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Heating the heath: How 23 years of experimental warming changes an alpine biodiversity hotspot

Gaute Eiterjord

Master of Science in Natural Resource Management

Acknowledgments

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Gaute Eiterjord

*«Musøyra heiter eg,
fjellmo for sume,
og her i høgfjellet høyrer eg til,
ei ørliti selje,
på berre ein tume
men endå eit tre,
det minste av alle, segjer Linné.»*

*Kulden er hard her
og vinden strid,
her kan ein kje stå
med krana vid
og susa som askar og almar i lid, -
ein lyt gjera seg liten
og krjupa på kne [...]»*

«Fjellblokka kallar deg meg òg» by
Olav H. Hauge (with permission from Samlaget)

Abstract

Climate change is increasing the temperature of Arctic and alpine areas, which can alter plant communities and lead to loss of biodiversity. One of the most species-rich plant communities in Scandinavian mountains are *Dryas* heaths, named after the dominant dwarf shrub *Dryas octopetala*. In 2000, an experiment with open top chambers (OTCs) was started to study the effects of higher temperatures on *Dryas* heaths at Mt. Sanddalsnuten (1554 m asl.) in Finse, southwest Norway. In 2023, I studied the effects of long-term warming on the plant community by performing a vegetation analysis with high taxonomic resolution for vascular plants, lichens, and bryophytes. I also measured vegetation height, soil moisture, normalized difference vegetation index (NDVI), and flower abundance.

Long-term warming led to a decrease in the cover and richness of lichens and bryophytes, a decline in community diversity and evenness, and altered species composition. The cover of litter and dead *Dryas* increased with warming, but the cover of vascular plant functional groups and vascular plant richness was not affected. Warmed plots had taller vegetation and *Dryas* canopies. Shading from taller vascular plant and their litter may have caused the decline in lichens and bryophytes. A drier environment could have contributed to this, as I found a non-significant trend of decreasing soil moisture in warmed plots. Increased cover of litter and dead *Dryas* could be due to extreme events, such as heatwaves or droughts, being amplified by experimental warming. The small response of vascular plants to warming could be a result of water and nutrient limitations, as the heath is situated on a dry ridge with shallow soil. It could also be because of the slow growth and longevity of Arctic-alpine plants, or because the dominance of *Dryas* leaves little room for other species in the community to increase. In addition, the existing high diversity in the *Dryas* heath could have provided stability and resistance to environmental changes. There was a non-significant trend of increasing flower abundance in *Dryas* in warmed plots, which could indicate a higher reproductive effort with increased temperatures.

My study shows that lichens and bryophytes responded most strongly to long-term warming in the *Dryas* heath. Given their importance for biodiversity and ecosystem functions in Arctic-alpine plant communities, lichens and bryophytes are important to include in studies of climate change. Dry and low-productive *Dryas* heaths may be more resistant to higher temperatures than other Arctic-alpine habitats, but long-term warming could eventually impoverish these diversity hotspots. Given the slow changes in these communities, long-term experiments are necessary to understand what effects higher temperatures can have on their biodiversity in the future.

Samandrag

Arktisk-alpine område blir varmare som følge av klimaendringane. Dette kan endra plantesamfunn og føra til tap av artsmangfald. Reinroseheier, dominert av dvergbusken reinrose (*Dryas octopetala*) er blant dei mest artsrike plantesamfunna som finst i skandinaviske fjell. For å studera effekten av høgare temperatur på reinroseheier blei det i 2000 sett i gang eit forsøk med oppvarmingskammer (open top chambers, OTC) på Sanddalsnuten (1554 moh.) på Finse. I 2023 undersøkte eg langtidseffekten av oppvarming på dette plantesamfunnet gjennom ein vegetasjonsanalyse med høg taksonomisk oppløysing for karplanter, mose og lav. I tillegg gjorde eg målingar av plantehøgde, jordfukt, vegetasjonsindeksen NDVI og blomsterriksdom.

Langtidsoppvarming førte til lågare dekning og artsriksdom av lav og mose. Mangfaldet og jamleiken i plantesamfunnet var lågare med oppvarming, og artssamansetning var annleis. Oppvarming ga høgare dekning av plantestrø og daud reinrose, men førte ikkje til endringar i dekninga av funksjonelle karplantegrupper eller artsriksdomen til karplantene. Vegetasjonen generelt, og reinrosa spesielt, var høgare med oppvarming. Saman med meir plantestrø kan det ha gitt meir skugge som førte til at lav- og moseartane gjekk tilbake. Eit tørrare miljø kan ha bidratt til dette, då eg fann ein ikkje-signifikant tendens mot tørrare jord med oppvarming. Auken i strø og daud reinrose kan skuldast at ekstremvær, som heitebølger og tørke, har blitt forsterka av eksperimentell oppvarming. At karplantene elles reagerte lite på høgare temperatur kan vera fordi dei er begrensa av vatn og næringsstoff, sidan dei veks på ein tørr rabb med tynt jordsmonn. Det kan òg skuldast at Arktisk-alpine planteartar er sakteveksande og langlevde, eller at reinrosa har ein sterk dominans i plantesamfunnet som gir lite plass til at andre artar kan auka i omfang. Høgt mangfald i plantesamfunnet kan òg ha bidratt til stabilitet og gjort det motstandsdyktig mot endringar. Reinrosa viste ein ikkje-signifikant tendens mot større blomsterriksdom med oppvarming, som kan tyda på at høgare temperatur kan gi større reproduksjonsevne.

Studien min viser at lav og mose blei mest påverka av langtidsoppvarming i reinroseheia. Det er derfor viktig å inkludera desse artsgruppene i studiar av klimaendringar då dei utgjer ein viktig del av artsmangfaldet og økosystemfunksjonane i Arktisk-alpine plantesamfunn. Lågproduktive og tørre reinroseheier kan moglegens vera meir motstandsdyktige mot høgare temperaturar enn andre Arktis-alpine naturtypar, men desse artsrike samfunna kan likevel bli fattigare med oppvarming over lengre tid. Sidan desse plantesamfunna endrar seg sakte er det viktig å oppretthalda langtidforsøk for å forstå kva slags konsekvensar framtidige temperaturstigningar kan ha for artsmangfaldet deira.

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Introduction

Global temperatures are increasing because of climate change (IPCC, 2023), and the effects of warming are especially pronounced in Arctic and alpine areas (Henry & Molau, 1997; Hock et al., 2022; Nogués-Bravo et al., 2007). A warmer climate is expected to change the structure and composition of these high latitude and elevation ecosystems, altering biodiversity along with ecosystem functions (Bjorkman et al., 2020; Elmendorf et al., 2012a; Elmendorf et al., 2012b; Walker et al., 2006). Species in Arctic-alpine plant communities are adapted to harsh environments, characterized by low temperatures and short growing seasons (Wookey et al., 1993). They are often slow-growing and low-statured, and at a competitive disadvantage against taller and faster-growing lowland species (Alexander et al., 2018; Baruah et al., 2017; Klanderud, 2005; Meineri et al., 2020; van Zuijlen et al., 2022b). With warming, Arctic-alpine species could be threatened by the expanse of more warm-adapted species, such as an increase of shrubs and graminoids within their communities or from lower latitudes and elevations (Alexander et al., 2018; Bjorkman et al., 2020; Criado et al., 2024 (preprint); Klanderud, 2008; Roos et al., 2023; Scharn et al., 2022; Steinbauer et al., 2018).

A synthesis of warming experiments in 27 Arctic and alpine sites in the Northern hemisphere showed that elevated temperatures can cause taller and more abundant vascular plants, increased litter production, and decreased abundances of lichens and bryophytes (Elmendorf et al., 2012a). However, such changes were not observed everywhere, and sites that were initially warm or moist were in general more affected by warming than drier and colder sites (Elmendorf et al., 2012a). This shows that local environmental conditions could enhance or impede temperature-driven changes in Arctic-alpine plant communities (Elmendorf et al., 2012a). In a more recent synthesis from Arctic sites Bjorkman et al. (2020) found similar changes in plant communities as a response to warming as Elmendorf et al. (2012a) in both experimental and long-term monitoring studies, although no change was also a common response.

Greater vascular plant cover and biomass can result in ecosystem “greening”, which has been observed over large areas in both the Arctic and in the European Alps through an increase in the Normalized Difference Vegetation Index (NDVI) (Myers-Smith et al., 2020; Rumpf et al., 2022). Higher temperatures are expected to increase plant height (Bjorkman et al., 2018), as well as flower abundance and seed production (Frei & Henry, 2022; Henry & Molau, 1997; Welker et al., 1997). On the other hand, climate change is also expected to cause more frequent extreme weather events, which may result in dead plant material and “browning” of ecosystems (Myers-Smith et al., 2020; Phoenix & Bjerke, 2016), as well as failures to reproduce (Panchen et al., 2022).

Biodiversity could be reduced in Arctic-alpine plant communities if warming makes low-stature species lose ground (Alexander et al., 2015; Gottfried et al., 2012; Klein et al., 2004; Odland et al., 2010; Vanneste et al., 2017; Walker et al., 2006). Lichens and bryophytes, often referred to as

cryptogams, are an important part of these communities as their contribution to species richness increase at higher latitudes and elevations (Lang et al., 2012; Lett et al., 2022; Turetsky et al., 2012). They are crucial for ecosystem functions such as nutrient cycling, retaining water, insulating the soil, reflecting energy through a high albedo, and affecting the recruitment of vascular plants (Lett et al., 2022; Turetsky et al., 2012; Vanneste et al., 2017; Aartsma et al., 2020). The cryptogams' reduced ability to compete with vascular plants could put them at risk when temperatures increase (Asplund et al., 2022; Cornelissen et al., 2001; Elmendorf et al., 2012a; Lang et al., 2012; Walker et al., 2006). Despite this, studies of vegetation and climate change often group cryptogams into broad categories, and do not identify them to the level of species (Alatalo et al., 2014; Lett et al., 2022; Vanneste et al., 2017). A higher taxonomic resolution of cryptogams in climate change studies is therefore needed. It might reveal ecosystem responses to environmental changes that are not apparent in vascular plants (van Zuijlen et al., 2022a).

Despite increasing temperatures in Arctic and alpine ecosystems over the last decades, many experimental and long-term monitoring studies have shown that plant communities do not necessarily change as rapidly, or in the same direction, as expected (Bjorkman et al., 2020). For example, warming is expected to lead to loss of beta diversity as widespread species grow more dominant across communities, but a recent study on vascular plants across 45 Arctic and alpine sites found no such effect (Criado et al., 2024 (preprint)). The discrepancy between predictions of biodiversity loss and actual observations in Arctic-alpine plant communities could be due to inherent lags in their rates of change (Alexander et al., 2018).

