergence, whereas recruitment is often reserved for seedlings surviving over a certain time span – typically at least one year – though sometimes these terms are used interchangeably.

At the low-elevation site, each plot measured 30 x 30 cm and was sectioned into 9 subplots of 10 x 10 cm. The vegetation analysis conducted in these plots was less extensive than at the high-elevation site due to time constraints; I recorded the number of seedlings and the percent cover for the different functional groups, living *Dryas*, litter, dead *Dryas*, bare soil, and biological crust, but not species presence or fertility. As such, this site was not included in the ordination analysis.

Figure 2. *Dicot seedling with cotyledons attached, likely* Potentilla crantzii. *Photo: Gaute Eiterjord.*

At both sites, I measured the height of the general vegetation and *Dryas* for all plots (Figure 3). For the high-elevation plots, the general vegetation was measured in 12 subplots whereas *Dryas* was measured in 6 subplots. For the low-elevation plots, the general vegetation was measured in 5 subplots and *Dryas* in 3 subplots. I used the same subplot for each height measurement when possible. If *Dryas* was not present in a given subplot, I instead measured the height in the nearest appropriate subplot. For the statistical analyses, measurements were averaged within each plot.

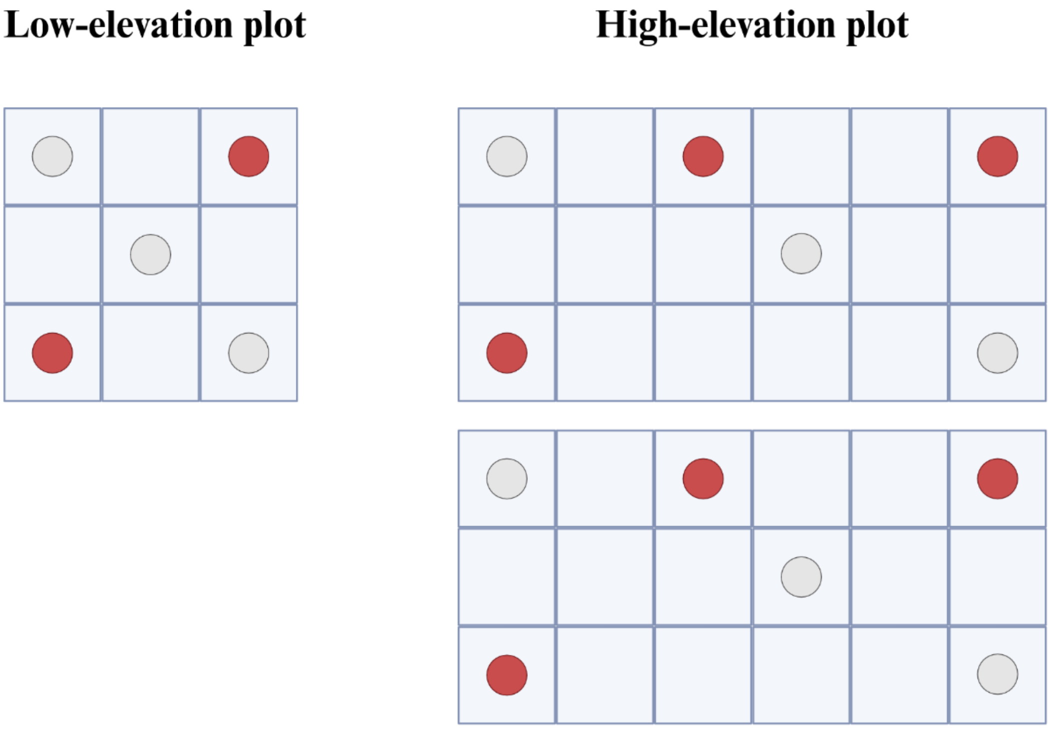

Figure 3. *Overview of the different subplots in low- and high-elevation plots. Grey dots mark subplots where both* Dryas *and vegetation height was measured, while red dots mark additional plots where only vegetation height was measured. The gap separating the high-elevation plot in two are a remnant from when the plots were established. The figure was created using BioRender (2025).*

2.4 Soil moisture and NDVI measurements

Soil moisture was measured in all plots at both sites on the 3rd and 12th of August using a SM150 moisture meter on the mineral soil setting (Delta-T Devices Ltd.). The moisture meter measured volumetric water content (% volume) at a soil depth of 6 cm. For the high-elevation plots, measurements were taken in four subplots. For the low-elevation plots, measurements were taken in two subplots. If it was not possible to obtain an accurate reading, e.g. due to shallow soil depth, I measured the nearest appropriate subplot. For the analyses, max readings were set to 100%. For the statistical analysis, measurements were averaged both within each plot and between the two measuring dates.

I measured NDVI (Normalised Difference Vegetation Index) in all plots at both sites on the 3rd of August using a GreenSeeker handheld crop sensor (Trimble Inc.). The device was aimed towards the centre of each plot and held just below hip-height, approximately 75 cm above the ground.

2.5 Dark diversity and community completeness index

In collaboration with PhD candidate Mikel Moriana Armendariz at NMBU, I compiled a list of vascular plant species found outside the established plots at the high elevation site. We largely followed the protocol outlined in Rixen et al. (2019), with some adjustments.

An overview of the survey method is shown in Figure 4. We began by identifying the exact point in the middle of all the established plots. We recorded all species found around the centre: first in two quadrats of increasing size (25 x 25 cm and 1 m^2) then walking in spiral transects with gradually increasing radii (1.25 m, 10 m, 20 m, 30 m, 40 m). Due to increasingly steep topography and time constraints, after having covered the entire area where the plots were located with the spiral transects, we opted for walking two line transects: one north towards the mountain summit, and one south towards, but not reaching, the low-elevation site. Each line transect measured approximately 100 metres from the centre.

The resulting species list was compared with the vascular plant species recorded inside the plots, i.e. the observed richness, including field recordings of the other 42 plots in 2023 (Eiterjord, 2024). The species not recorded inside the plots were assessed in terms of habitat suitability, relying on expert advice (Kari Klanderud, Siri Lie Olsen, Mikel Moriana Armendariz, personal communications). The full list of species recorded outside plots, along with an evaluation of habitat suitability, is provided in Appendix B. The number of species potentially able to inhabit the *Dryas* heath community was used as a measure of dark diversity. The number of species constituting dark diversity was used to calculate the community completeness index using the equation ln(observed richness/dark diversity), as proposed by Pärtel et al. (2013)

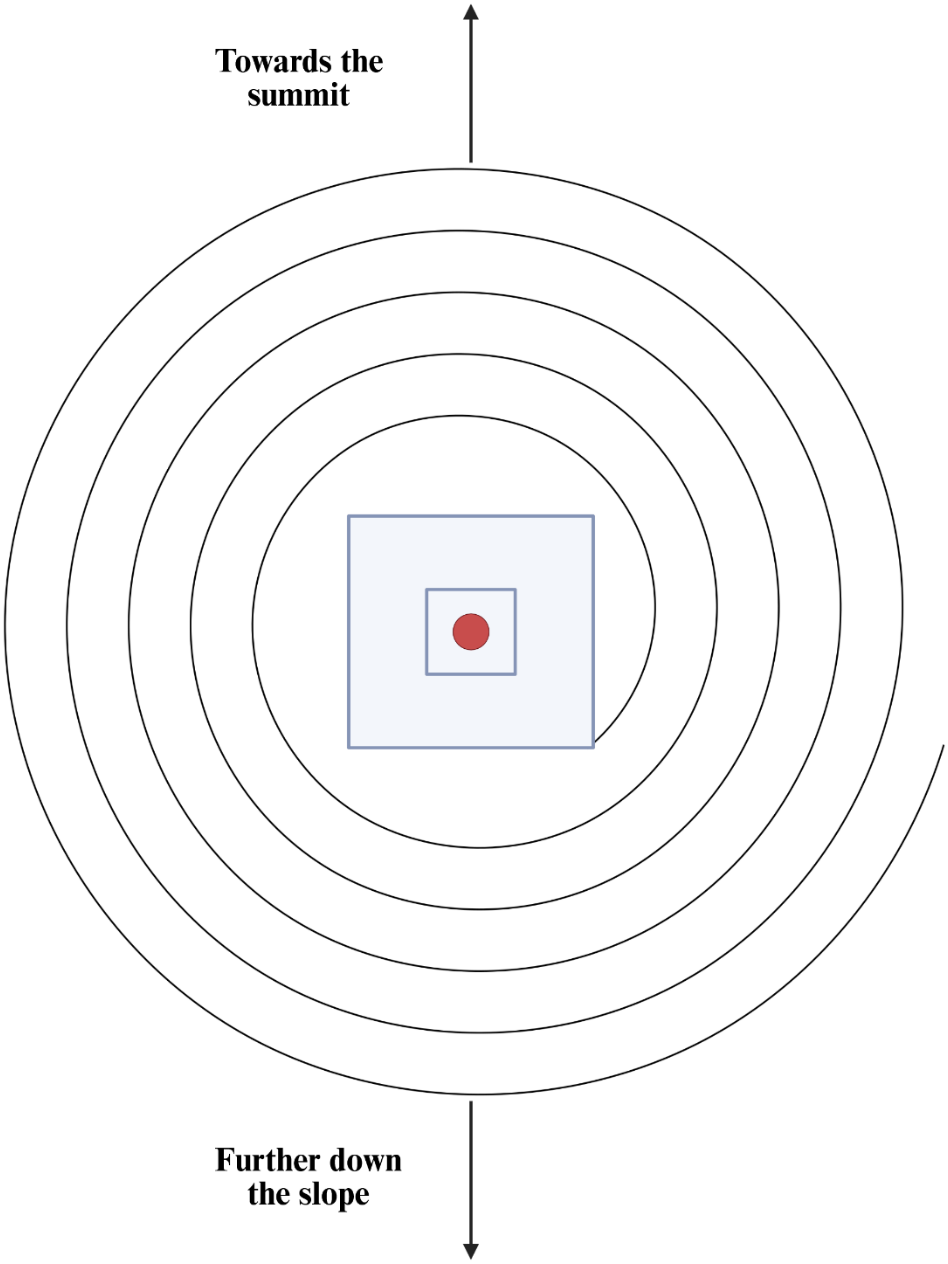

Figure 4. *Overview of the survey method used for recording species outside high-elevation plots. The red circle represents the centre of the high-elevation study site, and the two blue squares show the two quadrats examined. The black spiral illustrates the survey route used further away from the centre, and the two arrows indicate the general direction of the line transects; however, the length of the arrows is not indicative of the length of the transect. The figure was created using BioRender (2025).*