Long-term studies are needed to understand how vulnerable species and communities are to environmental changes (Lindenmayer et al., 2012). This is especially important in slowly changing Arctic and alpine ecosystems, where the effects of warming are expected to grow more pronounced with time (Jónsdóttir et al., 2023; Komatsu et al., 2019; Scharn et al., 2022). Warming experiments using open top chambers (OTCs) have been performed since the 1990s through the International Tundra Experiment (ITEX) to forecast changes in Arctic-alpine plant communities (Henry et al., 2022; Hollister et al., 2023). Still, in the synthesis of warming experiments by Elmendorf et al. (2012a), few studies had lasted more than ten years. Resurveying warming experiments with even more time can therefore reveal responses that were not apparent in the short term and allow for better predictions about the future (Alatalo et al., 2022).

At the ITEX site of Finse, southwest Norway, an experimental warming study on alpine *Dryas* heath has been ongoing since 2000 (Klanderud & Totland, 2007). *Dryas* heaths are dominated by the dwarf shrub *Dryas octopetala* (hereafter: *Dryas*) and are diversity hotspots compared to surrounding areas (Klanderud & Totland, 2005). The *Dryas* heath at Finse has shown resistance to warming, although the cover of lichens and bryophytes has been reduced (Hasvik, 2018; Roos et al., 2023; Sundsbø, 2019; van Zuijlen et al., 2022a). The small changes have been attributed to the

dryness at the site, as well as the high species diversity in the community (Klanderud & Totland, 2008; Roos et al., 2023). The last surveys at the site were performed in 2016 for vascular plants (Olsen in Hasvik (2018)), 2017 for lichens (Hasvik, 2018) and 2018 for bryophytes (Sundsbo, 2019). There has not been a simultaneous survey of the whole community since 2008 (Klanderud in Elmendorf (2012a)).

In this study I aim to evaluate the effect of 23 years of experimental warming on this alpine biodiversity hotspot. I present a survey of the whole plant community with high taxonomic resolution for vascular plants, lichens, and bryophytes, and how it has been affected by experimental warming. I seek to answer the following research questions:

- 1) How has experimental warming affected species richness, diversity, evenness, composition, cover of individual species, and cover of functional groups and litter?
- 2) Has experimental warming affected the cover, height, and flower abundance of *Dryas*, as well as vegetation height and number of flowering species?
- 3) Are there differences in NDVI and soil moisture between warmed and control plots?

I hypothesize that warmed plots will have increased cover of vascular plants, especially dwarf shrubs and graminoids, higher litter cover, and reduced cover of lichens and bryophytes, compared to control plots. Following this, I expect fewer and less abundant cryptogam species to reduce overall diversity and evenness and alter species composition in the plant community. With warming, I expect *Dryas* to have greater height, cover, and flower abundance than in control plots. I also expect that warming will have led to taller vegetation and a higher number of flowering species. Lastly, I expect that warmed plots will have higher NDVI because of an increase in vascular plants, but also lower soil moisture due to higher evaporation.

Method

Study area

The study was performed on the south-facing slope of the summit of Mt. Sandalsnuten (1554 m a.s.l.) in Finse (N 60.626 E 7.552), Ulvik municipality in southwest Norway (Fig. 1). The bedrock at the site is phyllite (Askvik, 2008), which is rich in calcareous minerals and gives rise to a diverse flora (Roos et al., 2023). There are domestic sheep grazing in the area, as well as wild reindeer (Strand et al., 2011). The snow at Mt. Sandalsnuten usually melts by the end of May or the start of June (Klanderud, 2005).

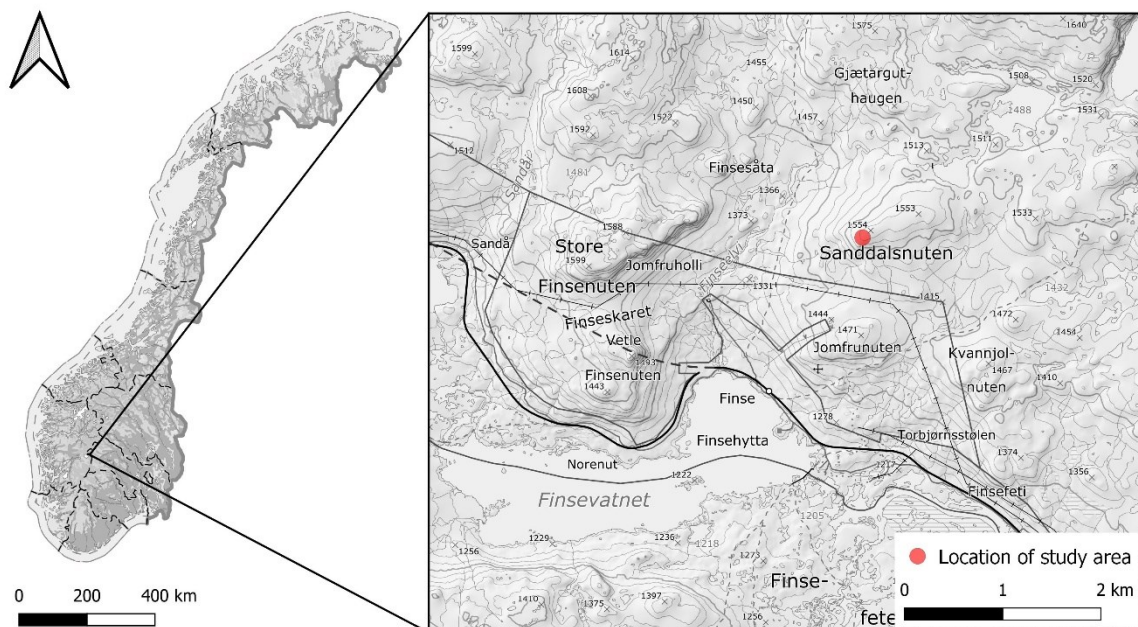


Fig. 1: Location of the study site. Made with QGIS version 3.28 (QGIS.org, 2024). Background map: Topographical map of Norway (Norwegian Mapping Authority, 2024).

From 1991-2020 the mean annual precipitation at Finse (1220 m a.s.l.) was 984 mm (The Norwegian Meteorological Institute, 2024). The average temperature in December and June was -8.2°C and 7.3°C , respectively (The Norwegian Meteorological Institute, 2024). Annual temperatures at Finse increased by 0.36°C per decade in the period 1970-2020 (Roos et al., 2023). The expected temperature increase for this region by 2071-2100 is between 1.2°C and 3.9°C compared to 1971-2000 (Hanssen-Bauer et al., 2017).

The dominant plant species at the study site is *Dryas octopetala* (*Dryas*), which grows in dense mats interspersed with a variety of other species (Klanderud & Totland, 2005). *Dryas* is an

evergreen dwarf shrub growing on dry, calcareous ridges in Arctic and alpine regions of the northern hemisphere (Klanderud & Totland, 2004; Reinhardt et al., 2013; Welker et al., 1997). *Dryas* has been shown to have both nursing and competitive effects on other species depending on its abundance (Klanderud & Totland, 2004). As an evergreen, *Dryas* keeps its leaves on for several years, but they turn brown in autumn until they rejuvenate in spring (Welker et al., 1997). *Dryas* as a species and its common habitat, exposed ridge, are red-listed (NT) in Norway due to the risk of overgrowth with increasing temperatures (Grytnes et al., 2018; Solstad et al., 2021). In addition, *Dryas* has limited opportunities for migration into higher mountain ranges because the calcareous bedrock it grows on is seldom found above 1500-1600 m a.s.l. in southern and 1000-1200 m a.s.l. in northern Norway (Solstad et al., 2021).

Besides *Dryas*, other common species at the site are the dwarf shrubs *Salix reticulata* and *Salix herbacea*; the forbs *Bartsia alpina*, *Bistorta vivipara*, *Cerastium alpinum*, *Potentilla crantzii*, *Saussurea alpina*, *Silene acaulis*, and *Thalictrum alpinum*; the graminoids *Carex vaginata*, *Carex rupestris*, *Carex atrata*, *Festuca ovina*, *Festuca vivipara*, and *Juncus trifidus*; the lichens *Flavocetraria nivalis*, *Flavocetraria cucullate*, *Cetraria islandica*, *Cetraria ericetorum*, *Cladonia arbuscula*, *Cladonia uncinalis*, and *Thamnolia vermicularis*; and the bryophytes *Hylocomium splendens*, *Ptilidium ciliare*, *Rhytidium rhugosum*, as well as species from the genera *Dicranum*, *Polytrichum*, and *Racomitrium*.

Experimental design

In the year 2000, 80 plots of 60 × 60 cm were established in the *Dryas* heath. 40 of them have been exposed to experimental warming by open top chambers (OTC) (Fig. 2) and 40 are control plots. The OTCs are designed according to ITEX standards as hexagonal polycarbonate chambers without a roof (Klanderud & Totland, 2007). The average heating effect inside the OTCs at Finse is +1.5°C in the air and +1°C in the soil (Klanderud & Totland, 2005). The chambers are left in place in winter, but melt-out dates are similar between warmed plots and control plots (Hollister et al., 2023; Klanderud & Totland, 2007). The design of OTCs allow rain, snow, pollinators, and small mammalian herbivores to enter them while providing a steady heating effect (Henry & Molau, 1997; Hollister et al., 2023; Kaarlejärvi et al., 2013). Larger grazers could avoid them, but OTCs have been shown to consistently provide similar effects on vegetation as increasing ambient temperatures over time (Elmendorf et al., 2015; Hollister et al., 2023), also when accounting for side-effects on grazing (Elmendorf et al., 2012a). When using OTCs, it is recommended to measure other physical impacts of the chambers that can affect the vegetation inside, such as eventual changes in soil moisture (Hollister et al., 2023).



Fig. 2: Field work in June 2023. To the left: An open top chamber (OTC) at the study site with flowering *Dryas* inside. To the right: Vegetation analysis in a split-plot. Photo: Gaute Eiterjord.

Vegetation analysis

I performed field work in the summer of 2023, from late June to mid-August. I surveyed 21 warmed plots and 21 control plots. Each plot is divided into two 30×60 cm split-plots (Fig. 2), with 18 subplots of 10×10 cm in each split-plot, leading to a total of 36 subplots per plot. In each plot I recorded the presence of every species of vascular plant, lichen, and bryophyte. For vascular plants, I recorded occurrences of flower buds, fully developed flowers, or fruits (hereafter referred to as “flowers”). In addition, I estimated the cover (%) of each species visually, as well as the cover of the following functional groups: Dwarf shrubs, forbs, graminoids, lichens, bryophytes, litter, bare soil, biological crust (algae or other miniscule growths on rock and soil), and dead *Dryas* (Fig. 3). Cover beneath 1 % was recorded as 0.1 % for the analyses. The pteridophytes *Huperzia arctica* and *Seliginella selaginoides* were sorted into the “forb” category in the analyses. Biological crust was left out of the analyses due to very low cover. When estimating cover of dead *Dryas* I did not discern between leaves that were loose on the ground as litter or dead leaves still attached to the plant, as this distinction was difficult to make when doing field work.

In each plot, I measured the height of the general vegetation in 12 of the subplots, using the same subplots in each plot. The height of *Dryas* was measured in six subplots in each plot in the same manner. If there was no vegetation present in a subplot, I used the nearest suitable one. Height values were averaged for each plot in the analyses.