2.6 Statistical analyses

The statistical analyses were conducted using R version 4.4.1 (R Core Team, 2024) and Rstudio (Posit team, 2024). I used the packages “readxl” (Wickham & Bryan, 2023) and “dplyr” (Wickham et al., 2023) for initial data wrangling. Plots were created using the package “ggplot2” (Wickham, 2016), as well as the “patchwork” (Pedersen, 2024) and “ggrepel” (Slowikowski, 2024) packages for merging figures and adjusting labels, respectively. Assistance with coding and interpretation of outputs was provided by AI technology through Sikt KI-chat, powered by OpenAI (2023).

2.6.1 Generalised linear models (GLMs)

To analyse the effects of elevation and experimental warming on the number of seedlings, environmental variables (i.e., NDVI and soil moisture), and community properties (i.e., cover of different functional groups, litter, and dead *Dryas*, as well as vegetation and *Dryas* height), generalised linear models (GLMs) were fitted using the package “glmmTMB” (Brooks et al., 2017). The distribution of each response variable was determined by visually inspecting histograms. For over-dispersed count data, i.e., the number of seedlings, a negative binomial distribution with a log link function (nbinom2) was selected for modelling. To account for different plot sizes at the high- and low-elevation site, the model included an offset term with the natural logarithm of plot size, effectively converting the count data into the rate of seedlings per unit area. For positively skewed continuous data, i.e., vegetation and *Dryas* height, a gamma distribution was selected. For continuous bounded variables, i.e., variables that always remained between 0 and 1, a beta distribution was selected, as proposed by Douma and Weedon (2019). The bounded variables in this study include soil moisture, NDVI measurements, and the percent cover of functional groups, litter, as well as living and dead *Dryas*. Percent cover and soil moisture were transformed into a proportion between 0 and 1 prior to fitting the models. All response variables were checked for zero and one values to assess if zero-/one-augmentation was necessary. Due to very sparse cover of bare soil, appropriate models could not be fitted for this variable.

To assess model fit, residuals were inspected using the package “DHARMa” (Hartig, 2024). If outliers were identified, I checked for possible errors in data punching and fitted models without outliers to see if the results were significantly different. Only the bryophyte-model revealed a significant outlier: when excluding this, the effect of warming went from almost significant to highly significant. All the models were fitted with and without the interaction between elevation and treatment. Unless the more complex models with interactions added significant explanatory power (i.e., the interaction was significant, $p < 0.05$) or significantly improved the model fit (i.e. compared using a Chi-squared test, $p < 0.05$), I opted for the simpler model. Additionally, I compared AIC and BIC values to guide model selection, though these values tended to show no distinguishable differences between the two models assessed. No interactions proved significant nor significantly improved model fit, so all the included GLMs are additive only. The models therefore only compared elevation and warming independently of each other, i.e. all warmed with all control plots, regardless of elevation, and all high-elevation plots with low-elevation plots, regardless of warming. Mean predicted values were back transformed and presented visually as bar charts, including 95% confidence intervals.

2.6.2 Ordination analysis

To assess the relationship between the number of seedlings and community properties including species composition in warmed and control plots, I conducted a non-metric multidimensional scaling (NMDS) ordination analysis with the species composition recorded at the high elevation site using the "vegan" package (Oksanen et al., 2024). Subplot frequencies were used as the measure of species' abundance in any given plot. I assessed the NMDS model by inspecting the stress levels, which were found to be suitable (0.12), as well as running a detrended correspondence analysis (DCA) to compare the correlation between the NMDS and DCA models. The models showed a strong correlation in a symmetric Procrustes rotation (0.88) and had highly significant similarities ($p < 0.001$). Additionally, I identified the length of the first DCA axis in order to decide between running a redundancy analysis (RDA), preferred when assessing a short environmental gradient (< 3), or canonical correspondence analysis (CCA), preferred when assessing a longer environmental gradient (> 3). The length of the first DCA axis was 1.2; thus, I opted for the RDA.

To add environmental variables to the NMDS ordination diagram and test their correlation with the ordination axes, I used the function "env_fit" from the "vegan" package (Oksanen et al., 2024). The number of seedlings was added as a variable, along with the cover of *Dryas*, dead *Dryas*, litter, bare soil, and different functional groups, vegetation and *Dryas* heights, NDVI, soil moisture, and the number of flowering species. The latter is the total number of different flowering species found in the plot, not the abundance of flowering individuals.

3. Results

3.1 Number of seedlings

The number of seedlings was significantly lower at the high-elevation site and in warmed plots compared to the low-elevations site ($p < 0.001$) and control plots ($p < 0.05$), respectively (Table 1, Figure 5).

Table 1. *Results from an additive generalized linear model (GLM) with a negative binomial distribution, using elevation and warming treatment as explanatory variables and number of seedlings as the response variable. Estimates are presented on the log scale, along with standard errors, Z values, and P values. Bold numbers indicate significance at $p < 0.05$. Significant intercept indicate that the number of seedlings in high-elevation control plots was significantly different from 0. n = 8 control and 9 warmed plots at high elevation, 5 control and 5 warmed plots at low elevation.*

Variable	Estimate	Std. error	Z value	P value
Number of seedlings				
Intercept	1.414	0.397	3.56	< **0.001**
Treatment	-0.804	0.393	-2.047	**0.041**
Elevation	-2.06	0.405	-5.089	< **0.001**

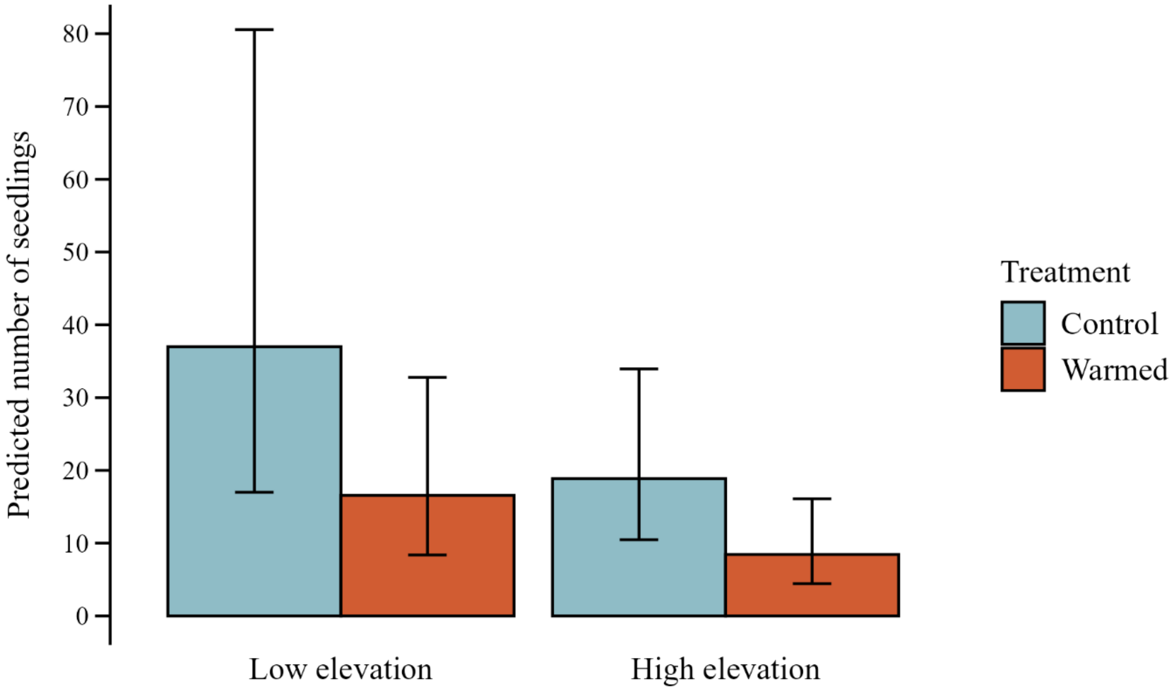

Figure 5. *Mean predicted number of seedlings from the negative binomial GLM in control (blue bars) and warmed plots (orange bars) ± 95% confidence intervals. n = 8 control and 9 warmed plots at high elevation, and 5 control and 5 warmed plots at low elevation.*

3.2 Cover of litter, dead *Dryas*, and different functional groups

The cover of litter was significantly higher in both warmed plots ($p < 0.05$) and dead *Dryas* showed almost significant increase in cover with warming ($p = 0.069$), but neither variables differed between the two elevation sites (Figure 6, Table 2).

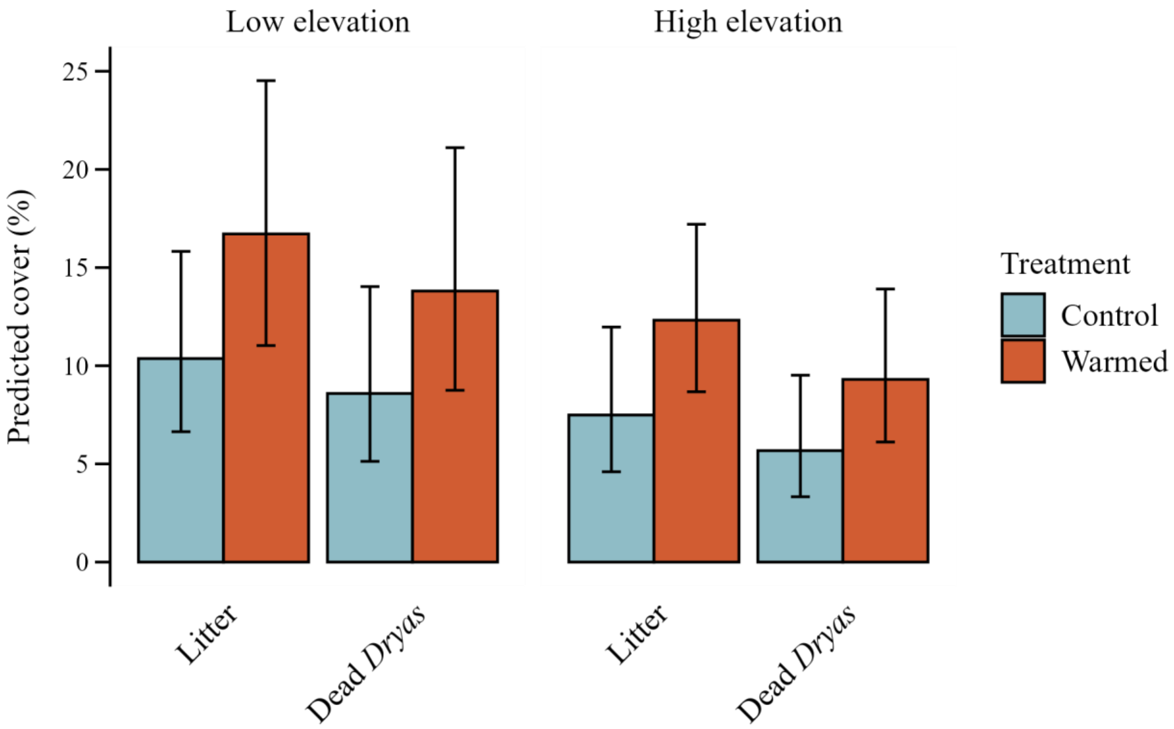

Figure 6. *Mean predicted cover of litter and dead* Dryas *from beta GLMs in control (blue bars) and warmed plots (orange bars) ± 95% confidence intervals. n = 8 control and 9 warmed plots at high elevation, and 5 control and 5 warmed plots at low elevation.*

The cover of dwarf shrubs, *Dryas*, forbs, and bryophytes differed significantly between elevational sites (Figure 7, Table 2). Dwarf shrubs, *Dryas*, and bryophytes had higher cover at the high elevation site ($p < 0.01$), whereas forbs had higher cover at the low elevation site ($p < 0.05$). There was no significant difference in the cover of any functional group with warming, except for an almost significant decrease in bryophyte cover ($p = 0.065$, Table 2). When excluding a significant outlier, the bryophyte cover decrease with warming was highly significant ($p < 0.001$).

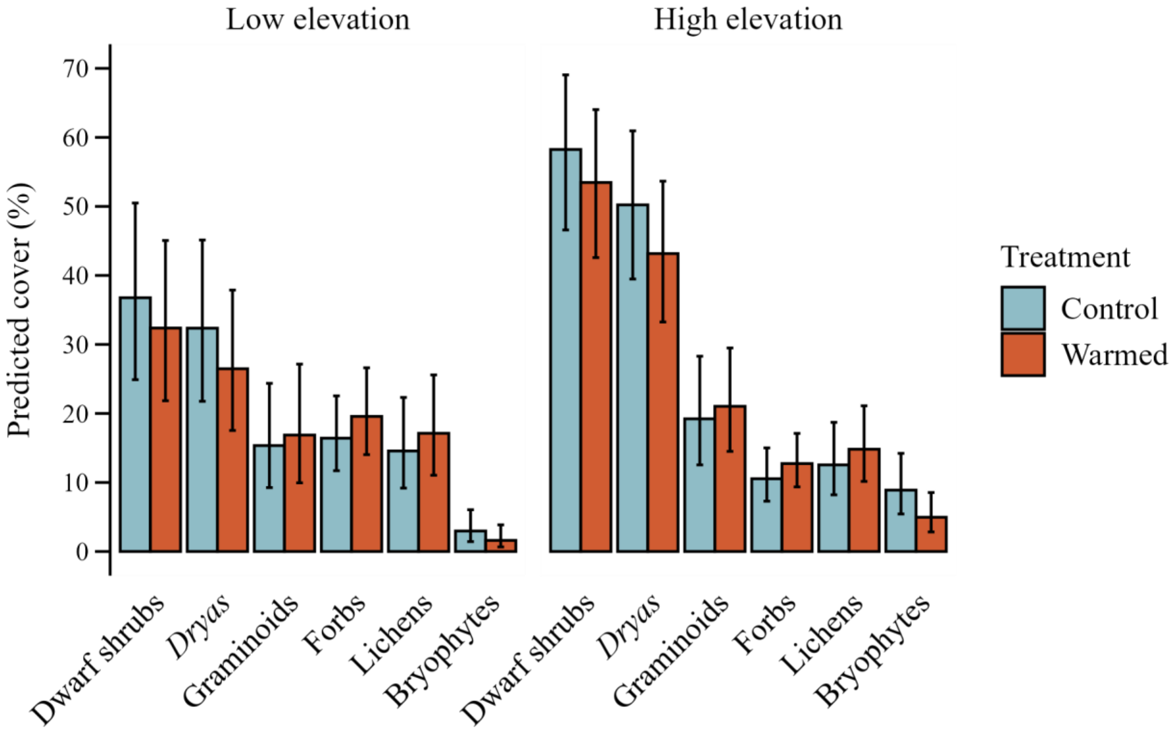

Figure 7. *Mean predicted cover of different functional groups and* Dryas *from beta GLMs in control (blue bars) and warmed plots (orange bars) ± 95% confidence intervals. n = 8 control and 9 warmed plots at high elevation, and 5 control and 5 warmed plots at low elevation.*

Table 2. *Results from additive generalized linear models (GLMs) with beta distributions, using elevation and treatment as explanatory variables and cover of litter, dead* Dryas, *living* Dryas, *and different functional groups as response variables. Estimates are presented on the log-odds scale, along with standard errors, Z values, and P values. Bold numbers indicate significance at p < 0.05. Significant intercept indicate that the response variable in high-elevation control plots was significantly different from 0. n = 8 control and 9 warmed plots at high elevation, 5 control and 5 warmed plots at low elevation.*

Variable	**Estimate**	**Std. error**	**Z value**	**P value**
Litter				
Intercept	-2.157	0.248	-8.702	< **0.001**
Treatment	0.551	0.272	2.029	**0.042**
Elevation	-0.356	0.269	-1.323	0.186
Dead Dryas				
Intercept	-2.365	0.282	-8.392	< **0.001**
Treatment	0.534	0.293	1.820	0.069
Elevation	-0.446	0.292	-1.528	0.127
Dwarf shrubs				
Intercept	-0.542	0.287	-1.892	0.059
Treatment	-0.194	0.289	-0.672	0.501
Elevation	0.875	0.302	2.903	**0.004**
Dryas				
Intercept	-0.737	0.277	-2.666	**0.008**
Treatment	-0.284	0.275	-1.032	0.302
Elevation	0.746	0.29	2.576	**0.01**
Graminoids				
Intercept	-1.708	0.293	-5.822	< **0.001**
Treatment	0.113	0.299	0.377	0.706
Elevation	0.272	0.314	0.866	0.386
Forbs				
Intercept	-1.627	0.201	-8.110	< **0.001**
Treatment	0.214	0.224	0.957	0.339
Elevation	-0.511	0.225	-2.274	**0.023**
Lichens				
Intercept	-1.769	0.266	-6.643	< **0.001**
Treatment	0.192	0.274	0.703	0.482
Elevation	-0.172	0.28	-0.616	0.538
Bryophytes				
Intercept	-3.487	0.38	-9.182	< **0.001**
Treatment	-0.626	0.34	-1.845	0.065
Elevation	1.161	0.381	3.043	**0.002**

3.3 Vegetation and *Dryas* height

The vegetation height was significantly taller with warming ($p < 0.05$, Figure 8A, Table 3), including non-signficiant trends of taller *Dryas* height in warmed plots ($p = 0.092$, Figure 8B, Table 3). Neither vegetation nor *Dryas* height differed significantly with elevation (Table 3).