Most species were identified in the field, following nomenclature in Elven et al. (2022) for vascular plants, Holien and Tønberg (2017) and the Natural History Museum (2024) for lichens, and Hallingbäck (2016) for bryophytes. When a species was difficult to identify in the field, I sampled it

outside the plot and studied it later under a microscope. The species that I could not identify to species level are described on the genus level. This concerns the graminoids *Festuca ovina* and *Festuca vivipara* and the bryophytes *Dicranum*, *Grimmia*, *Lophozia*, *Pohlia*, *Polytrichum*, and *Racomitrium*.



Fig. 3: Dead, grey leaves of *Dryas* inside an open top chamber (OTC) at the study site, August 2023. Photo: Gaute Eiterjord.

Soil moisture and NDVI measurements

I recorded soil moisture in 30 warmed plots and 30 control plots on the 28th of June, 21st of July, 1st of August, and 12th of August. I used a Delta-T SM150 moisture meter (Delta-T Devices Ltd., England) with the mineral soil setting to measure volumetric water content (% volume) at a soil depth of 6 cm. Soil moisture was recorded on four fixed locations in each plot. If there were rocks or too shallow soil for the moisture meter's pins to be fully covered, or if it gave an erroneous reading, another spot nearby was chosen. The NDVI was measured with a handheld Greenseeker (Trimble Inc., USA). One measurement of NDVI was done for 30 warmed plots and 30 control plots on the 28th of June, 21st of July, 1st of August, and 13th of August. I recorded and tested differences in soil moisture and NDVI for a higher number of plots than I did vegetation analysis in. This was because the original plan was to survey 60 plots, but weather and time constraints did not allow for this.

Statistical analyses

I performed statistical analyses with R (R Core Team, 2022) and RStudio (Posit team, 2023). The packages “readxl” (Wickham & Bryan, 2023), “dplyr” (Wickham et al., 2023), “ggplot2” (Wickham, 2016), “patchwork” (Pedersen, 2023), “ggrepel” (Slowikowski, 2023), and “reshape2” (Wickham, 2007) were used to organize data and make figures.

To measure plant community diversity I used species richness (number of species in a plot), Shannon’s diversity index (Shannon, 1948), and Pielou’s evenness index (Pielou, 1966). The diversity and evenness indices were calculated with the “vegan” package (Oksanen et al., 2022). Shannon’s diversity index is given by the following formula:

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

H is the index value, where the lowest value is 0 and a higher value indicates higher diversity. p_i is the relative abundance of the i th species in a plot, a value from 0 to 1 based on its presence in 0 to 36 subplots, and S is the total number of species. Pielou’s evenness index J was calculated by dividing the Shannon index by the logarithm of the total species number:

$$J = \frac{H}{\log (S)}$$

To test the assumptions of normally distributed data with equal variance, I visually inspected histograms and used Shapiro-wilk tests and Equal Variance F-tests. Several of the variables were right-skewed, and I therefore used a cube-root transformation on the following: Cover of forbs, graminoids, lichens, bryophytes, litter, dead *Dryas*; vegetation height; and *Dryas* flower abundance (% of subplots with flowers present). In all figures I present untransformed data.

For all variables I tested if the mean values were significantly different between the warmed plots and the control plots. The following variables met the assumptions of normal distribution and equal variance and were tested with a Student’s T-test: Shrub cover, *Dryas* cover, bryophyte cover, vascular plant species richness and vegetation height. Welch’s T-test was used for variables with unequal variance, these were: Cover of forbs, graminoids, lichens, litter, dead *Dryas*; bryophyte species richness; *Dryas* flowers; and Shannon’s diversity index. A non-parametric Mann-Whitney-Wilcoxon-test was used for the variables that did not meet the requirements of the other tests, even after transformation. These were: Cover of bare soil; total species richness; lichen species richness; and *Dryas* height. I used Mann-Whitney-Wilcoxon-tests to test if the cover of individual species differed between all the control plots and all the warmed plots. This test was used because many species had skewed distributions, making it difficult to fulfill the assumptions required of a Student’s or Welch’s T-test.

I tested the difference in soil moisture and NDVI between warmed and control plots with a mixed linear model with treatment as a fixed effect, using the package “lmerTest” (Kuznetsova et al., 2017). Because I did repeated measures of soil moisture and NDVI, I used plot ID and date of measurement as random effects to account for non-independent observations.

To examine differences in species composition between warmed plots and control plots, I used nonmetric multidimensional scaling (NMDS) with subplot frequency of species per plot as the abundance measure. The use of subplot frequency to some extent favours species with little cover. I consider this to be the case for many of the species I surveyed and therefore chose this method to best illustrate changes in species composition. I also performed the analyses using visual estimation of cover (%), these are shown in Appendix B. All ordination analyses were performed with the “vegan”-package (Oksanen et al., 2022). I used two dimensions in the NMDS as it reduced the stress below 0.2, which is generally considered to be an acceptable threshold (Dexter et al., 2018). To further test the validity of the NMDS model I ran a detrended correspondence analysis (DCA) (Økland, 1996) and compared the axes of the NMDS and DCA models with Kendall’s rank correlation coefficient. As the NMDS and DCA models correlated, I proceeded with the NMDS.

I used the function “env_fit” from the “vegan” package (Oksanen et al., 2022) to add the following environmental variables to the NMDS diagram: Cover of functional groups, litter, bare soil, vegetation height, soil moisture and NDVI. For these analyses I averaged soil moisture and NDVI values per plot across all measurement dates. To test if the NMDS-axes were correlated with environmental variables I used Kendall’s rank correlation coefficient. The correlations test used a Z distribution for all variables except soil moisture where it used a T-distribution. Lastly, I performed canonical correspondence and redundancy analyses (CCA and RDA, respectively) to test if the species composition differed between warmed plots and control plots. I used both methods to account for the possibility of both linear and unimodal distributions of species abundances along the main gradients (Lepš & Šmilauer, 2003; Økland et al., 1999). Due to the short length of the axes in the NMDS ordination diagram, the results from the RDA are presented. Results from the CCA are shown in Appendix B.

Results

Cover of functional groups, litter and bare soil

My survey of the *Dryas* heath 23 years after the experimental warming study started showed that there were significant decreases in bryophyte and lichen cover with warming, while litter cover was significantly higher (Fig. 4, Table 1). The cover of dwarf shrubs was unchanged in warmed plots. Cover of forbs and graminoids were slightly higher, and bare soil slightly lower, but none of these differences were significant.

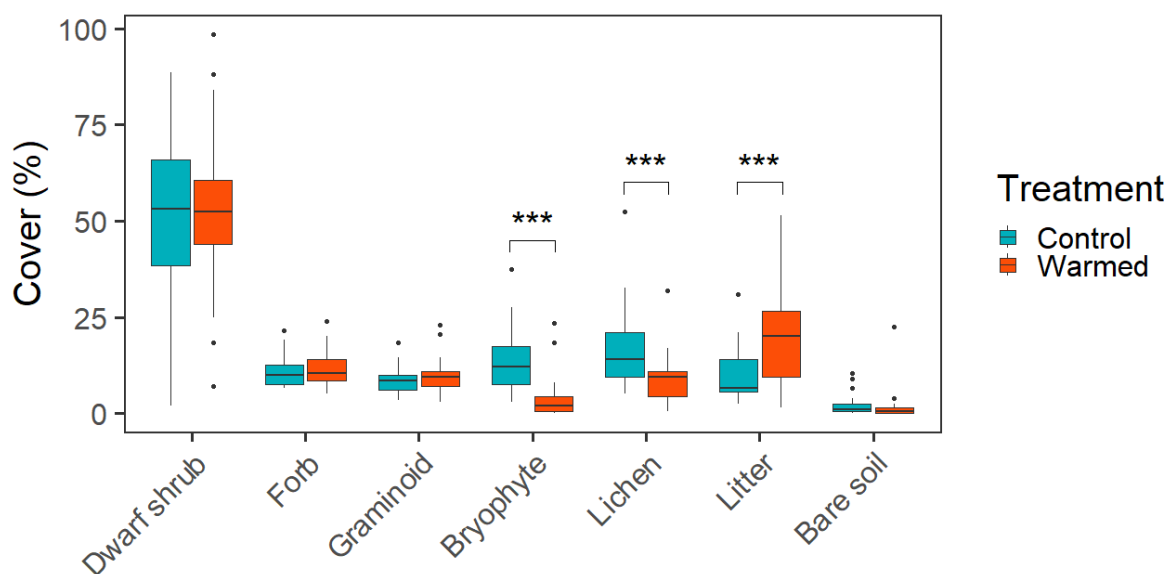


Fig. 4: Cover of functional groups, litter, and bare soil in control and experimentally warmed plots in the *Dryas* heath, 23 years after the experiment started. $n=21$ for both plot types. Asterisks indicate significant p -values: * = $p < 0.5$, ** = $p < 0.01$, *** = $p < 0.001$

Species richness, diversity and evenness

Total species richness, lichen richness and bryophyte richness were significantly lower in warmed plots (Fig. 5, Table 1). Vascular plant richness did not differ with warming. Both diversity and evenness were significantly lower with warming, but both warmed and control plots had high scores on these diversity metrics (Fig. 6, Table 1).

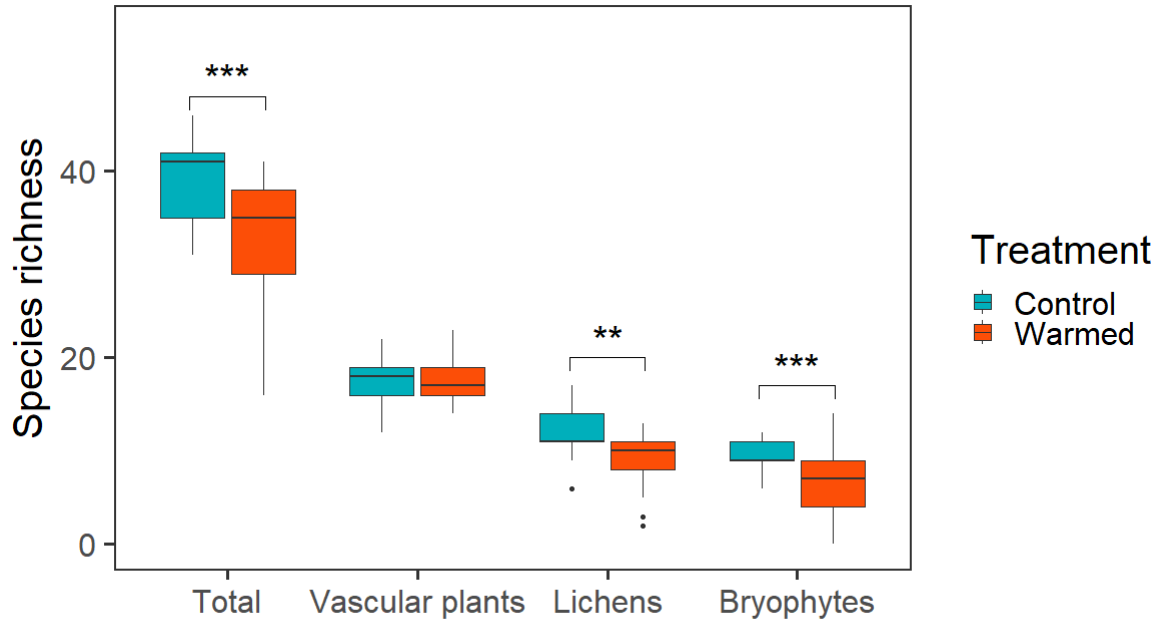


Fig. 5: Species richness in control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. $n=21$ for both plot types. Asterisks indicate significant p -values: * = $p<0.5$, ** = $p<0.01$, *** = $p<0.001$.