Table 3. *Results from additive generalized linear models (GLMs) with gamma distributions, using elevation and treatment as explanatory variables and vegetation and* Dryas *height as response variables. Estimates are presented on the log scale, along with standard errors, T values, and P values. Significant intercept indicate that the response variable in high-elevation control plots was significantly different from 0. Bold numbers indicate significance at $p < 0.05$. n = 8 control and 9 warmed plots at high elevation, 5 control and 5 warmed plots at low elevation.*

Variable	Estimate	Std. error	T value	P value
Vegetation height				
Intercept	0.546	0.099	5.529	< **0.001**
Treatment	0.242	0.104	2.333	**0.02**
Elevation	0.201	0.107	1.874	0.061
Dryas *height*				
Intercept	0.387	0.078	4.928	< **0.001**
Treatment	0.136	0.081	1.685	0.092
Elevation	0.035	0.084	0.414	0.679

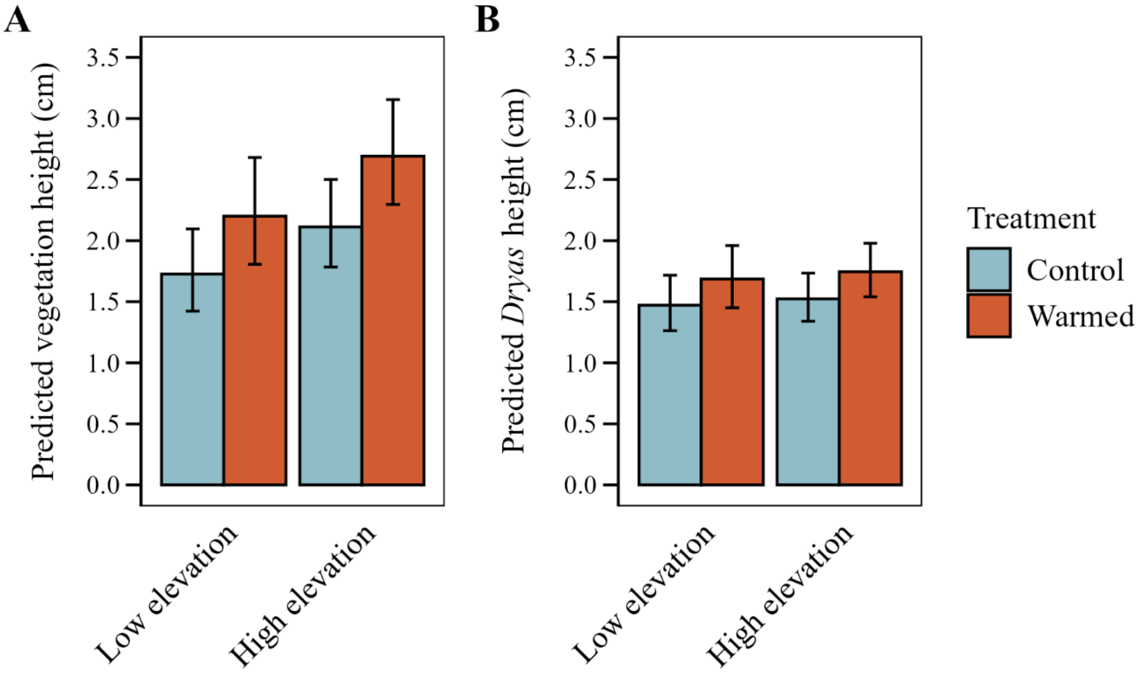

Figure 8. *A) Mean predicted vegetation height and B)* Dryas *height from the gamma GLM in control (blue bars) and warmed plots (orange bars) ± 95% confidence intervals. n = 8 control and 9 warmed plots at high elevation, and 5 control and 5 warmed plots at low elevation.*

3.4 Soil moisture and NDVI

Soil moisture was signifcantly lower at the high elevation site (p < 0.001, Figure 9A, Table 4), whereas NDVI was higher at the high elevation site (p < 0.01, Figure 9B, Table 4). Neither soil moisture nor NDVI differed significantly with warming (Table 4).

Table 4. *Results from additive generalized linear models (GLMs) with beta distributions, using elevation and treatment as explanatory variables and soil moisture and NDVI as response variables. Estimates are presented on the log-odds scale, along with standard errors, Z values, and P values. Bold numbers indicate significance at p < 0.05. Significant intercept indicate that the response variable in high-elevation control plots was significantly different from 0. n = 8 control and 9 warmed plots at high elevation, 5 control and 5 warmed plots at low elevation.*

Variable	Estimate	Std. error	Z value	P value
Soil moisture				
Intercept	-0.532	0.211	-2.517	**0.012**
Treatment	-0.252	0.241	-1.048	0.295
Elevation	-0.913	0.243	-3.752	**< 0.001**
NDVI				
Intercept	-0.047	0.118	-0.398	0.691
Treatment	-0.174	0.124	-1.412	0.158
Elevation	0.336	0.128	2.636	**0.008**

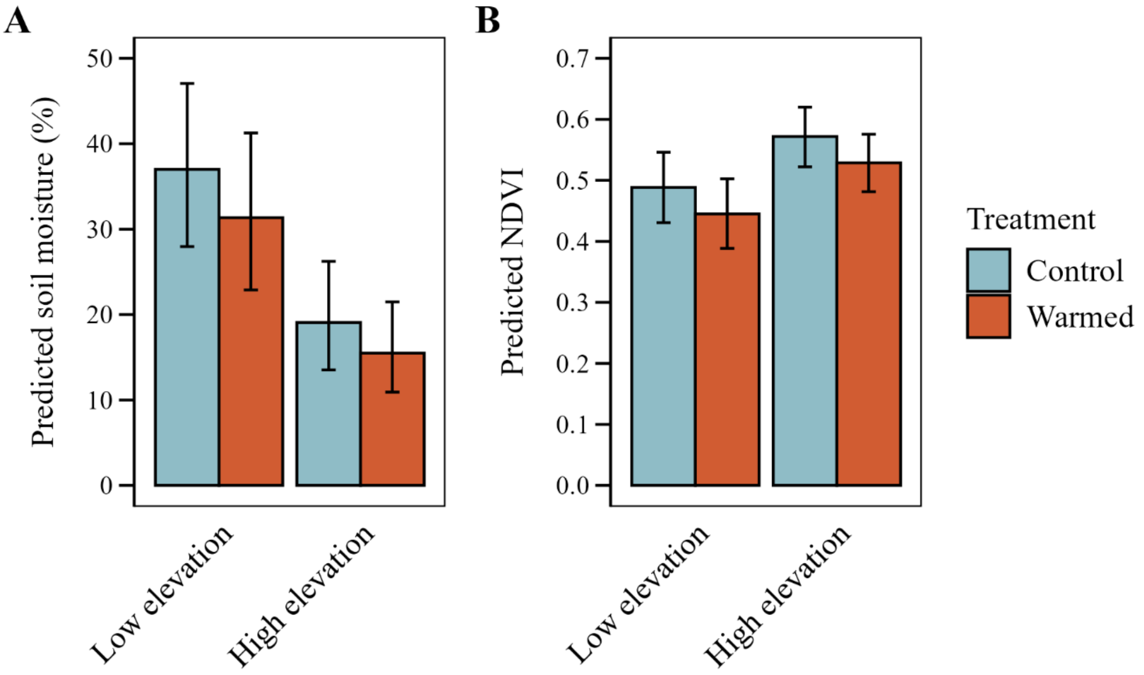

Figure 9. *A) Mean predicted soil moisture and B) NDVI from the beta GLM in control (blue bars) and warmed plots (orange bars) ± 95% confidence intervals. n = 8 control and 9 warmed plots at high elevation, and 5 control and 5 warmed plots at low elevation.*

3.5 Species composition at high elevation

In the NMDS ordination diagram, warmed and control plots formed two semi-overlapping clusters, indicating a change in species composition at the high-elevation site with warming (Figure 10). The plot illustrating species' distribution along the NMDS axes is included in Appendix C. The RDA confirmed that warming did have a significant effect on species composition ($p < 0.05$, Table 5).

Table 5. *Results from the redundancy analysis (RDA) testing the effect of warming on species composition, including degrees of freedom (Df), variance, f- and P-values. Subplot frequency was used as the measure of abundance. Permutations = 999.*

RDA	Df	Variance	F	P value
Treatment	1	0.31524	2.3376	**0.011**
Residual	15	2.02278		

As indicated by the general direction of the arrows (Figure 10), control plots were characterised by higher cover of forbs and bryophytes, both of which showed significant correlation with the ordination axes ($p < 0.01$, Table 6) and explained a substantial portion of the variance ($R^2 = 0.52$ for forbs, $R^2 = 0.75$ for bryophytes, Table 6). Warmed plots were more closely associated with higher cover of dwarf shrubs, including *Dryas*, and litter, including dead *Dryas*, as well as taller *Dryas* and overall vegetation. Dwarf shrubs, dead *Dryas*, and vegetation height were significantly correlated with the ordination axes ($p < 0.05$, Table 6), and could explain some of the variance ($R^2 = 0.46$ for dwarf shrubs, $R^2 = 0.41$ for dead *Dryas*, $R^2 = 0.36$ for vegetation height, Table 6). NDVI seemed to be higher in warmed plots, showing significant correlation with the ordination axes ($p = 0.001$, Table 6) and could explain a lot of the variance ($R^2 = 0.78$). There did not seem to be a very distinct pattern in the cover of lichens and graminoids, and neither showed significant correlation with the ordination axes (Table 6).

Control plots were positively associated with a higher number of seedlings, soil moisture, number of flowering species, and bare soil cover (Figure 10). Conversely, warmed plots were negatively associated with the number of seedlings, and positively associated with higher cover of litter, including dead *Dryas*, taller *Dryas* and overall vegetation, higher cover of *Dryas* and dwarf shrubs.