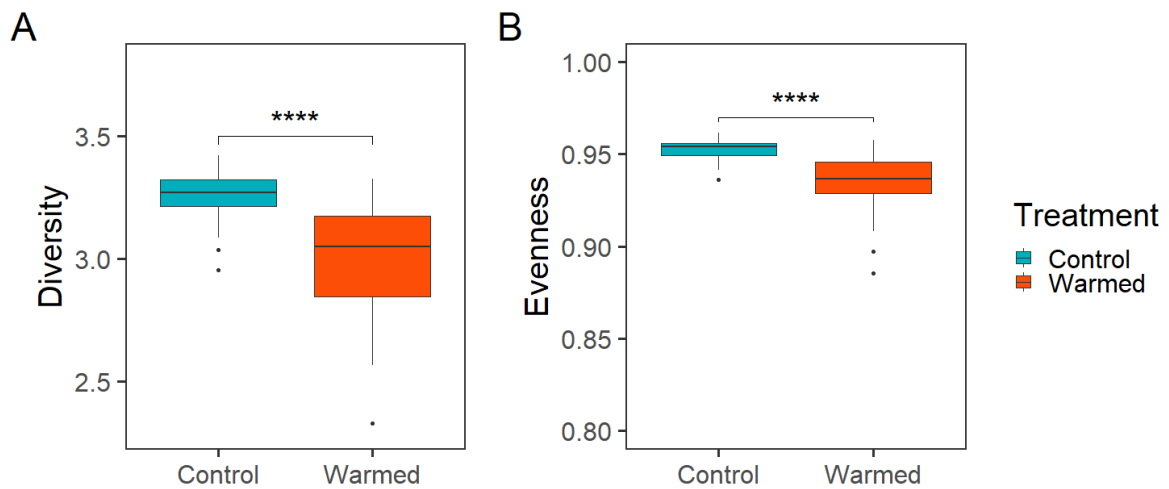


Fig. 6: A) Shannon's diversity index B) Pielou's evenness index in control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. Subplot frequency was used as the measure for species abundance. $n=21$ for both plot types. Asterisks indicate significant p -values: * = $p<0.5$, ** = $p<0.01$, *** = $p<0.001$.

Table 1: Results from tests comparing cover of functional groups, litter, bare soil, and diversity measures between control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. $n=21$ for both plot types. T -values are given for Student's T -tests and Welch's T -tests, W for non-parametric Mann-Whitney-Wilcoxon tests. Bold values are significant at $p < 0.05$.

Variable	W	T	df	p
Cover of functional groups (%)				
Dwarf shrub		-0.076	40	0.940
Forb		-0.317	40	0.753
Graminoid		-0.919	40	0.363
Lichen		3.022	40	0.004
Bryophyte		5.166	40	<0.001
Litter		-3.244	40	0.002
Bare soil	274.5			0.171
Diversity measures				
Species richness	345.6			0.002
Vascular plant richness		0.492	40	0.625
Lichen richness	322.5			0.010
Bryophyte richness		2.875	29.867	<0.001
Shannon's diversity index H		0.056	28.202	<0.001
Pielou's evenness index J	378			<0.001

Species composition

In the NMDS ordination diagram, warmed plots and control plots clustered near each end of the diagram (Fig. 7A). This indicates a difference in species composition depending on warming. The RDA showed that warming had a significant effect on species composition (Table 2), as did the CCA (Appendix B, Table 7). The NMDS diagram showed that most vascular plant species had a higher abundance in warmed plots, while lichen and bryophytes species were generally more abundant in the control plots (Fig. 7B).

There were significant correlations between some of the environmental variables and the NMDS-axes (Table 3). Bryophyte cover, lichen cover, and soil moisture had a moderately negative correlation with NMDS-axis 1, while dwarf shrubs and NDVI had a moderately positive correlation along this axis. Vegetation height showed a weak positive correlation with NMDS-axis 1. NMDS-axis 1 thereby represents a gradient from plots with high cryptogam abundance and soil moisture in one end, to greener plots with higher dwarf shrub cover and vegetation height in the other. The warmed plots were more abundant near the latter end of this gradient, while there were more control plots near the former (Fig. 7A).

NDVI and dwarf shrub cover had a moderately positive correlation with NMDS-axis 2, while graminoid and litter cover had a weak negative correlation along this axis (Table 3). NMDS-axis 2 thereby represents a gradient from greener, dwarf shrub-dominated plots in one end, to plots with higher litter and graminoid cover in the other. Warmed plots were more abundant near the latter end of this gradient than the control plots (Fig. 7A). Repeating the analyses with cover (%) data as the measure of species abundance resulted in similar patterns in the distribution of plots, species, and correlation of environmental gradients (Appendix B, Figs. 11A-11B, Tables 8-10).

Table 2: Results from a redundancy analysis (RDA) testing if species composition was different between control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. Subplot frequency was used as a measure for abundance. Permutations = 999. Bold values are significant at $p < 0.05$.

	Df	Variance	F	p
Treatment: Warming	1	0.220	5.796	0.001
Residual	40	1.517		

Table 3: Correlation between environmental variables and the two main axes in the non-metric multidimensional scaling (NMDS) ordination diagram of species composition in the Dryas heath, 23 years after the experimental warming study started. Subplot frequency was used as a measure of species abundance in the NMDS. Kendall's rank correlation coefficient τ was used to measure the correlation. Z values are given for every test except soil moisture where a T-distribution was used. Bold values are significant at $p < 0.05$.

Variable	Axis	T	Z	τ	p
Dwarf shrubs	NMDS1		3.837	0.412	<0.001
	NMDS2		3.425	0.368	0.001
Forbs	NMDS1		0.206	0.022	0.837
	NMDS2		-1.314	-0.143	0.189
Graminoids	NMDS1		-0.348	-0.038	0.728
	NMDS2		-2.978	-0.325	0.003
Lichens	NMDS1		-6.226	-0.672	<0.001
	NMDS2		-0.738	-0.080	0.461
Bryophytes	NMDS1		-5.833	-0.634	<0.001
	NMDS2		0.967	0.105	0.334
Litter	NMDS1		0.770	0.083	0.441
	NMDS2		-2.462	-0.266	0.014
Bare soil	NMDS1		-1.591	-0.179	0.112
	NMDS2		-0.508	-0.057	0.611
Vegetation height	NMDS1		2.406	0.258	0.016
	NMDS2		0.325	0.035	0.745
Soil moisture	NMDS1	242		-0.438	<0.001
	NMDS2	446		0.036	0.747
NDVI	NMDS1		3.642	0.391	<0.001
	NMDS2		3.230	0.347	0.001

Cover of individual species

There were several noteworthy effects of warming on the cover of individual species (Appendix A, Table 6). The bryophytes *Dicranum* sp., *Dicranella* sp., *Districhium capillaceum*, *Hylocomium splendens*, *Ptilidium ciliare*, *Racomitrium* sp., and *Sanonia uncinata* had significantly lower cover with warming. A significant decrease was also found for the lichens *Cetraria ericetorum*, *Ochrolechia frigida*, *Stereocaulon* sp., and *Vulpicida juniperinus*. Among the vascular plants, warming significantly decreased the cover of the dwarf shrubs *Harimanella hyponoides*, *Salix herbacea*, and *Salix reticulata*.

Dryas, height and flowers

The cover of *Dryas* decreased with warming, but the effect was not significant (Fig. 8A, Table 4). The cover of dead *Dryas* was significantly higher with warming. Warmed plots had significantly taller vegetation and *Dryas* canopies (Fig. 8B, Table 4). There was no effect of warming on the number of flowering species (Fig. 9A, Table 4). The abundance of *Dryas* flowers tended to be higher in warmed plots, but the difference was not significant (Fig. 9B, Table 4).

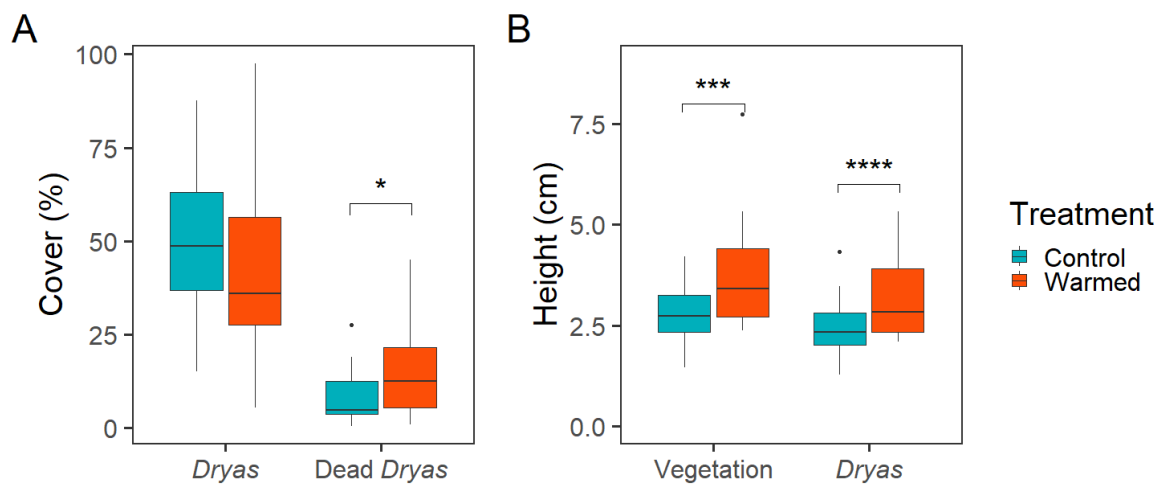


Fig. 8: A) Cover of *Dryas* and dead *Dryas* and B) height of the general vegetation and *Dryas* for control and experimentally warmed plots in the *Dryas* heath, 23 years after the experiment started. $n=21$ for both plot types. Asterisks indicate significant p -values: * = $p < 0.5$, ** = $p < 0.01$, *** = $p < 0.001$.