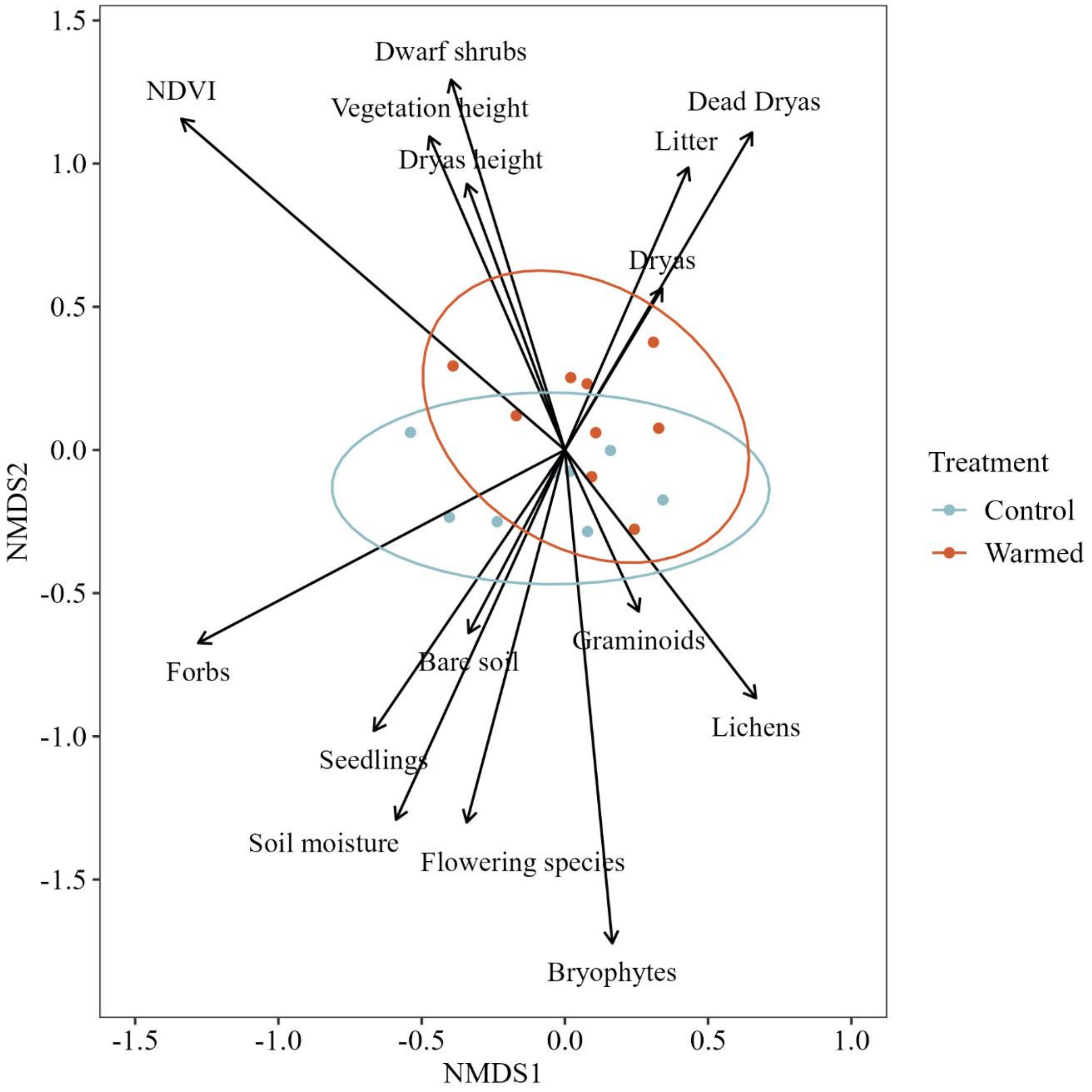

Figure 10. *Non-metric multidimensional scaling (NMDS) ordination diagram of plots at the high-elevation site. k = 2, stress = 0.12. The positioning of control plots (blue) and warmed plots (orange) along the two NMDS axes reflects similarities and dissimilarities in species composition, using subplot frequency as a measure of abundance, with ellipses representing 95% confidence intervals. Arrows represent environmental vectors, indicating the direction and strength of associations with the ordination axes and each other. n = 8 control and 9 warmed plots. Full species list used for the ordination is listed in Appendix A.*

Table 6. *Results from the envfit analysis assessing the correlation between environmental variables and the NMDS ordination axes, including* R^2 *and P values for each variable. Bold numbers indicate significance at* $p < 0.05$*. Permutations = 999.*

Variable	NMDS1	NMDS2	R^2	P value
Bare soil	-0.46540	-0.88510	0.1304	0.429
Bryophytes	0.09568	-0.99541	0.7488	**0.001**
Dead *Dryas*	0.50763	0.86158	0.4139	**0.018**
Dryas	0.51549	0.85690	0.1086	0.458
Dryas height	-0.34537	0.93847	0.2450	0.118
Dwarf shrubs	-0.29377	0.95588	0.4573	**0.018**
Flowering species	-0.25462	-0.9670	0.4523	**0.019**
Forbs	-0.88476	-0.46605	0.5231	**0.009**
Graminoids	0.41566	-0.90952	0.0961	0.480
Lichens	0.60986	-0.79251	0.2991	0.081
Litter	0.40018	0.91644	0.2896	0.082
Moisture	-0.41524	-0.9097	0.5034	**0.009**
NDVI	-0.75682	0.65363	0.7824	**0.001**
Seedlings	-0.56229	-0.82694	0.3518	**0.041**
Vegetation height	-0.39645	0.91806	0.3554	**0.038**

3.6 Dark diversity and community completeness at high elevation

There were a total of 50 vascular plant species found within the 17 plots examined at the high-elevation site in 2024 (Appendix B). When including the 42 plots analysed in 2023, one additional unique vascular plant species was recorded, resulting in an observed species richness of 51 across both seasons. There were 30 vascular plant species found exclusively outside the plots at the high-elevation site in 2024, of which 22 could likely inhabit the *Dryas* heath community, i.e. contributing to the dark diversity. This leads to a calculated community completeness index of 0.84, which can be interpreted as 84% of species in the local species pool having recently been recorded inside the high-elevation plots.

4. Discussion

My study found that long-term experimental warming resulted in reduced seedling recruitment within the *Dryas* heath. Fewer seedlings in warmed plots can potentially be linked to negative effects of increased litter cover, the majority of which consisted of dead *Dryas*, as well as taller vegetation, including non-significant trends of taller *Dryas*. The effect of warming did not differ between the two sites for any of the variables tested, suggesting that despite the two sites representing different environmental conditions within the *Dryas* heath, there was a seemingly uniform response to warming. Elevation had an even greater effect on seedlings than warming, with far fewer seedlings being recorded at the high-elevation site on average. The high-elevation site was characterised mainly by lower soil moisture, but also higher cover of *Dryas*, dwarf shrubs, and lower cover of forbs than at low elevation. Species composition was different between warmed and control plots at the high-elevation site, and the number of seedlings was positively associated with the number of flowering species. Dark diversity estimates were lower than expected and thus community completeness was higher than expected.

4.1 Reduced seedling recruitment with warming

Warmed plots had fewer seedlings than control plots at both elevations, as hypothesised. While increased temperatures are generally associated with positive effects on both germination and seedling emergence (e.g. Vázquez-Ramírez & Venn, 2021), higher temperatures can also lead to increased evapotranspiration resulting in topsoil desiccation (Walsh et al., 2020) – which has been proposed as one of the factors reducing seedling abundances at warmer sites (Giménez-Benavides et al., 2007, 2008; Meineri et al., 2013; Walck et al., 2011). The high-elevation site along the ridge is quite dry during the growing season (Roos et al., 2023), so it is possible that elevated temperatures might have impacted the recruitment process here by further limiting soil moisture availability. However, soil moisture was only non-significantly lower in warmed plots, a pattern which is often reported in OTCs (Hollister et al., 2023). Furthermore, the wetter, low-elevation site exhibited the same response to warming; thus, water limitations might not fully explain the reduced seedling recruitment with warming.

The cover of *Dryas* and different functional groups did not differ significantly with warming, except for a non-significant trend of decreased bryophyte cover. This trend became very significant when excluding an outlier warmed plot at the low-elevation site that had very high bryophyte cover. Reduced cover of bryophytes and lichens along with no significant differences in vascular plant cover was reported in the high-elevation plots surveyed in 2023 (Eiterjord, 2024), partially in line with my findings. Bryophytes responding negatively to warming is a general trend across ITEX sites (Elmendorf et al., 2012), and bryophytes can affect water availability in the soil (Cornelissen et al., 2007a). As such, lower bryophyte cover could also potentially have contributed to reduced seedling recruitment, supported by a similar alignment of bryophyte cover and the number of seedlings in the NMDS ordination of high-elevation plots. However, other studies indicate that the direction of this relationship might be very specific to both the bryophyte and seedling species (Lett et al., 2017; Lett et al., 2020), thus bryophyte cover is unlikely to explain the general effect of warming on seedlings. Lastly, warmed plots had a higher cover of litter and taller vegetation – in line with my hypotheses and other findings at alpine and Arctic sites (e.g. Elmendorf et al., 2012) – so these changes in the vegetation may be better suited to explain the reduced seedling recruitment with warming.

The increased cover of overall litter found with warming, as well as almost significant trends of increased dead *Dryas* cover specifically, may have inhibited seedling recruitment in the *Dryas* heath by altering the physical and chemical environment. While the effect of litter on seedlings is not directly tested in my study, the alignment of the number of seedlings and cover of litter and dead *Dryas* in the NMDS ordination of high-elevation plots lends support to my hypothesis. This is further substantiated by an earlier study of the *Dryas* heath at Finse, which suggested that litter in warmed plots could have negatively impacted the long-term establishment of sown alpine species (Olsen & Klanderud, 2014). Previous studies assessing the relationship between litter and naturally occurring seedlings in alpine ecosystems are seemingly rare and do not support my hypothesis; either finding no effect, neither positive nor negative (Forbis, 2009; Welling & Laine, 2000), or reporting positive sheltering effects of litter on seedling emergence (Venn & Morgan, 2009). This albeit sparse body of research contradicting my findings could indicate that site-specific conditions, e.g. the type of litter, in the *Dryas* heath contributed to the potential negative relationship between litter cover and seedling recruitment.

Litter can inhibit seedling recruitment by acting as a physical barrier reducing light penetration to both seeds and seedlings, as well as facilitating pathogens and releasing allelopathic compounds (Facelli & Pickett, 1991). Additionally, the physical and chemical structure of different types of litter is important factors to consider when assessing it as a mechanical barrier inhibiting seeds and seedlings (Facelli & Pickett, 1991). *Dryas* leaves are highly recalcitrant (Jónsdóttir et al., 2023) and made up the majority of litter in the heath (Eiterjord, 2024; personal observation). They also appear to remain attached to the stem after browning for numerous seasons before ultimately senescing (personal observation), which could limit wind dispersal. Leaves of evergreen shrubs in general have been noted to have slower rates of decomposition when compared to forbs and sedges (Cornelissen et al., 2007b) and could take over 10 years before fully decomposing in alpine ecosystems (Körner, 2021). As such, the shading effects of dead *Dryas*, whether it is still attached to the plant or not, on germinating seeds and emerging seedlings may be more pronounced than other types of litter. One proposed cause of the higher *Dryas* die-off reported in warmed plots at Sanddalsnuten in 2023 was previous extreme weather events (Eiterjord, 2024). Extreme weather events are predicted to increase in frequency with climate change and might be more impactful on ecosystems than the gradual increase in average temperatures (Roos et al., 2023; Walsh et al., 2020), with vegetation browning being an increasingly common response (Bjerke et al., 2014; Bjerke et al., 2017; Myers-Smith et al., 2020). To my knowledge, most studies examining seedling recruitment in alpine ecosystems have not had litter as the main focus unless the studied habitats are grasslands (Viard-Crétat et al., 2010; Yuan et al., 2016), emphasising the novelty of my findings. Further insight into the legacy effects of vegetation browning on seedling recruitment could be gained by assessing how different early life-stages of plants are affected by different types and depths of litter.

Finally, while the increased cover of litter can be indicative of vegetation browning, the increased vegetation height in warmed plots could also indicate increased productivity and vegetation greening. The presence of both browning and greening in response to warming could explain why NDVI did not differ significantly with warming and indicates that this might not be the best measure to catch small-scale patterns of browning. The taller vegetation and non-significant trends of taller *Dryas* in warmed plots could have similar shading effects on seedlings as litter, with the added element of increased competition for the same limited resources. This negative relationship is supported by the opposite alignment of the number of seedlings and taller vegetation and *Dryas* in the NMDS ordination of high-elevation plots. As the increased canopy height did not coincide with higher cover, it may limit the impact of competition somewhat. Competition reducing seedling recruitment is however widely reported, with gaps in vegetation acknowledged as important regenerative niches (Abbedissen, 2025; Forbis, 2009; Klanderud, 2010; Klanderud et al., 2017; Tingstad et al., 2015), and competition might increase with increasing temperatures (Olsen & Klanderud, 2014). The vegetation cover in the *Dryas* heath is quite dense, and bare soil was generally very low within the established plots in the *Dryas* heath; thus, accurate models for this variable could not be made in this study. My findings could suggest that gaps might become less common in the heath with warming as canopies grow taller and more ground is covered by litter, though decreased bryophyte cover could also open up new areas where individuals can establish. Over time, however, the availability of open microhabitats might decrease, and disturbances, like grazing, could become increasingly important for maintaining gaps in the vegetation and mitigating the effects of warming, as suggested by Klanderud et al. (2017).

4.2 The importance of soil moisture

The high-elevation site along the ridge and the low-elevation site at the leeside exhibit different abiotic conditions, including substantial differences in soil moisture levels – confirmed by the significantly lower soil moisture at the high-elevation site. With that in mind, elevation had an even greater impact on the number of seedlings than warming, and there were fewer seedlings recorded in high-elevation plots. The importance of soil moisture for both seed germination and early seedling establishment is widely recognised (e.g. Walck et al., 2011), and it has also been remarked as an important factor in alpine regions specifically (Abbedissen, 2025; Forbis, 2003; Klanderud & Totland, 2007; Körner, 2021; Rosbakh et al., 2022). My findings further support this relationship between soil moisture and naturally occurring seedlings, while indicating that soil moisture may be more limiting for seedling recruitment than any direct or indirect effects of warming in the *Dryas* heath. Furthermore, variation in soil moisture conditions and subsequent seedling recruitment likely exists within each site as well. In the NMDS ordination, higher soil moisture was positively associated with a higher number of seedlings within the high-elevation site, indicating that wetter microhabitats are influential for the spatial distribution of naturally occurring seedlings.

Warming acting together with changes in soil moisture may have greater impacts on seedlings than either variable on its own (Walck et al., 2011). Indeed, the combined effect of warming and lower soil moisture likely explains the lowest predicted number of seedlings being in warmed high-elevation plots. Contrary to what I expected, however, the effect of warming did not vary between the two sites for any of the variables tested in this study. Thus, my hypothesis of more severe effects of warming on the cover of litter and dead *Dryas* at the drier, high-elevation site was not supported. When assessing these results together, they indicates that the differences in soil moisture between the two sites could not buffer against the processes leading to increased vegetation browning with warming.

Lastly, the high-elevation site was not only characterised by lower soil moisture but also significantly higher NDVI measurements and a higher cover of *Dryas*, dwarf shrubs in general, and bryophytes, as well as lower cover of forbs. The higher NDVI at the high-elevation site was unexpected but could possibly be explained by the higher dwarf shrub cover. Lower NDVI readings at the low-elevation site could be due to warmed plots having had a couple of patches of bare soil from another experiment that the sensor might have detected (personal observation), as well as a slight tendency towards higher litter cover in all plots. This again highlights that NDVI might be more accurate for large-scale remote sensing, and its usage for predicting favourable conditions for seedlings may be limited. The differences in community composition, however, could have contributed to the difference in seedling recruitment between the two sites. Higher *Dryas* cover at the high-elevation site could have negatively impacted seedling recruitment, as indicated by the opposite alignment of *Dryas* cover and the number of seedlings in the NMDS ordination. *Dryas* has been linked to reducing species recruitment through competition (Klanderud & Totland, 2007), and might be a stronger competitor than other species. Furthermore, a higher cover of forbs was positively associated with the number of seedlings in the NMDS ordination of high-elevation plots, which may suggest that greater abundance of these species at the low-elevation site are less likely to exclude seedlings. In light of this, species-specific interactions could be an important factor when assessing the relative impacts of competition on seedling recruitment.

4.3 Species composition, dark diversity, and seedling recruitment dynamics

While I did not record the species of the seedlings, the most abundant seedling observed was the annual, hemiparasitic forb *Euphrasia wettsteinii* (personal observation). Most alpine plants are perennials (Körner, 2021), and this is true for the species within the *Dryas* heath as well. Abundant recordings of an annual forb should be kept in mind when interpreting my findings, though *E. wettsteinii* was present in around half of both control and warmed plots at the high-elevation site (Appendix A), and likely did not change the predicted effect of warming.

The species composition at the high-elevation site was significantly different in warmed and control plots, in line with previous findings in the other plots surveyed previously at the high-elevation site (Eiterjord, 2024). Changes in vascular plant species composition with warming could potentially impact seedling recruitment – as a positive relationship between neighbouring species richness and naturally occurring seedling densities has been identified before (Klanderud, 2010). In the NMDS ordination, the number of seedlings aligned with the number of different flowering species (i.e. flowering species richness), suggesting a positive relationship between these two variables as well. A higher diversity of flowering species could perhaps lead to higher local abundances of different types of seeds (e.g. small- vs. large-seeded, early- vs. late-germinating), which could in turn lead to higher seedling numbers due to a diversity of germination strategies. The positioning of the arrows in the ordination suggests a higher number of different flowering species in high-elevation control plots, which somewhat contrasts other studies reporting increased flowering (Fazlioglu & Wan, 2021) and seed production (Welker et al., 1997) in various alpine species in response to experimental warming. Further research into the relationship among flower abundance, flower diversity, and seedling recruitment could shed more light on how these variables interact.

The dark diversity estimate for the *Dryas* heath surrounding the high-elevation site was 22, which is lower than the average number of 30 species recorded across other ITEX sites (Daskalova et al. in prep). This was somewhat surprising, as I hypothesised that species could potentially have better recruitment success in microhabitats outside the plots that are less dominated by *Dryas*, due to the competitive role *Dryas* has on both species recruitment (Klanderud & Totland, 2007) and the surrounding vegetation (Klanderud & Totland, 2004). I therefore expected similar, if not higher, dark diversity estimates for the *Dryas* heath when compared to other ITEX-sites. One possible explanation could be the adjustments we made when surveying the surrounding area. The protocol specified walking in spiral transects up to a radius of 100 m, covering a total area of approximately 31,400 m^2, but we covered a substantially smaller area of approximately 5,000 m^2 using spiral transects. While we compensated for this by walking two line transects spanning 100 metres from the centre, it is not unlikely that more species would have been included in the local species pool if we had covered a larger region, and subsequent dark diversity estimates might have been higher.

The estimated community completeness when accounting for dark diversity in the *Dryas* heath was 84%. Community completeness allows for comparing biodiversity across different ecosystems (Pärtel et al., 2025), though caution should be exercised when comparing community completeness using different methods, as the resulting estimates often differ (Hostens et al., 2023; Lewis et al., 2016). This becomes apparent when comparing the estimates for the *Dryas* heath with those gathered from a recent article using species co-occurrences, wherein the global average at sites with low human impact was 35% and the highest estimates overall were at around 50% (Pärtel et al., 2025). As the data from other ITEX sites using a similar method to mine is not yet published, the comparative element of community completeness is somewhat limited as of now. Still, the high community completeness indicates that the established plots include the majority of plant species that could inhabit the *Dryas* heath at the summit, suggesting that local dispersal limitations are not strongly limiting species richness and recruitment.