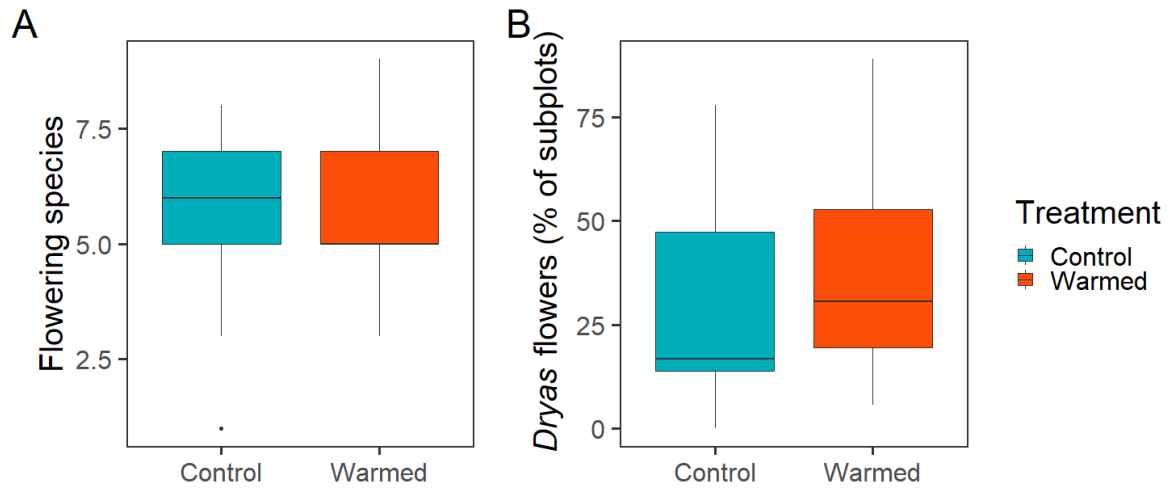


Fig. 9: A) Number of flowering species and B) *Dryas* flower abundance in control and experimentally warmed plots in the *Dryas* heath, 23 years after the experiment started. Subplot frequency was used to measure the abundance of *Dryas* flowers. $n=21$ for both plot types. Asterisks indicate significant p -values: * = $p<0.5$, ** = $p<0.01$, *** = $p<0.001$.

Table 4: Results from tests comparing cover of *Dryas*, dead *Dryas*, *Dryas* height and *Dryas* flowers, vegetation height, and flowering species in control plots and experimentally warmed plots in the *Dryas* heath, 23 years after the experiment started. $n=21$ for both plot types. T -values are given for Student's T -tests and Welch's T -tests, W for non-parametric Mann-Whitney-Wilcoxon tests. Bold values are significant at $p < 0.05$.

Variable	W	T	df	p
<i>Dryas</i> cover (%)		0.543	40	0.590
Dead <i>Dryas</i> cover (%)		-2.491	40	0.032
<i>Dryas</i> flowers (% of subplots)		-1.805	32.446	0.080
<i>Dryas</i> height (cm)	109.5			0.005
Vegetation height (cm)		-3.374	40	0.002
Flowering species		-0.466	40	0.644

Soil moisture and NDVI

Warmed plots showed a trend of lower soil moisture compared to the control plots, but the difference was not significant (Fig. 10A, Table 5). Warming had no effect on NDVI (Fig. 10B, Table 5).

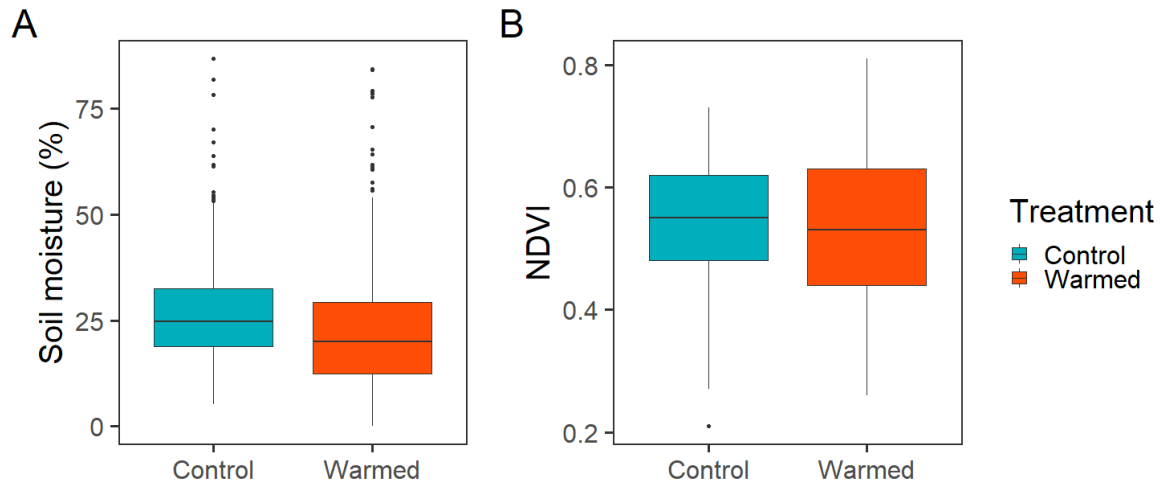


Fig. 10: A) Soil moisture and B) NDVI in control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. $n=30$ for both plot types.

Table 5: Results from mixed linear model tests for soil moisture and NDVI in control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. $n=30$ for both plot types. Bold values are significant at $p < 0.05$.

	Estimate	SE	Df	T	p
Moisture					
Intercept	26.988	1.814	33.128	14.874	<0.001
Treatment: Warming	-4.318	2.262	57.178	-1.909	0.061
NDVI					
Intercept	0.546	0.028	10.184	19.198	<0.001
Treatment: Warming	-0.013	0.028	57.280	-0.452	0.653

Discussion

I found 23 years of warming to result in reduced lichen and bryophyte cover and richness. Warmed plots also had lower community richness, diversity, and evenness. Species composition was altered with warming, as vascular plants were more abundant in warmed plots and cryptogams were more abundant in control plots. The cover of vascular plant functional groups and vascular plant richness did not change. The cover of litter and dead *Dryas* increased with warming, as well as vegetation height and *Dryas* height. I found non-significant trends of increasing *Dryas* flower abundance and lower soil moisture with warming. The NDVI and number of flowering species did not differ between warmed and control plots.

A decline in cryptogams reduced community diversity

Community changes with warming were driven by a strong decline in the cover and richness of lichens and bryophytes. This decline seems responsible for the significant decreases in community diversity and evenness, and the reason why species composition was altered, in line with my hypothesis. Furthermore, I found significant declines in the cover of several individual cryptogam species. These results are in line with other studies that report cryptogam species losing ground with warming (Alatalo et al., 2017; Alatalo et al., 2020; Cornelissen et al., 2001; Hollister et al., 2005; Klanderud, 2008; Lang et al., 2012; Vuorinen et al., 2017). Warming itself is not necessarily detrimental to cryptogams. Other experiments with OTCs have documented that they can increase in cover (Biasi et al., 2008) or show no response (Harris et al., 2022). Similarly, in long-term monitoring studies, lichen and bryophyte cover have been shown to increase with ambient warming (Alatalo et al., 2017; van Zuijlen et al., 2022a). The negative effects of higher temperatures on cryptogams could therefore depend on how strongly they are affected by the rest of the community, as other studies have found a negative correlation between plant canopy cover and lichens (Alatalo et al., 2017) and bryophytes (Jägerbrand et al., 2012).

In the *Dryas* heath at Finse, there was a dense cover of vascular plants, and both the general vegetation and *Dryas* was taller with warming. Warmed plots also had increased litter cover. These changes may have caused a negative shading effect on the cryptogams. Increased height can give plants a competitive advantage in acquisition for light, and have diminishing effects on smaller species (Baruah et al., 2017). In the same manner, litter can shade and bury cryptogams, which has been found to be the case in previous studies at Finse (van Zuijlen et al., 2022a; van Zuijlen et al., 2022b) and other Arctic and alpine sites (Alatalo et al., 2020; Cornelissen et al., 2001; Lang et al., 2012). These studies support the explanation that taller canopies and higher litter cover are behind the cryptogam decline in the *Dryas* heath. Furthermore, in studies that found no change, or increases in

cryptogam cover with warming, this was attributed to a sparse vascular plant cover (Biasi et al., 2008; Harris et al., 2022), which is not the case at Finse.

Most lichens and bryophytes tolerate desiccation (Kranter et al., 2008; Proctor et al., 2007), but they depend on water in their surroundings for growth (Alatalo et al., 2014; van Zuijlen et al., 2022b). My results showed a link between cryptogam cover and soil moisture. Reduced water availability with warming could be part of the reason why these species declined, as I found a non-significant trend towards lower soil moisture with warming. OTCs can cause lower soil moisture compared to control plots (Bokhorst et al., 2013; Dabros et al., 2010; Hollister et al., 2023), which makes it important to consider increased water stress as an unintended “chamber effect”. The exposed ridge at Finse is already a dry environment (Roos et al., 2023). The topsoil layer, on which the cryptogams grow, appeared drier inside the chambers than outside (personal observation), which has also been reported in other studies (Hollister et al., 2023). Then again, moisture limitation and droughts could increase as dry sites get warmer with climate change (Bjorkman et al., 2018; Walsh et al., 2020). Bryophytes especially are known to be negatively affected by drier soils (Alatalo et al., 2017; Elmendorf et al., 2012a; Lett et al., 2022) and might therefore be most impacted if *Dryas* heaths get drier with warming.

Lichens are favoured over bryophytes in drier conditions (Hudson & Henry, 2010), and it is noteworthy that both were diminished in the warmed plots at Finse. This suggests that increased shading may have been the most detrimental effect of warming, at least for lichens. In a synthesis of climate change experiments on lichens in 14 Arctic sites, negative effects of warming were consistent across watered and non-watered treatments (Cornelissen et al., 2001). Still, it is important to consider how potential changes in air humidity within OTCs could affect lichens, as many species depend on moist air for photosynthesis (Alatalo et al., 2017). To investigate this, experimental warming studies should measure air humidity (e.g. Dabros et al., 2010) to see how the chambers affect the microclimate of cryptogams as well as other species.

The cryptogam decline in the *Dryas* heath at Finse is notable because few studies identify cryptogams to species or genus, even though they can have a variety of responses to environmental changes (Lett et al., 2022). Over half of the 85 taxa I identified in the *Dryas* heath were lichens or bryophytes, illustrating their large contribution to the richness of this community and the importance of a high taxonomic resolution. Including lichens and bryophytes in vegetation studies can increase our understanding of how plant communities respond to environmental changes (St. Martin & Mallik, 2017), and possibly function as an early-warning system (van Zuijlen et al., 2022a). Their decline with long-term warming at Finse could show that perhaps they are the canary in the coal mine for low-stature Arctic-alpine plants threatened by climate change.

Most vascular plants showed small responses

The lack of change in vascular plants ran contrary to my hypothesis and was surprising given that other studies in Arctic and alpine sites have shown that shrubs and graminoids often increase with warming (Criado et al., 2024 (preprint); Elmendorf et al., 2012a; Elmendorf et al., 2012b). The vascular plants in the *Dryas* heath at Finse seem to be responding to long-term warming in a very modest way, as I did not find any significant increases in cover of functional groups or individual species. Neither was the NDVI higher with warming, contrary to my hypothesis. This result was surprising given the general trend of greening in Arctic and alpine areas (Myers-Smith et al., 2020; Rumpf et al., 2022), but is as expected when warming did not cause larger changes in the vascular plants. That long-term warming did not affect the vascular plants more could indicate a stability that has also been observed in other studies of *Dryas* heaths exposed to warming for 8 (Wahren et al., 2005), 15 (Hudson & Henry, 2010), 17 (Jónsdóttir et al., 2023), and 26 years (Scharn et al., 2022). There could be several reasons for this apparent stability, both abiotic and biotic.