4.4 Future implications for alpine ecosystems

In order to persist through anthropogenic climate change, sessile organisms can stay and adapt or shift their ranges to track their existing niches. Both of these overarching strategies rely on seedling recruitment to either evolve or effectively colonise new areas (Walck et al., 2011). If recruitment can be inhibited by direct or indirect effects of increased temperatures, both in dry and wetter areas, as my results suggest, this carries wide-reaching implications for future population dynamics in alpine ecosystems. Furthermore, temperatures may increase beyond the warming effect that open-top chambers provide (Henry & Molau, 1997; IPCC, 2023), resulting in greater impacts than this type of experimental warming study accounts for.

Reduced seedling recruitment with warming could influence the resilience of alpine species. Alpine species existing close to the summit have limited possibilities of expanding further upwards (Körner, 2021; Steinbauer et al., 2018). Although phenotypic plasticity is generally high in alpine plants and has been linked to rapid responses to warming (Arnold et al., 2024; Henn et al., 2018), it might have a limited effect in increasing resilience to extreme weather events (Arnold et al., 2022; Geange et al., 2017; Notarnicola et al., 2021). Furthermore, seedling recruitment in a long-lived alpine plant has been reported to be more common in favourable years, whereas clonal offspring are higher in less favourable years (Weppler et al., 2006). As extreme weather events are projected to increase in frequency with climate change (Walsh et al., 2020), this could indicate that sexual reproduction might become more important to the persistence of alpine plants but simultaneously less accessible due to extreme weather events.

Reduced seedling recruitment with warming could potentially buffer against the establishment of new individuals, preventing the elevational range shift of lowland species establishing at higher elevations as observed at other study sites (e.g. Steinbauer et al., 2018). How persistent this inhibiting effect is will likely be highly dependent on both the decomposition of litter and the frequency of events leading to increased vegetation browning. Additionally, vegetation greening resulting in increased competition will likely play an increasingly important role under higher temperatures (Olsen & Klanderud, 2014). As competition increases, the smaller seeded alpine species may even be at a disadvantage in competing for light when compared to the generally larger seeds of boreal and generalist species (Klanderud et al., 2017). These findings together suggest that warming-induced changes in the vegetation may reduce seedling recruitment, especially that of small-seeded alpine species. Furthermore, alpine species have been reported to lack the competitive traits required to prevent the arrival of lowland competitors (Meineri et al., 2020), though contradicting findings have also been observed (Abbedissen, 2025). Understanding how receptive alpine habitats are to seedling recruitment under elevated temperatures may be critical for understanding future biodiversity shifts.

Finally, climate change is associated not only with increasing temperatures but also with changes in precipitation patterns (IPCC, 2023). The higher number of naturally occurring seedlings at the wetter, low-elevation site suggests that increased soil moisture may make areas more open to seedling recruitment. Seedling recruitment in alpine areas with predicted increases in precipitation may be facilitated by a wetter future, while the opposite may be true for areas with predicted decreases in precipitation. In this region of Norway, precipitation is expected to increase (Hanssen-Bauer et al., 2017), which could lead to greater snowfall during the winter and increased soil moisture availability during the summer. In the *Dryas* heath, this may be more impactful at the lower elevation leeside, as the higher elevation ridge generally remains quite dry during the summer and the high wind-exposure allows only thin snow cover during the winter despite already high annual precipitation (Roos et al., 2023). Including predicted changes in precipitation in future studies could be useful to fully understand the impacts of climate change on seedling recruitment.

5. Conclusion

Over 20 years of experimental warming of the *Dryas* heath resulted in lower seedling recruitment. My findings indicate that warming indirectly inhibited early life-stages of plants through increased vegetation browning and taller canopies, which could suppress the recruitment of new individuals under elevated temperatures. The long-term negative effects on recruitment will likely depend on both the frequency of events leading to increased vegetation browning and how fast litter decomposes, and it remains to be seen how this could affect the arrival of new migrants and adaptability of alpine plants within this biodiverse *Dryas* heath. Further research on how different types and depths of litter affect the recruitment process could be increasingly important at sites with observed vegetation browning. Experimental warming had a similar impact on both the ridge at higher elevation and the leeside at lower elevation, though the combined effect of warming and lower soil moisture likely explains the much lower seedling numbers predicted in high-elevation warmed plots. Furthermore, low dark diversity estimates at high elevation indicate that that local dispersal limitations are not strongly limiting species richness and recruitment. Wetter areas may be more open to seedling recruitment and further research could benefit from also considering how precipitation patterns are predicted to change in the future.

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Appendix A – Recorded species at high-elevation site

I recorded 90 taxa inside the plots at the high-elevation site. All taxa are listed in Table 7, including the abbreviations, scientific names, Norwegian names, and number of plots the species was recorded.

Table 7. *All species recorded inside control and warmed plots at the high-elevation site of the* Dryas *heath, with abbreviations, full scientific and Norwegian names, as well as the number of plots the species was present in. n = 8 control and 9 warmed plots.*

			Presence in plots	
Abbreviation	**Scientific name**	**Norske navn**	**Control**	**Warmed**
Dwarf shrubs				
Dry oct	*Dryas octopetala*	Reinrose	8	9
Emp nig	*Empetrum nigrum*	Krekling	2	1
Har hyp	*Harrimanella hypnoides*	Moselyng	2	1
Sal her	*Salix herbacea*	Museøre	7	6
Sal ret	*Salix reticulata*	Rynkevier	7	5
Vac uli	*Vaccinium uliginosum*	Blokkebær	0	2
Forbs				
Ant alp	*Antennaria alpina*	Fjellkattefot	4	7
Ant dio	*Antennaria dioica*	Kattefot	5	3
Ast alp	*Astragalus alpinus*	Setermjelt	0	1
Bar alp	*Bartsia alpina*	Svarttopp	4	6
Bis viv	*Bistorta vivipara*	Harerug	8	9
Cam rot	*Campanula rotundifolia*	Blåklokke	5	5
Car bel	*Cardamine bellidifolia*	Høyfjellskarse	1	0
Cer alp	*Cerastium alpinum*	Fjellarve	5	4
Che bif	*Cherleria biflora*	Tuearve	1	1
Com ten	*Comastoma tenellum*	Småsøte	0	1
Eri uni	*Erigeron uniflorus*	Småbakkestjerne	5	5
Eup wet	*Euphrasia wettsteinii*	Småøyentrøst	5	5
Gen niv	*Gentiana nivalis*	Snøsøte	2	0

Hie alp	*Hieracium alpinum*	Fjellsveve	1	0
Oxy lap	*Oxytropis lapponica*	Reinmjelt	3	3
Par pal	*Parnassia palustris*	Jåblom	2	3
Pot cra	*Potentilla crantzii*	Flekkmure	5	6
Ran sp.	*Ranunculus sp.*	Soleieslekten	2	0
Rho ros	*Rhodiola rosea*	Rosenrot	0	1
Sau alp	*Saussurea alpina*	Fjelltistel	8	9
Sax opp	*Saxifraga oppositifolia*	Rødsildre	1	1
Sil aca	*Silene acaulis*	Fjellsmelle	8	9
Sil wah	*Silene wahlbergella*	Blindurt	1	0
Tar sp.	*Taraxacum sp.*	Løvetannslekten	2	0
Tha alp	*Thalictrum alpinum*	Fjellfrøstjerne	8	9
Tof pus	*Tofieldia pusilla*	Bjørnebrodd	0	2
Vis alp	*Viscaria alpina*	Fjelltjæreblom	1	3
Pteridophyte				
Sel sel	*Selaginella selaginoides*	Dvergjamne	6	5
Graminoids				
Ant odo	*Anthoxanthum odoratum*	Gulaks	1	2
Car atr	*Carex atrata*	Svartstarr	6	3
Car cap	*Carex capillaris*	Hårstarr	2	3
Car myo	*Carex myosuroides*	Rabbetust	1	2
Car rup	*Carex rupestris*	Bergstarr	8	9
Car vag	*Carex vaginata*	Slirestarr	7	7
Fes ovi	*Festuca ovina*	Sauesvingel	8	4
Fes viv	*Festuca vivipara*	Geitsvingel	7	3
Jun big	*Juncus biglumis*	Tvillingsiv	1	0
Jun trif	*Juncus trifidus*	Rabbesiv	1	1
Luz con	*Luzula confusa*	Vardefrytle	2	0
Luz spi	*Luzula spicata*	Aksfrytle	6	3
Luz sp.	*Luzula sp.*	Frytleslekten	7	4
Poa alp	*Poa alpina*	Fjellrapp	4	3
Tri spi	*Trisetum spicatum*	Svartaks	1	2