Arctic-alpine plant growth is not only restricted by temperature, but also soil moisture and nutrients (Barrett & Hollister, 2016; Bjorkman et al., 2020; Elmendorf et al., 2012a; Scharn et al., 2022). With warming, dry sites often change less than wet ones (Bjorkman et al., 2020). Water limitation was a possible cause for limiting plant growth on a dry ridge in a 15-year warming and monitoring study in Atkasuk, Alaska (Hollister et al., 2015). On the other hand, 17 years of warming in a *Dryas* heath in Endalen, Svalbard, resulted in an increase in evergreen shrub abundance and a significantly different species composition, despite dry soils (Jónsdóttir et al., 2023). The compositional changes in Endalen were, however, regarded as small, even with long-term warming (Jónsdóttir et al., 2023). The need for water conservation might make plants in dry environments adhere to conservative growth strategies with warming (Bjorkman et al., 2018), which could be the case at Finse. In addition, *Dryas* heaths often have shallow, dry, and nutrient-poor soils (Reinhardt et al., 2013; Welker et al., 1997), which could have limited further community changes. A combined fertilization and warming experiment at Finse illustrated this, as it turned a dwarf shrub-dominated *Dryas* heath into a graminoid and forb meadow (Klanderud & Totland, 2005; Klanderud, 2008). Water and nutrient limitations might therefore be more important for changes in vascular plants in *Dryas* heaths than increasing temperatures. Warming in Arctic and alpine areas may cause larger changes at sites with deeper and more nutrient-rich soils (Alatalo et al., 2022; Roos et al., 2023; Töpper et al., 2018; van Zuijlen et al., 2022b).

Longevity, clonal growth, and high trait plasticity are central to the life history strategies of many Arctic-alpine plant species and provide a buffering capacity to withstand interannual environmental changes (Hudson & Henry, 2010; Jónsdóttir et al., 2023). Such traits may have caused vascular plants in the *Dryas* heath to resist the effects of higher temperatures. In addition, the dominance of *Dryas* could have prevented larger structural changes. By being a strong competitor to

other species in the community (Klanderud & Totland, 2004), *Dryas* leaves little space for other species to establish or increase in abundance (Olsen & Klanderud, 2014). The high species richness and diversity at the site could also have maintained stability under warming. Such an explanation would be in line with the hypothesis of more stability in diverse communities, as diversity increases the number of possible responses to environmental changes and interactions between species (Elton, 1958; Klanderud & Totland, 2008; Tilman et al., 2014). Even though community diversity decreased with warming, both warmed and control plots had high diversity and evenness. This could enable the community to withstand further structural changes, at least under current temperature levels.

The changes that did occur among the vascular plants with warming were an increase in canopy height and litter cover, as hypothesized. These effects of warming have been documented in other studies of Arctic-alpine vegetation in general (Baruah et al., 2017; Bjorkman et al., 2018; Elmendorf et al., 2012a; Klein et al., 2004) and *Dryas* heaths in particular (Hudson et al., 2011; Jónsdóttir et al., 2023; Welker et al., 1997). Such changes with warming may cause vascular plants to affect other species in their community, even if they do not increase in cover, as illustrated with the cryptogam decline. In the same manner, taller plants and more litter may have contributed to the decreases in the cover of the smaller dwarf shrubs *Salix herbacea*, *Salix reticulata* and *Harimanella hypnoides*. Prostrate dwarf shrubs could be poor competitors when other plants grow taller (Klanderud, 2008), and a number of studies have found increased plant height and litter to negatively impact low-stature Arctic-alpine plants (Alatalo et al., 2022; Elmendorf et al., 2012a; Klein et al., 2004; Scharnagl et al., 2019; Yang et al., 2018). While I did not find vascular plant richness to be reduced with warming, the detrimental effects on *S. herbacea*, *S. reticulata*, and *H. hypnoides* could show that the smallest and least competitive species might be the first to decline, and potentially disappear, as temperatures rise.

Increased litter and dead *Dryas* may result from extreme events

Dwarf shrub cover and NDVI both increased towards the same plots in the *Dryas* heath, while litter cover was not linked to either of these and increased with warming. Although I did not discern between dead *Dryas* that were on the ground or still attached to the plant, much of the litter was identifiable as *Dryas* (personal observation). This browning effect with warming could be another reason why the NDVI was not higher in warmed plots. A negative correlation between dead *Dryas* and NDVI was found in a snow-depth study in Adventdalen, Svalbard (Cooper et al., 2019), supporting such an explanation. Higher litter cover due to warming has been reported in both experimental warming (Alatalo et al., 2020; Elmendorf et al., 2012a) and long-term monitoring studies (Harris et al., 2022; Scharnagl et al., 2019). OTCs can limit wind dispersal of dead plant matter (Alatalo et al., 2020; Løkken et al., 2019), making it important to consider litter accumulation as a side effect of the chambers rather than warming. However, given that long-term monitoring

studies also have reported increased litter cover, it seems unlikely that OTCs themselves are the only reason for this at Finse.

The higher cover of dead *Dryas* with warming is noteworthy as the species is an evergreen dwarf shrub (Welker et al., 1997). In warming experiments, *Dryas* has been found to have small contributions to increased litter compared with deciduous dwarf shrubs (Welker et al., 2004). A possible explanation for the *Dryas* die-off at Finse could be that the heath has experienced one or more extreme weather events. Droughts, heatwaves, winter warming, and frost nights in spring could happen more frequently with climate change (Bokhorst et al., 2013; Marchand et al., 2006; Panchen et al., 2022; Phoenix & Bjerke, 2016; Walsh et al., 2020; Zona et al., 2014). Such events can cause die-offs in dwarf shrubs (Bokhorst et al., 2009; Schaefer, 2023). OTCs amplify extreme warming events (Bokhorst et al., 2013) and could therefore have had a more severe effect on the vegetation in warmed plots than in the controls.

Southern Scandinavia experienced a very warm and dry summer in 2018 (Bastos et al., 2020) that could have affected a dry site such as the *Dryas* heath at Finse. *Silene acaulis*, which is abundant in this community, was noticeably impacted by this event (Klanderud, personal communication). Alpine plants can be susceptible to heatwaves with their prostrate growth forms, specialized at capturing heat (Körner, 2021, pp.187-192). Furthermore, transplant experiments in the European Alps have shown that alpine plant communities can be especially vulnerable to the combined effects of extreme heat and water stress (De Boeck et al., 2016; Schuchardt et al., 2023). Another possible cause for the die-off in *Dryas* could be that enhanced temperatures in warmed plots have led to lower frost tolerance (Fazlioglu & Wan, 2021; Wookey et al., 1995), which can make dwarf shrubs more vulnerable to frost damage in spring (Scharn et al., 2022). A non-significant trend of increasing frost events during the growing season has been found at Finse between 1970 and 2020 (Roos et al., 2023), which may have affected the *Dryas* heath. A further investigation of the frequency and magnitude of extreme weather events at Finse could shed more light on this issue. In addition, drought experiments could be performed to study the resilience of *Dryas* heaths to heat and water stress.

With a changing climate, more frequent extreme events may cause larger changes than steady temperature increases (Roos et al., 2023; Turner et al., 2020). The consequences of such events can be particularly severe in alpine ecosystems because they are slow to recover (De Boeck et al., 2018). Furthermore, heatwaves and droughts have been shown to reduce the resistance of alpine plant communities to invasion of lowland species (Schuchardt et al., 2023). If warming weakens *Dryas* as the dominant species in *Dryas* heaths, it might make room for other taller and more competitive species. I found both litter and graminoid cover to increase in plots with lower dwarf shrub cover, which might indicate such a tendency. On the other hand, *Dryas* has recalcitrant litter (Jónsdóttir et al., 2023) which could be a barrier to the establishment of other species (Olsen & Klanderud, 2014). Increased litter may either way have a long-lasting effect on this community. If higher temperatures

result in less moisture, decomposition may slow down (Christiansen et al., 2017), which was found as a possible effect of warming in a litterbag study at Finse (Karr, 2017). Future studies could investigate the legacy of dead *Dryas*, for example its impact on vascular plant seedlings.

Mixed effects on reproductive efforts

I hypothesized that warming would increase the number of flowering species and flower abundance for *Dryas*, as a higher reproductive effort is expected with higher temperatures (Fazlioglu & Wan, 2021; Panchen et al., 2022; Welker et al., 1997). My hypothesis for *Dryas* was almost supported, as there was a non-significant trend of increasing flower abundance with warming. In another study performed at Finse in 2023 in the same plots, the abundance of *Dryas* flowers significantly increased with warming when counting each individual flower (Finne, 2023). This illustrates that sampling methods are important, as my use of subplot frequency underestimated actual flower abundance. Sexual reproduction can improve the ability of a species to adapt to environmental changes (Müller et al., 2011), abide in its community (Panchen et al., 2022), or migrate to other habitats (Kullman, 2010). Increased reproductive effort could therefore be important for species in *Dryas* heaths if climate change makes their current habitat less suitable. Increasing flower abundance could also be important for other parts of the ecosystem such as pollinating insects, although they will also be affected by an eventual contraction of the flowering season (Høye et al., 2013).

Many Arctic-alpine plants need several consecutive growing seasons to build up the resources necessary to flower (Panchen et al., 2022). I therefore expected that long-term warming would have caused a higher number of flowering species in the *Dryas* heath. This was not the case. It might be that despite higher temperatures, there is still a lot of interannual variation in reproductive effort. A one-summer study like mine might not have been sufficient to capture changes in flower abundance, if some species for instance had flowered the year before or were storing up resources to do so next year. Other factors than temperature could also limit flowering, such as nutrients (Barrett & Hollister, 2016), which could be important in low-productive habitats such as *Dryas* heaths. Plants could also respond to increased competition by allocating resources towards vegetative, rather than reproductive growth (Barrett & Hollister, 2016), but as I did not see changes in the cover of most vascular plants, this does not seem the case at Finse. Extreme events could also have contributed to reproductive failures and counteracted the positive effects of higher temperatures (Frei & Henry, 2022; Panchen et al., 2022). A study of the flowering phenology of *Dryas* at Finse showed that a very cold summer in 2020 drastically affected flowering and seed production compared to more benign temperatures in 2021 (Roos et al., 2024 (unpublished)). Further studies on how long-term warming affects flower abundance in *Dryas* heaths should investigate the effect of interannual temperature variation by performing measurements over several years.

Past studies and the future of *Dryas* heaths

Previous studies in the *Dryas* heath at Finse found that short-term (four years) warming did not cause significant changes in the community in terms of litter, height, richness or composition (Klanderud & Totland, 2005; Klanderud, 2008). In the longer term (17 and 18 years), warming resulted in increased vegetation height and litter cover, and reduced lichen richness and bryophyte cover (Hasvik, 2018; Sundsbø, 2019; van Zuijlen et al., 2022a). The larger changes in community diversity, richness, and composition after 23 years suggest that *Dryas* heaths respond slowly to warming, but eventually change. This underscores the value of maintaining long-term experiments and performing regular surveys. Studying changes over time in the control plots would be beneficial to see if the community changes in the same direction with ambient warming as with experimental warming.

By the end of this century, temperatures at Finse could potentially increase more than the effect of the OTCs (Hanssen-Bauer et al., 2017). If so, *Dryas* heaths could change far more than what is shown in warming studies such as this one. Other factors are also important for how Arctic-alpine vegetation is affected by climate change, such as in changes in precipitation and snow cover (Roos et al., 2023). Precipitation is expected to increase in the western part of Norway, resulting in heavier snowfall in alpine areas (Hanssen-Bauer et al., 2017). At Finse, the *Dryas* heath is situated on a windswept ridge with thin snow cover in winter, that is otherwise quite dry and well-drained in the growing season (Roos et al., 2023). Plant communities on exposed ridges could therefore be less affected by changes in snow cover than other alpine habitats such as snowbeds (Reinhardt et al., 2013). On the other hand, warming could make it easier for other species to establish on ridges, such as those that grow in leesides (Klanderud, 2008; Reinhardt et al., 2013). My results show that also within existing ridge communities, warming can have diminishing effects on lichens, bryophytes, and smaller dwarf shrubs.

Alpine *Dryas* heaths have a high species richness and are important for rare and endangered species (Klanderud & Totland, 2005; Reinhardt et al., 2013). Even though I found small responses in the vascular plants, there might be inherent lags in how fast alpine plant communities change with warming (Alexander et al., 2018). This can cause a growing extinction debt with climate change that could become evident only with time (Dullinger et al., 2012). *Dryas*, and its associated community, grow on calcareous bedrock (Reinhardt et al., 2013) and have limited opportunities for upwards migration with warming (Solstad et al., 2021). It is therefore important to continue monitoring such hotspots so that we may know how the rich diversity they harbour will fare in the future.

Conclusion

Long-term effects of experimental warming in the *Dryas* heath were severe for lichens, bryophytes, and small dwarf shrubs but otherwise the plant community showed small responses. This suggests that dry, low-productive, and diverse *Dryas* heaths may have a better capacity to withstand climate change than other Arctic and alpine habitats. However, the large increases in litter and dead *Dryas* indicate that extreme events such as heatwaves and droughts can have large impacts on alpine communities. It remains to be seen what the legacy effect of this browning will be in the community, and how the decline of cryptogams will affect ecosystem functions. Experiments with droughts could be performed to study the resilience of *Dryas* heaths to more frequent extreme weather. Maintaining long-term studies, and surveying both vascular plants and cryptogams, is necessary to further understand the impact of higher temperatures in slowly changing Arctic-alpine plant communities.

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Appendix A – Recorded species

I recorded a total of 85 taxa during my survey of the 42 plots in the *Dryas* heath. A list of all taxa, their average cover, and if they increased or decreased in cover with warming is shown in Table 6. Among the recorded species there were 40 vascular plants, 28 lichens and 17 bryophytes. Average richness per plot \pm standard error was 36.0 ± 1.0 species in total, 17.5 ± 0.4 vascular plants, 10.6 ± 0.5 lichens and 7.9 ± 0.5 bryophytes. Dwarf shrubs were the dominant functional group, covering on average 51.9 ± 3.4 % per plot. *Dryas* was the dominant species covering 46.5 ± 3.4 % per plot.

Table 6: Recorded species during the survey of control and experimentally warmed plots in the *Dryas* heath, 23 years after of experiment started. Mean values \pm standard error is given for the cover (%) across all warmed/control plots, along with results from a non-parametric Mann-Whitney-Wilcoxon-test comparing if the cover was different with warming. Counts are given for all the times a species was observed in a plot, while the test uses cover values across all control/warmed plots. Bold values are significant at $p < 0.05$.

↓ = less abundant in warmed plots ↑ = more abundant in warmed plots, - = equally abundant
c = only found in control plots w = only found in warmed plots

Abbreviation	Species/taxon	Counts		Mean cover (%) \pm SE		Test results		
		Control	Warmed	Control	Warmed	W	p	Change
Dwarf shrubs								
Dry oct	<i>Dryas octopetala</i>	20	21	47.41 \pm 5.01	42.86 \pm 4.83	255	0.392	↓
Emp nig	<i>Empetrum nigrum</i>	2	3	1.43 \pm 1.43	1.53 \pm 1.38	210.5	0.671	↑
Har hyp	<i>Harimanella hypnoides</i>	13	6	0.5 \pm 0.14	0.11 \pm 0.06	309.5	0.015	↓
Sal her	<i>Salix herbacea</i>	18	6	0.71 \pm 0.2	0.14 \pm 0.07	356.5	<0.001	↓
Sal ret	<i>Salix reticulata</i>	20	16	2.21 \pm 0.39	1.15 \pm 0.29	308.5	0.027	↓
Vac uli	<i>Vaccinium uliginosum</i>	2	6	0.1 \pm 0.07	6.12 \pm 2.35	172.5	0.081	↑
Forbs								
Ant alp	<i>Antennaria alpina</i>	9	7	0.19 \pm 0.08	0.32 \pm 0.12	226	0.885	↑
Ast alp	<i>Astragalus alpinus</i>	6	2	0.35 \pm 0.22	0.01 \pm 0.01	266.5	0.095	↓
Bar alp	<i>Bartsia alpina</i>	11	15	0.43 \pm 0.16	0.72 \pm 0.19	169	0.184	↑
Bis viv	<i>Bistorta vivipara</i>	21	21	3.48 \pm 0.35	3.45 \pm 0.25	217	0.939	↓

Cam rot	<i>Campanula rotundifolia</i>	5	6	0.07±0.05	0.11±0.07	208	0.695	↑
Cer alp	<i>Cerastium alpinum</i>	12	14	0.16±0.06	0.33±0.12	188.5	0.398	↑
Com ten	<i>Comastoma tenellum</i>	1	2	0.01±0.01	0.01±0.01	210	0.573	-
Eri uni	<i>Erigeron unifloris</i>	7	8	0.17±0.1	0.23±0.09	203.5	0.626	↑
Eup wet	<i>Euphrasia wettsteinii</i>	8	5	0.2±0.14	0.02±0.01	257	0.262	↓
Gen niv	<i>Gentiana nivalis</i>	1	1	0.01±0.01	0.01±0.01	220.5	1	-
Hup arc	<i>Huperzia arctica</i>	4	0	0.15±0.1				c
Oxy lap	<i>Oxytropis lapponica</i>	7	5	0.12±0.07	0.14±0.12	242	0.504	↑
Par pal	<i>Parnassia palustris</i>	1	2	0.01±0.01	0.05±0.05	209.5	0.554	↑
Pot cra	<i>Potentilla crantzii</i>	16	19	0.42±0.1	0.71±0.18	173	0.22	↑
Rho ros	<i>Rhodiola rosea</i>	2	0	0.1±0.07				c
Sau alp	<i>Saussurea alpina</i>	21	21	2.1±0.19	2.6±0.28	178	0.285	↑
Sax opp	<i>Saxifraga oppositifolia</i>	2	1	0.01±0.01	0.01±0.01	231	0.573	-
Sel sel	<i>Seliginella selaginoides</i>	12	13	0.21±0.09	0.23±0.07	204	0.669	↑
Sil aca	<i>Silene acaulis</i>	20	19	3.34±0.56	3.47±0.71	231	0.801	↑
Tar sp.	<i>Taraxacum</i> sp.	0	3		0.12±0.08			w
Tha alp	<i>Thalictrum alpinum</i>	21	21	1.51±0.21	1.2±0.2	266.5	0.245	↓
Tof pus	<i>Tofieldia pusilla</i>	2	1	0.05±0.05	0.1±0.1	230	0.612	↑
Vis alp	<i>Viscaria alpina</i>	1	0	0.01±0.01				c

Graminoids

Ant odo	<i>Antoxanthum odoratum</i>	3	6	0.15±0.1	0.34±0.14	188	0.261	↑
Car atr	<i>Carex atrata</i>	9	15	0.77±0.26	1.03±0.19	168.5	0.174	↑
Car cap	<i>Carex capillaris</i>	6	7	0.34±0.14	0.4±0.24	216	0.902	↑
Car rup	<i>Carex rupestris</i>	21	21	2.04±0.24	2.17±0.23	208.5	0.77	↑

Car vag	<i>Carex vaginata</i>	20	21	3.24±0.34	3.81±0.39	186	0.388	↑
Fes sp.	<i>Festuca sp.</i>	20	18	2.47±0.64	2.52±1.03	251.5	0.442	↑
Jun tri	<i>Juncus trifidus</i>	8	7	1.52±0.52	1.6±0.8	233.5	0.714	↑
Luz con	<i>Luzula confusa</i>	0	1		0.1±0.1			w
Luz spi	<i>Luzula spicata</i>	6	10	0.16±0.08	0.46±0.14	166.5	0.121	↑
Luz sp.	<i>Luzula sp.</i>	13	8	0.46±0.12	0.47±0.33	282	0.099	↑
Poa alp	<i>Poa alpina</i>	2	2	0.05±0.05	0.01±0.01	221.5	0.98	↓

Lichens

Ale nig	<i>Alectoria nigricans</i>	4	0	0.06±0.05				c
Ale och	<i>Alectoria ochroleuca</i>	7	4	0.08±0.04	0.06±0.05	251.5	0.318	↓
Bry div	<i>Bryocaulon divergens</i>	11	8	0.28±0.19	0.06±0.03	259	0.282	↓
Cet eri	<i>Cetraria ericetorum</i>	21	20	4.34±0.68	2.18±0.27	330	0.006	↓
Cet isl	<i>Cetraria islandica</i>	20	19	1.84±0.28	1.45±0.23	248.5	0.485	↓
Cla arb	<i>Cladonia arbuscula</i>	20	19	1.68±0.42	2.43±0.6	182	0.335	↑
Cla gra	<i>Cladonia gracilis</i>	20	19	0.33±0.08	0.31±0.11	243	0.517	↓
Cla unc	<i>Cladonia uncialis</i>	16	16	0.66±0.21	0.48±0.16	238.5	0.651	↓
Cla ran	<i>Cladonia rangiferina</i>	0	1		0.05±0.05			w
Cla sty	<i>Cladonia stygia</i>	0	1		0.05±0.05			w
Cla sp.	<i>Cladonia sp.</i>	10	8	0.05±0.01	0.08±0.05	236.5	0.652	↑
Fla cuc	<i>Flavocetraria cucullata</i>	18	15	1±0.28	1.11±0.41	243.5	0.562	↑
Fla niv	<i>Flavocetraria nivalis</i>	20	20	4.07±1.73	1.77±0.47	242	0.593	↓
Lec sp.	<i>Lecanorina sp.</i>	1	0	0.01±0.01				c
Lep dac	<i>Lepra dactylina</i>	1	0	0.143±0.143				c
Och fri	<i>Ochrolechia frigida</i>	17	6	1.72±0.6	0.25±0.12	350	0.001	↓