Bryophytes				
And sp.	*Andreaeopsida sp.*	Sotmoser	2	0
Bra alb	*Brachythecium albicans*	Bleiklundmose	7	6
Bry sp.	*Bryum sp.*	Vrangmoseslekten	8	7
Dicranella sp.	*Dicranella sp.*	Grøftemoseslekten	0	1
Dicranum sp.	*Dicranum sp.*	Sigdmoseslekten	8	9
Dis cap	*Districhium capillaceum*	Puteplanmose	6	6
Hyl spl	*Hylocomium splendens*	Etasjemose	6	7
Hyp sp.	*Hypnum sp.*	Flettemoseslekten	0	1
Lop sp.	*Lophozia sp.*	Flikmoseslekten	8	9
Pla por	*Plagiochila porelloides*	Berghinnemose	2	0
Pla sp.	*Plagiomnium sp.*	Fagermoseslekten	1	1
Poh sp.	*Pohlia sp.*	Nikkemoseslekten	1	1
Pol sp.	*Polytrichum sp.*	Bjørnemoseslekten	8	6
Pti cil	*Ptilidium ciliare*	Bakkefrynse	8	9
Rac sp.	*Racomitrium sp.*	Gråmoseslekten	7	6
Rhy rug	*Rhytidium rugosum*	Labbmose	2	3
San unc	*Sanionia uncinata*	Klobleikmose	8	7
Syn sp.	*Syntricia sp.*	Hårstjerneslekten	1	1
Lichens				
Ale nig	*Alectoria nigricans*	Jervskjegg	1	0
Ale och	*Alectoria ochroleuca*	Rabbeskjegg	2	3
Bry div	*Bryocaulon divergens*	Fjelltagg	3	3
Cet eri	*Cetraria ericetorum*	Smal islandslav	7	9
Cet isl	*Cetraria islandica*	Islandslav	5	8
Cla arb	*Cladonia arbuscula*	Lys reinlav	8	9
Cla gra	*Cladonia gracilis*	Syllav	7	8
Cla ran	*Cladonia rangiferina*	Grå reinlav	3	3
Cla unc	*Cladonia uncialis*	Pigglav	7	7
Cla sp.	*Cladonia sp.*	Begerlavslekten	4	4
Col sp.	*Collema sp.*	Glyelav	3	0
Fla cuc	*Flavocetraria cucullata*	Gulskjerpe	6	7

Fla niv	*Flavocetraria nivalis*	Gulskinn	6	8
Och fri	*Ochrolechia frigida*	Fjellkorkje	4	0
Pel aph	*Peltigera aphtosa*	Grønnever	4	3
Pel mat	*Peltigera malacea*	Mattnever	0	1
Pel sp.	*Peltigera sp.*	Peltigera	0	1
Sol sp.	*Solorina sp.*	Skållav	1	0
Sph glo	*Sphaerophorus globosus*	Brun korallav	2	4
Ste sp.	*Stereocaulon*	Saltlav	8	7
Tha ver	*Thamnolium vermicularis*	Makklav	5	6
Vul jun	*Vulpicida juniperinus*	Einerlav	2	0
Lichen sp.	*Unknown*	Ukjent		

Appendix B – Dark diversity species

I recorded a total of 30 vascular plant species outside the plots at the high-elevation site. All species are listed in Table 8, including the scientific and Norwegian names, distance from the centre of the high-elevation site where the species was first observed, as well as an evaluation of whether the species was considered probable of inhabiting the *Dryas* heath based on habitat suitability.

Table 8. *All species recorded outside the plots at the high-elevation site of the* Dryas *heath, with location of first observation, scientific and Norwegian names, functional group, and habitat suitability. Line transect is someplace between 40-100 metres from the centre. Bolded species were excluded from dark diversity estimates.*

First observation	Scientific name	Norske navn	Functional group	Habitat suitability
1 m quadrant	*Festuca rubia*	Rødsvingel	Graminoid	Yes
10 m radius	*Deschampsia alpina*	Fjellbunke	Graminoid	Yes
10 m radius	*Huperzia appressa*	Fjell-lusegras	Pteri	Yes
10 m radius	*Veronica alpina*	Snøveronika	Forb	Yes
10 m radius	*Saxifraga cespitosa*	Tuesildre	Forb	Yes
10 m radius	*Draba fladnizensis*	Alperublom	Forb	Yes
10 m radius	*Botrychium lunaria*	Marinøkkel	Pteridophyte	Yes
20 m radius	***Saxifraga cernua***	Knoppsildre	Forb	Unlikely, more common in snowbeds
20 m radius	*Arctous alpina*	Rypebær	Dwarf shrub	Yes
20 m radius	***Arabsis alpina***	Fjellskrinneblom	Forb	Unlikely, more common in wetter soils, snowbeds, or along streams
20 m radius	*Leontodon autumnalis*	Føllblom	Forb	Yes
30 m radius	*Saxifraga aizoides*	Gulsildre	Forb	Yes
40 m radius	*Alchemilla sp.*	Marikåpeslekten	Forb	Yes
40 m radius	*Sibbaldia procumbens*	Trefingerurt	Forb	Yes

40 m radius	*Diphasiastrum alpinum*	Fjelljamne	Pteri	Yes
40 m radius	*Sagina saginoides*	Seterarve	Forb	Yes
Line transect	*Juncus triglumis*	Trillingsiv	Graminoid	Yes
Line transect	*Avenella flexuosa*	Smyle	Graminoid	Yes
Line transect	*Omalotheca supina*	Dverggråurt	Forb	Yes
Line transect	*Epilobium anagallidifolium*	Dvergmjølke	Forb	Yes
Line transect	*Phleum alpinum*	Fjelltimotei	Graminoid	Yes
Line transect	***Rumex acetosa***	Matsyre	Forb	Unlikely, more common in meadows
Line transect	***Omalotheca norvegica***	Setergråurt	Forb	Unlikely, more common in meadows
Line transect	***Poa flexuosa***	Mykrapp	Graminoid	Unlikely, more common in more exposed areas
Line transect	***Petasites frigidus***	Fjellpestrot	Forb	Unlikely, more common in wetter soils
Line transect	***Eriophorum vaginatum***	Torvull	Forb	Unlikely, more common in wetter soils
Line transect	*Pinguicula vulgaris*	Tettegras	Forb	Yes
Line transect	*Dactylorhiza viridis*	Grønnkurle	Forb	Yes
Line transect	***Micranthes tenuis***	Grannsildre	Forb	Unlikely, more common in snowbeds
Line transect	*Equisetum variegatum*	Fjellsnelle	Pteridophyte	Yes

Appendix C – NMDS ordination diagram with species

The NMDS ordination diagram showing the position of each species is shown in Figure 11. There is a slight trend of bryophytes and lichens clumping together towards the bottom right part of the diagram, whereas the other functional groups seem more broadly dispersed.

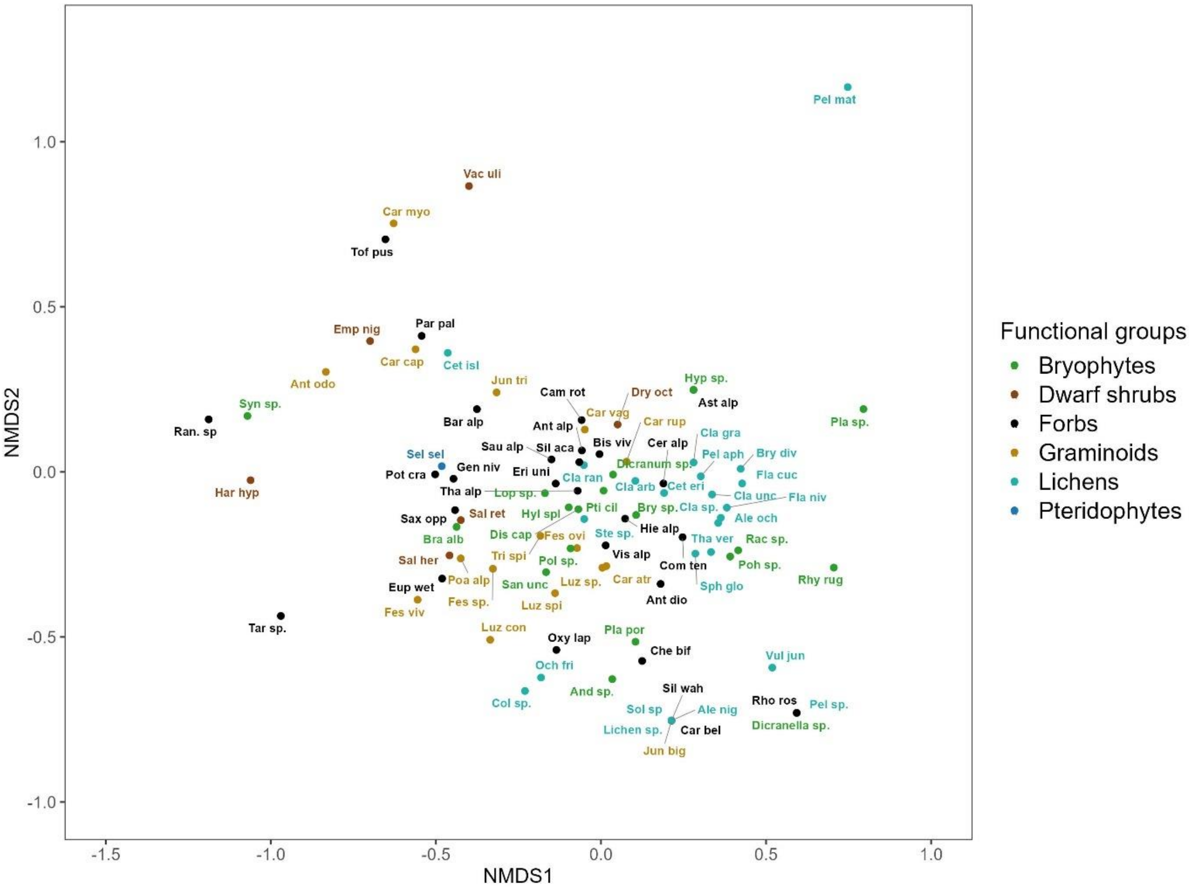

Figure 11. *Species distribution in the NMDS ordination. The positioning of several species have been adjusted to avoid overlapping, lines connect them to the original point. Functional groups are colour-coded according to the legend to the right. Full species names are listed in Appendix A.*

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