Pel apt	<i>Peltigera aphthosa</i>	6	5	0.58±0.27	0.38±0.16	232.5	0.708	↓
Pel mat	<i>Peltigera malacea</i>	3	2	0.1±0.07	0.05±0.05	231.5	0.638	↓
Rhi sp.	<i>Rhizocarpon</i> sp.	3	0	0.01±0.01				c
Sol bis	<i>Solorina bispora</i>	1	1	0.05±0.05	0.01±0.01	221	1	-
Sol sac	<i>Solorina saccata</i>	0	1		0.05±0.05			w
Sol spo	<i>Solorina spongiosa</i>	1	0	0.05±0.05				c
Sol sp.	<i>Solorina</i> sp.	1	0	0.01±0.01				c
Sph glo	<i>Sphaerophorus globosus</i>	3	0	0.01±0.01				c
Ste sp.	<i>Stereocaulon</i> sp.	15	9	0.56±0.15	0.06±0.03	320	0.008	↓
Tha ver	<i>Thamniolium vermicularis</i>	18	15	0.71±0.14	0.33±0.1	296	0.053	↓
Umb cyl	<i>Umbilicaria cylindrica</i>	1	0	0.01±0.01				c
Vul jun	<i>Vulpicida juniperinus</i>	8	2	0.24±0.1	0.05±0.05	284	0.033	↓

Bryophytes

Bra alb	<i>Brachythecium albicans</i>	16	11	0.1±0.03	0.05±0.01	278.5	0.088	↓
Bry sp.	<i>Bryum</i> sp.	9	10	0.06±0.03	0.24±0.09	190.5	0.408	↑
Dicranum sp.	<i>Dicranum</i> sp.	21	20	5.69±1.24	2.58±0.8	351	0.001	↓
Dicranella sp.	<i>Dicranella</i> sp.	10	2	0.11±0.05	0.01±0.01	306.5	0.006	↓
Dis cap	<i>Districhum capillaceum</i>	15	4	0.09±0.03	0.02±0.01	338	0.001	↓
Gri sp.	<i>Grimmia</i> sp.	1	0	0.01±0.01				c
Hyl spl	<i>Hylocomium splendens</i>	15	8	1.75±0.9	0.26±0.15	308	0.021	↓
Hyp sp.	<i>Hypnum</i> sp.	3	1	0.01±0.01	0.01±0.01	241.5	0.311	↓
Lop sp.	<i>Lophozia</i> sp.	10	8	0.05±0.01	0.04±0.01	241.5	0.548	↓
Pla por	<i>Plagiochila porelloides</i>	5	1	0.02±0.01	0.01±0.01	262.5	0.085	↓
Poh sp.	<i>Pohlia</i> sp.	1	0	0.01±0.01				c

Pol sp.	<i>Polytrichum</i> sp.	13	9	0.32±0.1	0.13±0.06	275	0.143	↓
Pti cil	<i>Ptilidium ciliare</i>	19	17	2.11±0.48	0.94±0.3	307.5	0.028	↓
Rac sp.	<i>Racomitrium</i> sp.	17	13	3.64±1.08	0.26±0.11	337	0.003	↓
Rhy rug	<i>Rhytidium rugosum</i>	7	8	0.21±0.14	0.15±0.08	212	0.813	↓
San unc	<i>Sanonia uncinata</i>	20	14	0.52±0.15	0.27±0.17	316.5	0.007	↓
Syn sp.	<i>Syntrichia</i> sp.	4	9	0.18±0.17	0.06±0.03	171	0.127	↓

Appendix B – Supplementary statistics

Table 7: Results from a Constrained Correspondence Analysis (CCA) testing if species composition was different between control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. Subplot frequency was used as a measure of species abundance. Permutations = 999. Bold values are significant at $p < 0.05$.

	Df	ChiSquare	F	p
Treatment: Warming	1	0.091	3.545	0.001
Residual	40	1.027		

Table 8: Results from a redundancy analysis (RDA) testing if species composition was different between control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. Percent cover was used as a measure of species abundance. Permutations = 999. Bold values are significant at $p < 0.05$.

	Df	Variance	F	p
Treatment: Warming	1	0.002	1.349	0.219
Residual	40	0.074		

Table 9: Results from a Constrained Correspondence Analysis (CCA) testing if species composition was different between control and experimentally warmed plots in the Dryas heath, 23 years after the experiment started. Percent cover was used as a measure for abundance. Permutations = 999. Bold values are significant at $p < 0.05$.

	Df	ChiSquare	F	p
Treatment: Warming	1	0.088	2.104	0.002
Residual	40	1.682		

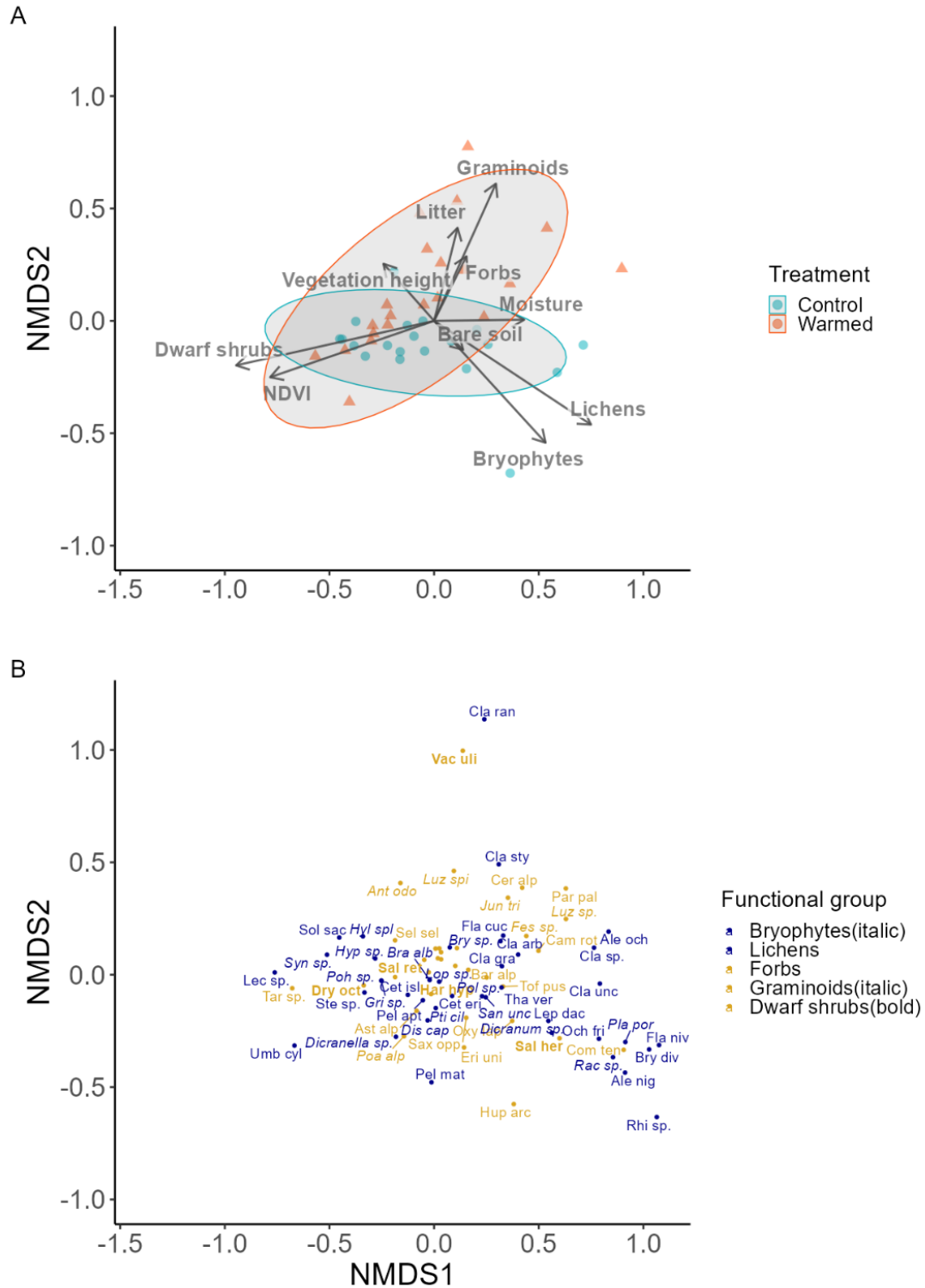


Fig. 11: Non-metric multidimensional scaling (NMDS) ordination of plots and species in the Dryas heath, 23 years after the experimental warming study started. Percent cover was used as a measure of species abundance. $k = 2$, stress = 0.15. A) Distribution of control plots (blue) and warmed plots (red) along the two main NMDS-axes. Arrows show the correlation between the NMDS-axes and cover of functional groups, litter, and bare soil; vegetation height; soil moisture; and NDVI. Directions of the arrows show positive, negative, or neutral correlations; lengths show the strength of the relationships. Ellipses show the 95 % confidence interval of plot treatment (control/warmed). B) Species' distribution along the two main NMDS-axes. The position of some species has been adjusted to avoid overlaps, actual locations are shown with lines. Vascular plants are in yellow, cryptogams in blue. Full species names are given in Appendix A.

Table 10: Correlation between environmental variables and the two main axes in the non-multidimensional scaling (NMDS) ordination of species composition in the Dryas heath, 23 years after the experimental warming study started. Percent cover was used as a measure of species abundance in the NMDS. Kendall's rank correlation coefficient τ was used to measure the correlation. Z values are given for every test except soil moisture where a T-distribution was used. Bold values are significant at $p < 0.05$.

Variable	Axis	T	Z	tau	p
Dwarf shrubs	NMDS1		-7.002	-0.752	<0.001
	NMDS2		-2.125	-0.228	0.034
Forbs	NMDS1		0.684	0.074	0.494
	NMDS2		2.118	0.230	0.034
Graminoids	NMDS1		2.978	0.325	0.003
	NMDS2		3.630	0.396	<0.001
Lichens	NMDS1		5.054	0.545	<0.001
	NMDS2		-1.063	-0.114	0.288
Bryophytes	NMDS1		3.421	0.372	<0.001
	NMDS2		-1.879	-0.204	0.060
Litter	NMDS1		1.139	0.122	0.255
	NMDS2		2.045	0.221	0.040
Bare soil	NMDS1		1.348	0.152	0.178
	NMDS2		-0.022	-0.002	0.982
Vegetation height	NMDS1		-1.192	-0.128	0.233
	NMDS2		0.802	0.086	0.423
Soil moisture	NMDS1	563		0.308	0.004
	NMDS2	426		-0.010	0.931
NDVI	NMDS1		-5.311	-0.570	<0.001
	NMDS2		-1.322	-0.142	0.186



Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway