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Warming without warning? Significant thermophilization amidst seemingly stable alpine plant communities in Filefjell, Norway

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Abstract

Global warming is driving rapid climatic changes, with profound effects on Arctic and alpine ecosystems. Climate-driven shifts in alpine plant communities have already been observed, including upward movements in species distributions and increased species richness in some areas. These changes vary across habitat types, making ecological responses to climate change in alpine environments inherently complex. In this study, I resurveyed the highest altitudinal occurrences of vascular plant species on 12 mountain summits in Filefjell, Norway. The aim was to assess changes in species richness, altitudinal distribution, and climatic indicator values, and to identify which habitat types are most frequently colonized by new species over a 14-year period. Additionally, polygons and estimations of habitat types were recorded and unsupervised classification was conducted to explore its potential for systematic and effective classification of alpine habitat types.

No significant changes were found in species richness, composition, or altitudinal distribution on the summits over the study period, possibly due to time lags in species' responses to climate change. In contrast, a significant increase in Dahl-R climatic indicator values was observed, indicating ongoing thermophilization of summit vegetation. This discrepancy suggests that thermophilic species are becoming more frequent on the summits, but not yet to a degree that results in substantial species turnover or noticeable shifts in overall diversity patterns. Boulderfields had a tendency of having the highest proportion of new species on the summits, while ridges had the lowest. Furthermore, habitat types and environmental variables explained only a small portion of the variation in species composition. While the unsupervised classification approach did not produce meaningful results for habitat mapping, remote sensing remains a promising tool for future alpine habitat classification. This study highlights the importance of incorporating detailed abundance data and full altitudinal and cardinal range information for plant species, as such data can help detect subtle ecological shifts that may otherwise go unnoticed. Given the potential for delayed responses to climate change, long-term ecological monitoring remains essential.

Sammendrag

Global oppvarming fører til raske klimaendringer som har stor innvirkning på arktiske og alpine økosystemer. Endringer i alpine plantesamfunn er blitt observert, blant annet ved at arter flytter seg oppover i høyden og ved økt artsrikdom i enkelte områder. Alpine områder innehar en bratt gradient av habitater, og klimaendringers påvirkning på alpine økosystemer varierer derfor mye på grunn av mangfoldet av naturtyper i disse områdene. Dette gjør at responsene på klimaendringer i alpine områder er svært komplekse. I denne studien har jeg gjennomført ny kartlegging av de høyeste forekomstene av karplanter på fjelltopper i Filefjell, Norge. Målet var å undersøke endringer i artsrikdom, høydefordeling og klimatiske indikatorverdier, samt å identifisere hvilke naturtyper nye arter oftest koloniserer, over en studieperiode på 14 år. I tillegg ble polygoner og dekning av naturtyper kartlagt og usupervisert fjernanalyse ble anvendt for å utforske potensialet for habitatklassifisering i alpine områder.

Ingen signifikante endringer ble funnet i artsrikdom, artssammensetning eller høydefordeling på fjelltoppene i løpet av studieperioden, som kan forklares av tidsforsinkede responser på klimaendringer hos artene. Det ble imidlertid observert en signifikant økning i klimatiske indikatorverdier (Dahl-R), noe som indikerer en pågående termofilisering av vegetasjonen på toppene. Dette antyder at varmekjære arter blir vanligere på fjelltoppene, men ennå ikke i et omfang som fører til betydelig utskifting av arter eller merkbare endringer i mønstrene for artsmangfold. Blokkmark hadde en tendens av å ha høyest forekomst av nye arter, mens rabbe hadde færrest. Videre forklarte verken naturtyper eller miljøvariabler mye av variasjonen i artssammensetning. Den usuperviserte klassifiseringen ga ikke meningsfulle resultater for kartlegging av naturtyper på toppene, men fjernanalyse har fortsatt et stort potensial for klassifisering av alpine naturtyper. Denne studien fremhever viktigheten av å inkludere detaljerte data knyttet til abundans av arter i tillegg til deres fullstendige høydemessige og kardinale utbredelse, ettersom slike data kan bidra til å avdekke subtile økologiske endringer som ellers kan forbli uoppdaget. Gitt potensialet for forsinkede responser på klimaendringer i alpine plantesamfunn, er langsiktig økologisk overvåkning avgjørende.

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Introduction

Global warming is leading to changes in climate, affecting ecosystems worldwide (IPCC, 2023). Arctic and alpine ecosystems are more susceptible to the impacts of climate change than ecosystems in lower latitudes and altitudes, due to biological and chemical processes being more temperature-sensitive in these areas (Kirschbaum, 1995). Additionally, Arctic amplification is leading to an increased rate of climate change in the high northern latitudes (Delworth et al., 2016; Serreze et al., 2011). Direct effects of climate change are elevated temperatures, shifts in precipitation and increased frequency of extreme events, such as droughts and heat waves (IPCC, 2023), imposing substantial impacts on alpine plant communities (Ernakovich et al., 2014).

Changes in alpine plant communities have already been observed as a response to climate change. The altitudinal distribution of alpine plant species is shifting upward (Klanderud et al., 2003; Lenoir et al., 2008; Pauli et al., 1996), with shrubs and woody plants expanding rapidly in alpine areas (Cannone et al., 2007; Odland et al., 2010). This upward movement has led to an increase in species richness, exemplified by an 87% rise in plant species richness on European mountain summits over the past 145 years (Steinbauer et al., 2018). However, other biotic and abiotic factors also play important roles in the response alpine ecosystems has to climate change. For example, differences in bedrock type and substrate calcareousness affect how alpine plant species respond to climate change. Siliceous bedrock has been associated with increased species richness after 14 years of climate warming, while calcareous bedrock has shown a decline (Nicklas et al., 2021). In addition, human and animal activities impact summit vegetation. Grazing pressure, hiking trails, and roads contribute to changes in species composition by facilitating seed dispersal and enabling the colonization of new areas by lowland plants which can establish in higher altitudes due to the changing climate (Austrheim et al., 2001; Austrheim et al., 2008; Bhatta et al., 2018; Haider et al., 2018; Koyama et al., 2025; Speed et al., 2012). Considering these interacting factors is therefore crucial for predicting and understanding how vascular plant species respond to a changing climate.

Models of future responses to climate change is another important facet in understanding and predicting alpine plant communities' responses to climate change. Such models are projecting high local extinctions of plant species in mountainous areas (Dullinger et al., 2012a). However, abiotic drivers of plant distribution often act on a smaller scale than the spatial resolution used in such models (Carlson et al., 2013). Microtopography, microclimate and substrate may be more important for alpine species facing climate change, than macroclimatic conditions (Kulonen et al., 2018; Körner, 2023). Mountains exhibit steep climatic gradients over short distances, resulting in high microclimatic heterogeneity (Körner, 2004). This heterogeneity can create microrefugia, which are specific areas where conditions are favourable for certain species, and that protect species against climate-driven range contractions and potential extinctions (Alexander et al., 2018; Dagnino et al., 2020; Scherrer et al., 2011; Suggitt et al., 2018). Because of this, alpine ecosystems, despite their apparent harshness, often support a wide diversity of microhabitats and microclimatic conditions which harbour many different species. These fine-scale features make species' responses to climate change highly complex and context-dependent. Therefore, when evaluating shifts in alpine plant distributions, it is essential to consider microclimatic variation and species' associations with specific microhabitats (Kulonen et al., 2018). Nevertheless, to the best of my knowledge, few studies have explored this topic within Scandinavian alpine ecosystems.

Remote sensing analysis has become an essential tool in ecological research for monitoring environmental changes and forecasting ecosystem responses to climate change (Gandhi et al., 2015; Pettorelli et al., 2014; Pettorelli et al., 2005). Numerous studies have utilized remote sensing to examine phenomena such as treeline shifts and variations in Normalized Difference Vegetation Index (NDVI) across mountainous regions (Chhetri et al., 2019; Guo et al., 2014; Muradyan et al., 2019; Pettorelli et al., 2005; Rumpf et al., 2022). These methods provide valuable insights into current habitat type distributions and enable projections of how ecosystems may shift under future climatic scenarios (Rwanga et al., 2017). On the other hand, such methods assess overall vegetation cover but lack detail on species composition and habitat types, limiting our understanding of species and habitat responses to climate change. A deeper understanding of how different habitat types respond ecologically under climate pressure improves our ability to model and predict alpine transformations. Furthermore, by identifying which habitats are most likely to support establishing species or lose existing ones, remote sensing may help pinpoint areas of expected ecological change and inform future conservation strategies.

To investigate how alpine plant communities are responding to climate change, I resurveyed vascular plant species on mountain summits in Filefjell, Norway. The altitudinal distribution of vascular plant species on these mountain summits was first recorded in the 1970s (Lye, 1973). In 2010, after almost 40 years of climate change, Odland et al. (2010) resampled the summits, comparing the findings to Lye (1973). The study found significant changes in both species' composition and richness, as well as an elevational advance of woody plants and shrubs (Odland et al., 2010). Odland et al. (2010) also found an increase in vascular plants Dahl-R climatic indicator values, indicating a change towards environments more advantageous for thermophilic species on the summits. In this study, I aim to evaluate the effects of 14 years of climate change on vascular plant species' communities on these summits. Additionally, a pilot study using remote sensing analysis is presented to explore its potential for systematically and effectively classifying habitat types in alpine areas. On that note, I seek to answer the following research questions:

1) Have there been changes in vascular plant species richness (in total and within different functional groups), species composition and altitudinal distribution on the summits since 2010?
2) Have changes in environmental indicator values based on vascular plant species indicated climatic shifts on the summits since 2010?
3) How does the occurrence of new species vary across different habitat types, and are certain nature types associated with a higher frequency of newly recorded species?
4) Do environmental variables such as elevation, bedrock type, the abundance of habitat types, and distance to roads and hiking trails influence species richness and composition on the summits?
5) Can unsupervised classification, using satellite imagery, be used for determining habitat types on the mountain summits?

I predict a significant increase in plant species richness, both in total and for all functional groups, along with upward shifts in altitudinal distribution, changes in species composition, and higher Dahl-R climatic indicator values on the summits since 2010. Additionally, the occurrence of new species is expected to vary across habitat types, with a higher prevalence in habitats such as snowbeds due to expected changes in snowcover duration. Environmental variables such as proximity to hiking trails and roads are likely to increase species richness in combination with climate change, as well as alter species composition at higher elevations by facilitating seed dispersal. In contrast, higher elevations may have a negative effect on species richness on the summits. Finally, remote sensing using unsupervised classification with satellite imagery will be an effective tool for identifying the dominant habitat types on mountain summits.

Materials and methods

Study area

This study was performed in Filefjell, Norway, during the first three weeks of August in 2024. Filefjell is a mountain area in the western part of Norway, situated within 61˚06’- 61˚14’N and 7˚52’-8˚15’E (fig. 1). The 12 summits visited in this study are the same as in Lye (1973) and Odland et. al. (2010) and range from 1515 to 1814 meters above sea level (m.a.s.l.) (table 1). Due to unforeseen events, one summit, Krekanosi S, was not visited this time. The studied summits are in proximity to each other with a valley separating Suletinden and Storeknippa from the rest (fig. 1). The bedrocks on the summits are mainly granite, but also monzodiorite, metagabbro and gabbro (table 1), and most of the summits are in areas with very low calcareous bedrocks (table 1, Appendix A: Fig 1). The vegetation on the summits is sparse, with mostly scattered individuals of vascular plants in cracks on bare rocks or in between boulders. On the lower summits, medium to large patches of vegetation were found, mostly on ridges, leesides and early snowbeds. The ridges were dominated by *Carex bigelowii, Juncus trifidus, Festuca vivipara, Empetrum nigrum* and *Vaccinium vitis-idaea.* The leesides vegetation was dominated by *Vaccinum myrtillus, Sabbaldia procumbens, Saussurea alpina* and *Anthoxantum odoratum,* while boulderfields consisted of scattered individuals of species such as *Beckwithia glacialis* and *Cryptogramma crispa*. Patches in snowbeds consisted mostly of *Salix herbacea* and moisture- and frost- adapted forbs, such as *Beckwithia glacialis, Omalotheca supina* and species from the genus *Saxifraga,* as well as graminoids such as *Luzula arcuata* and *Poa alpina var. vivipara*. Later snowbeds mostly consisted of bryophytes and the lichen S*olorina crocea*.

There are both domestic sheep and semi-domestic reindeer grazing in the area (Kartverket, 2015, 2018). The summits Graveggi, Loppenosi, Rjupeskareggen, Slettningseggi and Suletinden were affected by sheep grazing (Appendix A: fig 2), while semi-domestic reindeer only grazed at the summits Storeknippa and Suletinden (Appendix A: fig 3). Some of the summits had hiking trails close to or crossing the summits, as well as roads in proximity.

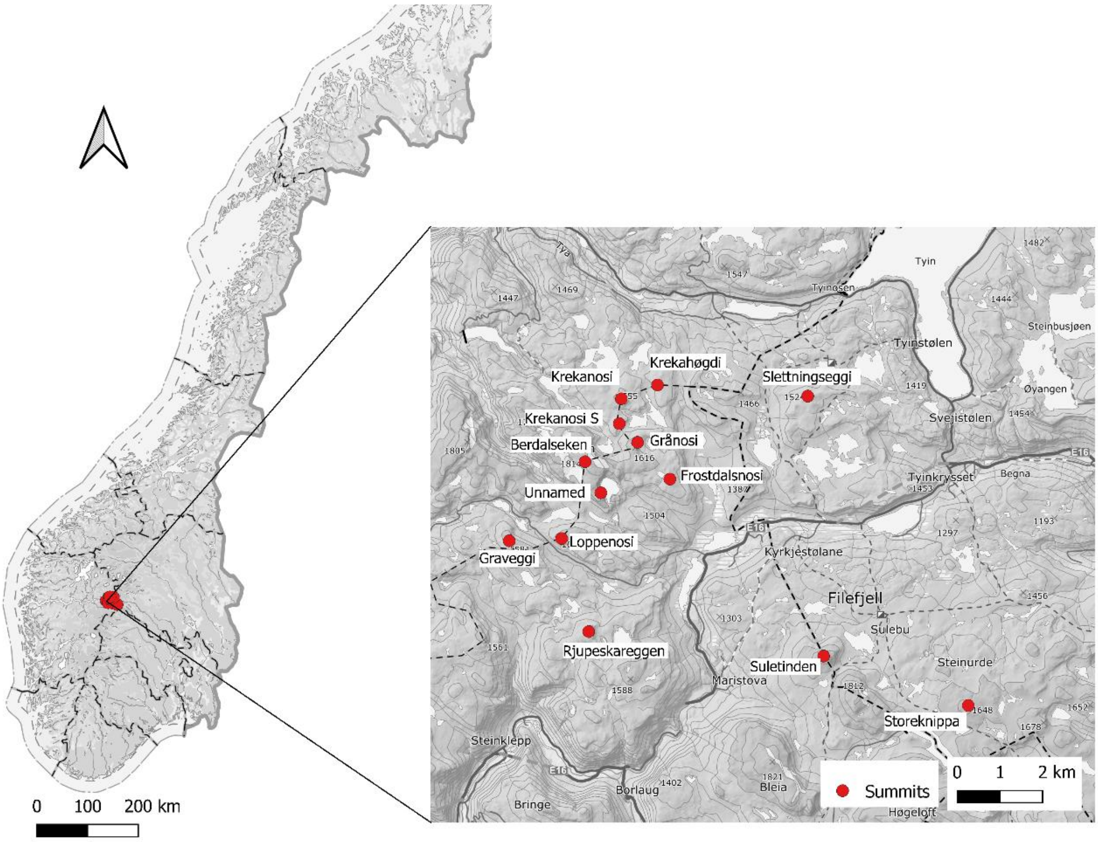

Fig. 1: *Location of the study area with red dots representing each summit. Made with QGIS version 3.26.3 (QGIS.org, 2024). Background map: Topographical map of Norway (Norwegian Mapping Authority, 2024).*

Table 1. *The summits visited in this study, their altitude (M.a.s.l.), size (decare) (Odland et al., 2010), bedrock (NIBIO, n.d.) and calcareousness (Kartverket, 2024).*

Summits	**M.a.s.l.**	**Size (daa)**	**Bedrock**	**Calcareousness**
Berdalseken	1814	10.0	Granite	Very low
Frostaldsnosi	1536	9.7	Monzodiorite	Very low
Graanosi	1619	3.3	Monzodiorite	Very low
Graveggi	1582	9.0	Metagabbro/granite	Low and high
Krekahøgdi	1515	5.5	Granite	Very low
Krekanosi	1558	12.1	Granite	Very low
Loppenosi	1613	5.4	Granite	Very low
Rjupeskareggen	1561	7.2	Granite	Very low
Slettningseggi	1528	2.0	Granite	Very low
Storeknippa	1649	14.0	Monzodiorite	Low
Suletinden	1784	3.1	Monzodiorite/granite	Very low
Unnamed	1654	9.2	Granite	Very low

Weather data was collected from Maristova, Asbjørsbråten and Kyrkjestølane weather stations due to their proximity to the study area. Maristova and Kyrkestølane are located at Filefjell, while Asbjørsbråten is located approximately 90 km SE of the study area. Asbjørsbråten weather station was used for temperature data, as it is the only weather station in the area that has long-term historical temperature data, while the other weather stations nearby only have temperature data from the past 10-15 years. There has been an increased annual temperature of 0.07 degrees Celsius per decade from 1923 to 2017 (Asbjørsbråten weather station, 60.9225° N - 9.29482° E, 639 m. a. s. l.), as well as an increased annual precipitation of 33 mm per decade from 1923 to 2022 (Maristova weather station, 61.1098838° N - 8.0368593° E, 806 m. a. s. l.) (MET, n.d.). There was not available temperature data for the whole study period in this area, but at the weather station Kyrkjestølane, Filefjell (61.178 N, 8.1125 E, 956 m. a. s. l), the average temperature increase from 2011 to 2024 was 0.032 degrees Celsius per year, while the average precipitation had decreased by -9.37 mm per year in the same timeframe (MET, n.d.).

Study design

In 1972, Lye (1973) collected data on altitudinal distribution of vascular plants on 13 summits in Filefjell, Norway (fig. 1, table 1). In the months of August and September of 2008-2009, Odland et. al (2010) went back and collected new data using the same methods, comparing the data to the historical data from Lye (1973). For the current study, the same methods were used during fieldwork on 12 of the summits. The altitude of the uppermost individual of each species on each summit was recorded by using a GPS (Garmin etrex 10) (Appendix B, table 1).

In addition to collecting altitudinal data on the vascular plants, I mapped the habitats of each species according to Nature in Norway version 2.3 (NiN). NiN is a framework used for mapping ecosystems in Norway (Halvorsen et al., 2020). In this study, I used mapping units, as they provide important information about habitats at multiple scales (table 2). For certain statistical analyses (see below), these mapping units were grouped into major types (table 3), as this level of aggregation was more appropriate for the purpose of comparing habitats and species composition. According to Halvorsen et al. (2020, *Supplementary Material*, Appendix S1, Table S1.1), *mapping units* are defined as "type, aggregate of types, or variable from an attribute system, used to delineate map objects adapted to a pre-defined map scale" and were specified at a 1:5000 mapping scale. *Major type* is defined as "a convex subspace of the ecodiversity level and satisfying a set of additional criteria," where the *ecodiversity level* refers to "a level in the hierarchy of increasing complexity towards broader spatial scales at which biotic and abiotic components and their interactions […] are considered together." To avoid confusion and enhance clarity throughout the thesis, I have chosen to refer to *major types* as *major habitat types*. While this is not the formal NiN term, it better communicates the ecological meaning in this context.

The mapping units at the location of the highest occurrence of each plant species at each summit was recorded. Additionally, to obtain information on mapping units and their distribution on the summits, I estimated and mapped the cover (%) of the different mapping units according to NiN. Due to the extent of this task, habitat mapping was performed in the following two ways:

1) On four summits, the landscape was mapped following the NiN mapping guideline (Bratli et al., 2022; Bryn et al., 2021; Halvorsen et al., 2020) and polygons covering the uppermost 32 meters in altitude were made (Appendix A: fig. 4 - 7), using mapping units and a minimum size of 250m^2 for each polygon. The app ArcGIS Field Maps version 24.2.2 (Esri, 2024) was used on a mobile device to make polygons, which were then downloaded to a computer using ArcGIS Online.

2) On six summits the cover (%) of the mapping units that were 250 m^2 or larger was visually estimated.

Due to unforeseen events, there were no estimates or polygons of mapping units made for the summits Loppenosi and Storeknippa.

Table 2. *Description of the major habitat types that were used in this study (Bryn & Naas, 2021).*

Major habitat types	**Description**
T1	**Bare rock:** Areas on open and solid rock on mountains without soil cover. The rock can be vegetation free or include some cover of bryophytes and lichens
T3	**Alpine heath, leeside and tundra**: Soilcovered solid ground in the mountains or north of the forest limit, which is not conditioned by environmental stress such as frost, wind, avalanches or late snowcover. The vegetation is characterised by shrubs and/or dwarf shrubs as well as forbs
T7	**Snowbed:** Soilcovered solid ground conditioned by long-lasting snowcover and a short growing season in alpine and arctic regions
T13	**Landslide area**: Unstable parts of a landslide hill under steep rock walls, where disturbance by avalanches is so high that there is no established soil cover
T14	**Ridge:** Land on elevated terrain in alpine or arctic areas characterised by wind exposure, especially because there is a lack of stable snowcover in winter
T22	**Alpine grass heath and grass tundra:** The gradual distinction between low-alpine to mid-alpine zone with vegetation dominated by, or including, “dry-grass”
T27	**Boulderfield:** Continuous areas dominated by boulders or rocks that are not disturbed by avalanches
V3	**Ombrotrophic bog:** Includes mires where the surface peat has no contact with groundwater, and the species receive water and mineral nutrients exclusively from precipitation
V6	**Wet snowbed and snowbed spring:** Long lasting snowcovered areas in the mountains that are provided with melting water from overlying snowpatches or glaciers through long periods of the growing season

Table 3. *Description of the mapping units that were used in this study (Bryn & Naas, 2021).*

Mapping units (1:5000)	**Description**
T1C1	Low desiccation-exposed and very low to low calcareous bare rock
T1C2	Desiccation-exposed and very low to low calcareous bare rock, rock walls and outcrops
T1C4	Desiccation-exposed low to intermediate calcareous bare rock, rock walls and outcrops
T1C9	Weakly intermediate to more calcareous windswept rock
T3C2	Low calcareous alpine heathland, moderate desiccation risk
T3C3	Low calcareous alpine lichen heath, high desiccation risk
T7C1	Very low calcareous moderate snowbed (early snowmelt and longer growing season)
T7C2	Fairly low calcareous moderate snowbed (early snowmelt and longer growing season)
T7C4	Intermediate calcareous late snowbed (late snowmelt and shorter growing season)
T7C5	Intermediate calcareous extreme snowbed (very late snowbed, short growing season)
T13C1	Low calcareous coarse scree
T14C1	Low to intermediate calcareous ridge
T22C3	High calcareous grass-snowbed
T27C1	Low to intermediate calcareous boulderfield
T27C2	High calcareous boulderfield
T27C5	Boulderfield in vegetation free snowbed
T27C6	Low to intermediate calcareous ridge-like boulderfield
V6C1	Low to intermediate calcareous moderate wet snowbed

Data analysis and statistics

I preformed the statistical analysis using R version 4.3.1 (R Core Team, 2023) and RStudio 2024.12.0+467 (RStudioTeam, 2024). I used the following packages for organizing data and making figures: readr (Wickham et al., 2024), tidyverse (Wickham et al., 2019), ggplot2 (Wickham et al., 2009), patchwork (Pedersen, 2019), reshape2 (Wickham, 2022) and ggrepel (Slowikowski et al., 2023).

ChatGPT (OpenAI, 2025) and Microsoft Copilot (Microsoft, 2025) were used for helping in writing codes for statistical analysis, and as aid for proofreading paragraphs and translations.

To test the assumptions of normally distributed data, I performed Shapiro-wilk tests as well as visually inspecting histograms. For testing assumptions for normally distributed residuals in the linear mixed models (see below), I visually inspected qq-plots of the residuals and then preformed a Shapiro-Wilk test to make sure they were normally distributed, as well as using the *simulateResiduals* function in the DHARMa-package (Hartig, 2024) to generate simulated residuals for assessing model fit. The function detects biases, dispersion issues, and autocorrelation using uniform residuals and diagnostic plots.

Species richness, functional groups, altitudinal distribution and Dahl-R values

To test for changes in species richness on the summits, I first calculated species richness on each summit for both years before preforming a paired Student's T-test. To test for changes in the number of species within the functional groups dwarf shrubs, shrubs, forbs and graminoids on the summits between the two years, I used a Wilcoxon Signed-Rank Test, as the data was not normally distributed.

Changes in the species altitudinal distribution on the summits from 2010 to 2024 was tested by first calculating each species distance to the summits' highest point for both years, before fitting a linear mixed model with lmer4-package (Bates et al., 2015) and lmerTest-package (Kuznetsova et al., 2017). The calculated distance was used as response variable, while year was used as explanatory variable. The distance-data was log+1 transformed as the data contained many values at and around zero. Summit and species were included as random variables. This statistical analysis used to measure changes in the species altitudinal distribution in my study includes all species, also the species that where lost and the ones that were new in 2024. New species may be colonizing at the lowest part of the study area, contributing to an overall increased distance from the summits highest point, while the species that was lost may have been situated on the higher parts of the summits in 2010. To investigate if this was the case, I divided the dataset into three groups; species present both years, new species in 2024 and lost species in 2024 on each summit, and then performed a Wilcoxon Singed-Rank Test to test if new species in 2024 were situated at significantly different altitudes than the species lost since 2010.

Dahl-R values were used to test for changes in indicator values on the summits between 2010 and 2024. Both temperature and precipitation has increased in the area of the summits in this study (MET, n.d.), but traditional weather station data often fail to reflect the microclimatic conditions actually experienced by small alpine plants, especially in sheltered or snowbed habitats (Scherrer et al., 2010). In this context, ecological indicator values such as Dahl-R can offer more sensitive measures of changing plant-climate relationships and were used to investigate further changes in microclimatic conditions. Dahl-R values also appear to perform better than other climatic indicator values when describing the decreasing temperatures along an altitudinal gradient (Odland, 2009), which was relevant in this study as species' altitudinal distribution along an altitudinal gradient was studied. Dahl-R values are based on plants respiration and the non-linear relationship between plants respiration and temperature, and from these calculations the plants have been assigned values from 0 (high altitudinal plants) to 2 (lowland) (Dahl, 1998). Dahl-R values for the species were obtained from Dahl (1998). To test for changes in Dahl-R values, I fist calculated the mean Dahl-R value for each summit in both years before performing a paired Student's t-test. To compare the Dahl-R values of new and lost species in 2024 to look for trends in changes within the climatic indicator values, I divided the dataset into two groups of new and lost species for each summit in 2024. I further calculated the mean Dahl-R values in each group and performed a paired Student's t-test. Dahl-R values existed for 70% of the species included in this study, and the species without values were excluded from the analyses.

Ratio of new species in different nature types

To examine whether certain major habitat types had a higher ratio of new species, I fitted a linear mixed model using the lme4 package (Bates et al., 2015). The response variable was the ratio of new species within each major habitat type on each summit, while major habitat type was included as the explanatory variable. Summit was included as a random variable to account for variation among summits. To identify differences between specific major habitat types, I conducted a post-hoc Tukey's test using the *emmeans* function from the emmeans package (Lenth et al., 2025).

Species composition

To test for similarities in species composition between the years 2010 and 2024, I used both the Jaccard Index (JI) and Sørensen Similarity Index (SSI). By using both methods, I can compare the results to get a more robust analysis. The JI and SSI are based on presence/absence data, and they do not take into account the abundance of species (Verma et al., 2020). The SSI adds more weight on the joint occurrences, therefore emphasizing similarities, while the JI emphasises differences, and is usually preferred when there are many joint occurrences in the samples (Clifford et al., 1975).

For both methods, the following data was used:

a = number of species present in both samples (joint occurrences)

b = number of species present only in the first sample

c = number of species present only in the second sample

The following formulas (Krebs, 1998) was used to calculate the indexes from both summits:

Sørensen Similarity Index (SSI)

$$SSI = \frac{2a}{2a + b + c}$$

Jaccard Index (JI)

$$JI = \frac{a}{a + b + c}$$

Both the JI and the SSI are a number between 0 and 1, where 0 means there are no common elements between the two samples, and 1 means the samples are identical (Krebs, 1998). For these analyses the values were multiplied by 100 to get the percent similarity between the two years.

To further examine differences in species composition between 2010 and 2024, I used nonmetric multidimensional scaling (NMDS) using the *metaMDS*-function from the vegan-package (Oksanen et al., 2025). The analysis was based on a presence/absence matrix of species per summit per year and by using two dimensions (k = 2). The analysis was done with trymax = 500 to increase the probability of reaching the global minimum and assure reproducible results. I further used the *envfit*-function from the vegan-package (Oksanen et al., 2025) for testing how well the environmental variables explained the variation in species composition. The *envfit*-function performs a permutation-test to test how well a variable explains the variation in species composition in the NMDS-ordination. The following environmental variables were added to the NMDS: distance to nearest road, distance to nearest hiking trail, altitude (m.a.s.l.), summit size (in decare), bedrock and calcareousness. The distance to nearest road and hiking trail was calculated manually using the app Norgeskart Friluftsliv 3.27.1 (Kartverket, 2017). It is important to note that not all hiking trails are registered in Norgeskart Friluftsliv or other map-services. Lastly, I preformed canonical correspondence and redundancy analyses (CCA and RDA, respectively) to test if the species composition differed between the two years, using year as conditional factor. I chose to use both tests for elevating the robustness of the analysis.

Since data on the cover of mapping units were only collected from 10 summits - 6 based on estimates and 4 derived from polygons - I performed a separate NMDS analysis for these summits using the same method as described above. In this analysis, mapping units cover was included as environmental variables using the *envfit* function. To incorporate mapping unit cover as an environmental variable in the NMDS with all 12 summits, I conducted a Procrustes analysis (from the *vegan* package; Oksanen et al., 2025) to compare the NMDS results from the 10-summit and 12-summit datasets. Since the Procrustes analysis indicated a strong similarity between the two NMDS configurations (Appendix C: table 2), I proceeded with the NMDS based on data from all 12 summits and incorporated the mapping unit cover variables derived from the 10-summit dataset.

Processing of polygons and remote sensing analysis

The polygons of major habitat types was processed in QGIS 3.26.3 (QGIS.org, 2025). Overlap between polygons was removed using the function *difference* in the Processing toolbox by calculating the average space in the overlap and applying half of this equally to each polygon. The habitat type bare rock (T1) was not recorded in the field, and all areas without polygons were assigned this in QGIS after fieldwork. Polygons of less than 250 m^2, and these polygons were deleted, and their area replaced with the nearest mapping unit. If there were more than one polygon bordering to this polygon, I evenly distributed the empty space to the bordering major habitat types.

Unsupervised classification was chosen to perform the remote sensing analysis, as it is a commonly used approach in vegetation cover mapping, offering the advantage of automatically transforming spectral image data into thematic maps (Xie et al., 2008). Sentinel-2 satellite images, bands 2, 3 and 4 were selected for conducting the unsupervised classification and was collected from the Copernicus database (Copernicus, n.d.). The chosen images were from 8th of August 2024, the same timeframe in which fieldwork for this study was conducted. A maximum cloud-cover of 20% was selected.

The classification was performed using QGIS 3.26.3 (QGIS.org, 2025) and R version 4.3.1 (R Core Team, 2023). The function *K-means Clustering* was used to conduct the unsupervised classification in QGIS. This function groups data into clusters based on spectral similarity. I did unsupervised classification with both mapping units and major habitat types. The polygons included 14 mapping units, so the unsupervised classification was performed using 14 clusters. For major habitat types, which comprised only 6 types, I selected 6 clusters for the classification. To compute statistical values for the polygons and the clusters created by *K-means clustering,* each of the vector data (polygons) and raster layer (clusters) for both mapping units and major habitat types were run through the function *Zonal statistics* in QGIS. The statistics of *majority* was chosen for the raster cluster. Majority statistics calculates the raster values that falls within the different polygons' borders, counting how many times there is a unique value. The output data was further processed using the *confusionMatrix*- function from the caret package (Kuhn et al., 2024) in R to check for the overall accuracy of the unsupervised classification compared to the ground truth data.

Results

Species richness

Species richness increased slightly on all but three summits (Graveggi, Krekahøgdi and Suletinden) from 2010 to 2024 (fig 2a). The overall mean richness on all summits had slightly increased, but not significantly (t = -0.587, df = 21.97, p-value = 0.565, fig. 2b).

Fig. 2. *a) Species richness on all summits in 2010 and 2024. b) Richness of vascular plants in 2010 and 2024, showing the median (bold line) and minimum and maximum values within the 1.5 interquartile range (whiskers).*

Species richness did not change significantly within functional groups on the summits from 2010 to 2024 (W = 4, p-value = 1), with very few changes in species richness within the functional groups (table 4).

Table 4. *Species richness within the different functional groups in 2010 and 2024.*

Functional group	**2010**	**2024**
Dwarf shrub	9	8
Shrub	6	6
Graminoid	28	31
Forb	63	64

Changes in altitudinal distribution

The species' altitudinal distributions did not change significantly from 2010 to 2024, indicating no significant altitudinal change of the species on the summits during this timeframe (table 5). Half of the summits had a decline in the average distance to the summits highest point, while the rest had an increase (fig. 3a & 3b).

There were significant differences between the new species' distance to the summits' highest points compared to the distances of the species lost in 2024 (W = 5510.5, p-value = 0.006), with new species having an average distance of 18.8 meters (N = 124) and lost species had an average of 22.0 meters (N = 72).

Table 5. *Results of the linear mixed model of the species' altitudinal distribution on the summits, with model estimates shown in log-scale, including the estimate, standard error (Std. Error), degrees of freedom (Df), t-value and p-value for the explanatory variable.*

	Estimate	**Std. Error**	**Df**	**t-value**	**P-value**
Intercept (2010)	2.450	0.159	17.55	15.41	<0.001
2024	-0.001	0.003	922.76	-0.353	0.724

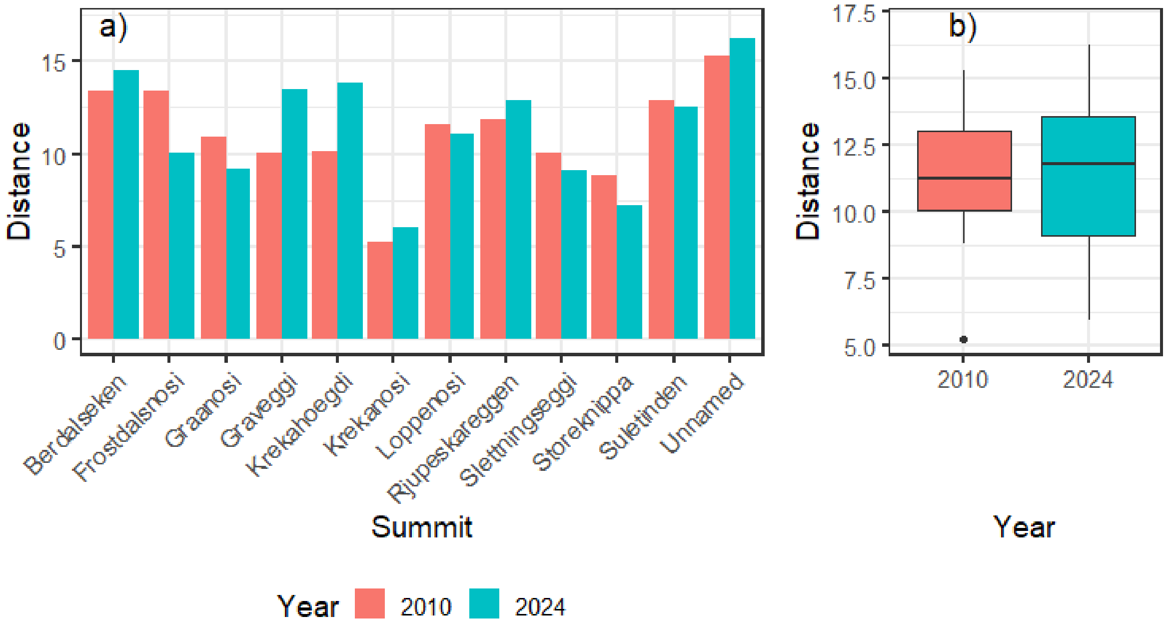

Fig. 3. *a) Species' average distance to the summits' highest point on all summits in year 2010 and 2024. b) Species' distance to the summits' highest point in year 2010 and 2024 based on the average distances, showing the median (bold line) and minimum and maximum values within the 1.5 interquartile range (whiskers), dots represent outliers.*

Changes in Dahl-R values

Dahl-R values increased on all but three summits, where the summit Unnamed had identical values in 2010 and 2024, and Graveggi and Krekahøgdi exhibited a decrease (fig. 4a). There was a significant increase in mean Dahl-R values on the summits since 2010 ($t = -2.8994$, p-value = 0.014, fig. 4b), indicating a climatic shift in the species composition on the summits towards species thriving in lowland climatic conditions. There were non-significant differences within the new and lost species' average Dahl-R values on the summits in 2024 ($t = 0.754$, df = 11, p-value = 0.467), where the species lost exhibited an average Dahl-R value of 0.342 ($N = 52$) and new species had an average Dahl-R value of 0.359 ($N = 92$).

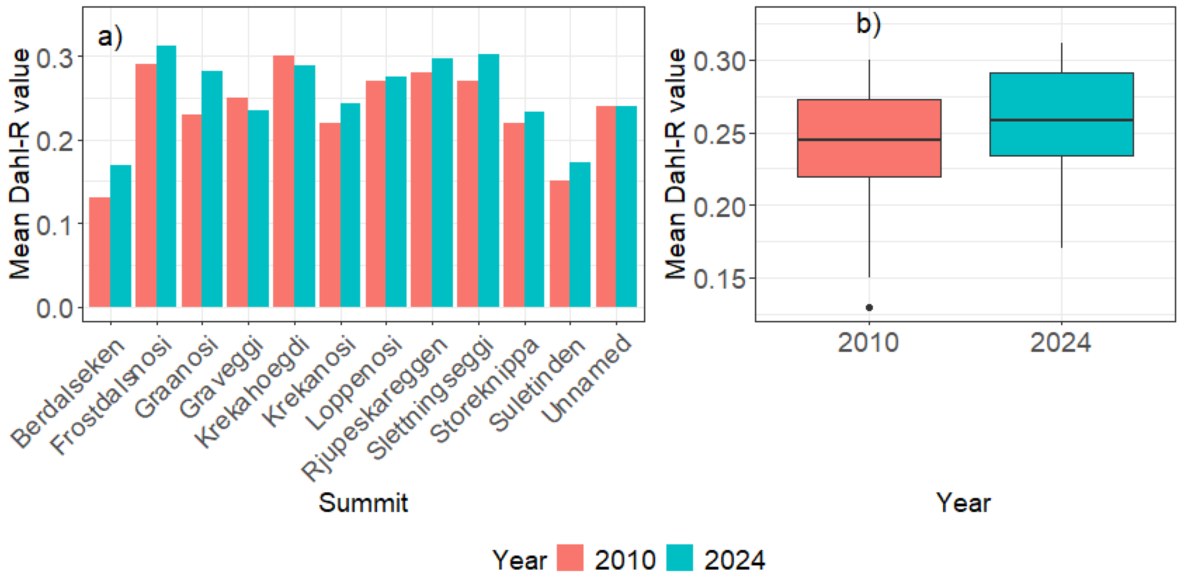

Fig 4. *a) Mean Dahl-R values on all summits the two years. b) Dahl-R values in year 2010 and 2024, showing the median (bold line) and minimum and maximum values within the 1.5 interquartile range (whiskers), dots represent outliers.*

Major habitat types and new species

The most prevalent mapping units on the summits in Filefjell was within the major habitat types *bare rock* (T1), *snowbed* (T7), *rigde* (T14) and *boulderfield* (T27) (fig. 5). The mapping units *desiccation-exposed and very low to low calcareous bare rock, rock walls and outcrops* (T1C2) and *highly calcareous boulderfield* (T27C2) where dominat on the summits, followed by *low desiccation-exposed and very low to low calcareous bare rock* (T1C1), *low to intermediate calcareous boulderfield* (T27C1) and *fairly low calcareous moderate snowbed* (T7C2) (fig. 5).

The prevalence of new species varied among major habitat types. A visual inspection of the ratio of new species and total number of species suggested that *ridge* (T14) had the lowest ratio, meaning that ridges had a lower amount of new species compared to the total number of species in this nature type, while *boulderfield* (T27) had the highest ratio, followed by *alpine grass heath and grass tundra* (T22), *alpine heath, leeside and tundra* (T3), *snowbed* (T7) and *bare rock* (T1) (fig. 6). *Ridge* (T14) had a tendency of having lower ratio of new species compared to *bare rock* (T1), but not significantly (table 6). The statistical test showed that *Boulderfield* (T27) had a significant higher ratio of new species (table 6). The pairwise comparison in the post-hoc test of *ridge* (T14) – *boulderfield* (T27) showed a close to significant difference between them (appendix C: table 3). The rest of the major habitat types showed no significant differences in ratio of new species (appendix C: table 3).

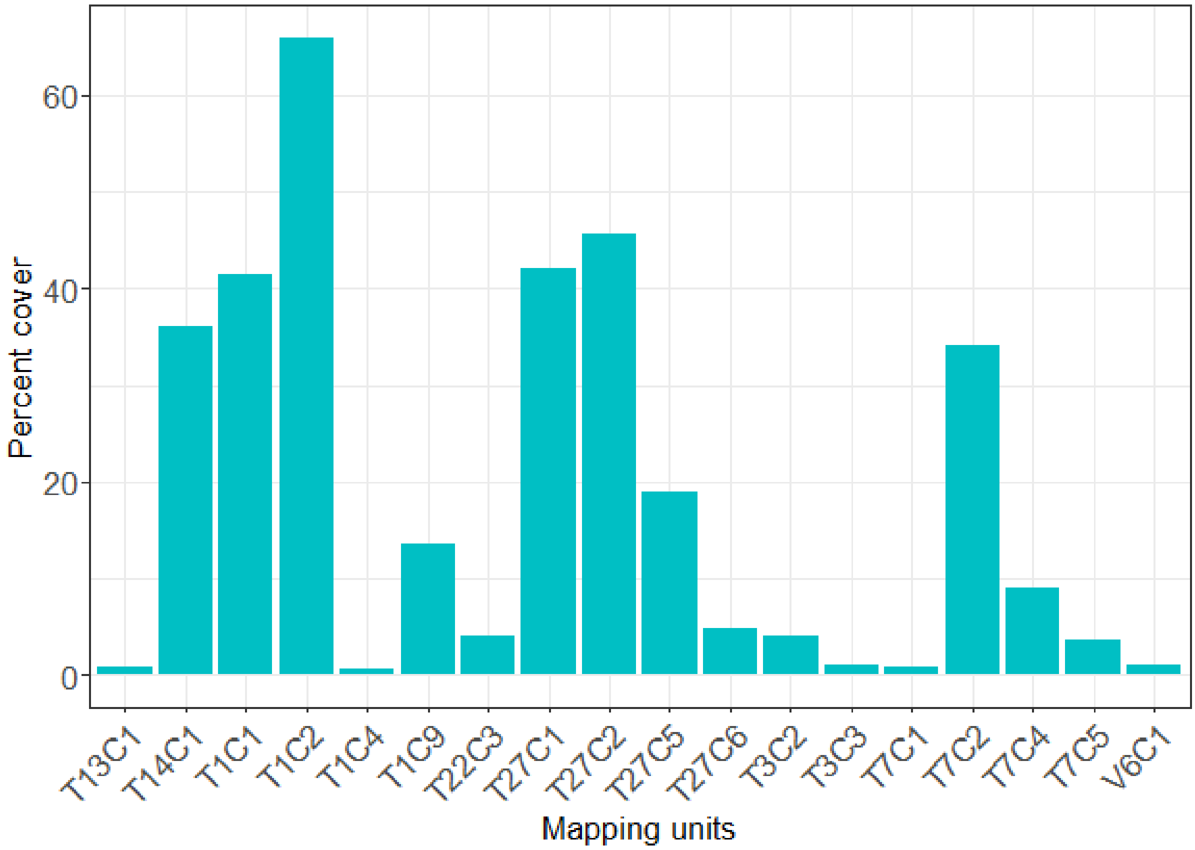

Fig.5. *The cover (%) of each mapping unit on the ten summits in 2024, based on both polygons and estimations in the field. See table 3 for description of the mapping units.*

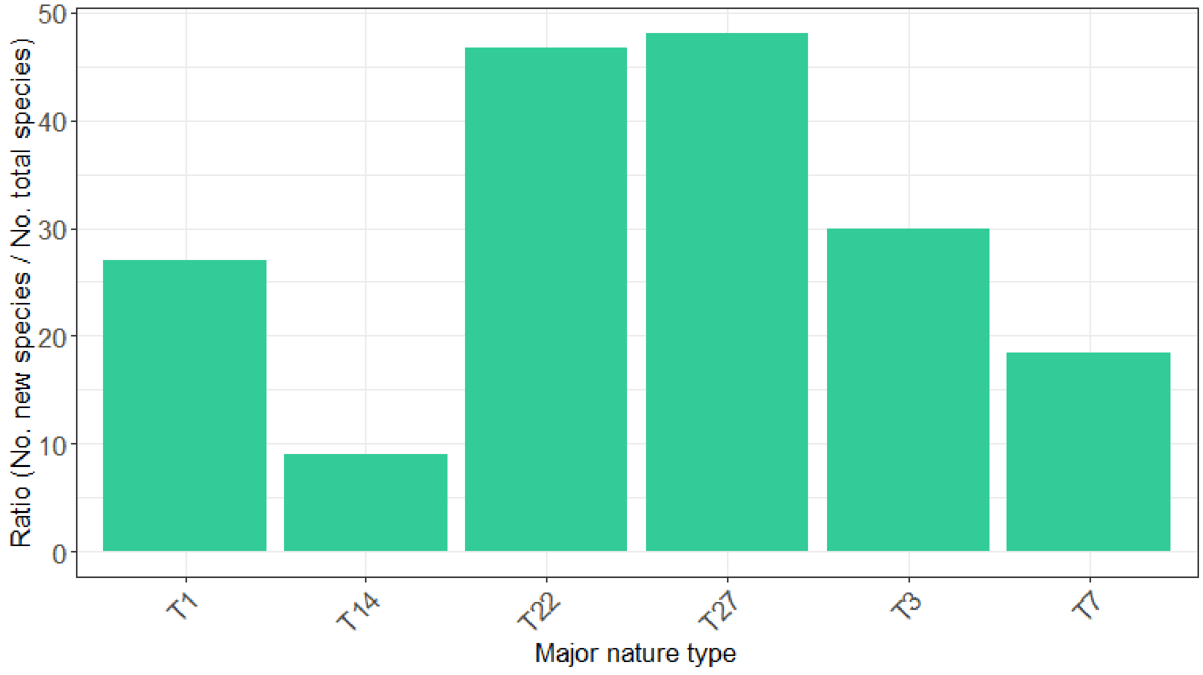

Fig. 6. *Ratio between number of new species and total number of species within each major habitat type. Values for major nature types V3 and V6 were not included as they had values = 0. See table 3 for description of the mapping units.*

Table 6. *Results of the linear mixed model with the ratio of number of new species and total number of species as response variables and each major habitat type as explanatory variables, showing estimate, standard error (Std. Error), degrees of freedom (Df), T (t-value) and p-value (* = significant, ● = close to significant). See table 2 for descriptions of the major habitat types.*

	Estimate	**Std. Error**	**Df**	**T**	**P-value**
T1 (Intercept)	26.58	6.43	29.8	4.13	< 0.001*
T14	-18.05	10.45	94.3	-1.73	0.087●
T22	16.61	11.11	98.4	1.50	0.138
T27	20.67	10.30	98.0	2.01	0.048*
T3	8.21	12.26	99.9	0.67	0.505
T7	-7.03	7.36	94.1	-0.95	0.342
V3	-22.49	31.74	100.0	-0.71	0.481
V6	-21.67	31.61	99.4	-0.69	0.495

Species composition

Both Sørensen Similarity index (SSI) and Jaccard Index (JI) showed high similarities across all summits since 2010 (table 7), meaning that species composition on the summits was very similar in the years 2010 and 2024. Both indexes showed the lowest similarity at Graanosi, with the highest similarity indicated by SSI at Frostdalsnosi and by JI at Rjupeskareggen (table 7).

***Table** 7. Sørensen similarity indexes and Jaccard indexes for all summits, comparing species composition in 2010 and 2024. The mean values of SSI and JI are shown in bold.*

Summits	**Sørensen Similarity Index (%)**	**Jaccard Index (%)**
Graanosi	71.0	60.3
Graveggi	72.6	74.5
Krekanosi	75.3	67.4
Berdalseken	78.6	71.4
Unnamed	83.3	81.8
Suletinden	84.2	81.0
Krekahøgdi	85.5	86.3
Slettningseggi	85.5	89.9
Storeknippa	87.0	88.2
Loppenosi	89.6	86.1
Rjupeskareggen	89.9	90.1
Frostdalsnosi	91.4	87.2
Mean	**82.9**	**80.4**

The NMDS showed a trend of the summits' species composition changing in the same direction and becoming more similar from 2010 to 2024 (fig. 7). Species composition changed the most on Graanosi and Krekanosi, illustrated by the longer arrows in the plot. Species composition on Berdalseken differed markedly from the other summits due to its low species richness. However, by 2024, the composition had shifted toward a higher number of species, becoming more like that of some of the other summits (fig. 7 & 8). Still, there was no significant change in species composition from 2010 to 2024 (table 8). Both the CCA and RDA showed that the summits explained most of the variation in species composition, while year only explained 3% (table 8).

None of the environmental factors significantly correlated with the NMDS ordination (table 9). However, it is interesting to observe some trends in the environmental factors. Firstly, the environmental variables showed trends opposite to those observed in species composition change (fig. 7 & 9), indicating they do not influence the changes in species composition. Secondly, bedrock had the highest R^2 value, indicating some correlation with the NMDS ordination, but this was not statistically significant. Distance to nearest road, size of the summits and the altitude seemed to be correlated with each other (fig. 9), which can indicate that higher summits were larger and were also further away from roads, and by its' position in the diagram, it correlated with the species composition on the summit Unnamed (fig. 9). There was a negative correlation between these factors and the distance to the nearest hiking trail, indicating that summits that were large, high and far away from roads, often were close to hiking trails, correlating with the species composition on Suletinden (fig. 9).

Overall, the mapping units had little correlation with the species composition in the ordination (table 10). However, the mapping unit *low calcareous coarse scree* (T13C1) had a significant correlation with the NMDS ordination, with a strength of 27%, meaning it explained 27% of the variation in the species composition in the ordination (table 10). *Low calcareous coarse scree* (T13C1) was located towards the right side of the x-axis, indicating a correlation on the species composition in the direction of change (fig. 7 & 10). Other mapping units that were also located in the direction of species composition change was *intermediate calcareous moderate snowbed* (T7C4), *low calcareous alpine heathland with moderate desiccation risk* (T3C2), *desiccation-exposed low to intermediate calcareous bare rock / rock walls/ outcrops* (T1C4) and *fairly low calcareous moderate snowbed* (T7C2) (fig. 7 & 10), but they were not significantly correlated with the NMDS ordination (table 10). *Boulderfield in vegetation free snowbed* (T27C5) and *low to intermediate calcareous ridge-like boulderfield* (T27C6) had a close to significant correlation with the NMDS ordination, with a strength of almost 30% and 15%, respectively (table 10). These mapping units were located close together in the ordination plot, towards the lower left part, indicating they had a correlation with the species composition of few or no species (fig. 8 & 10).

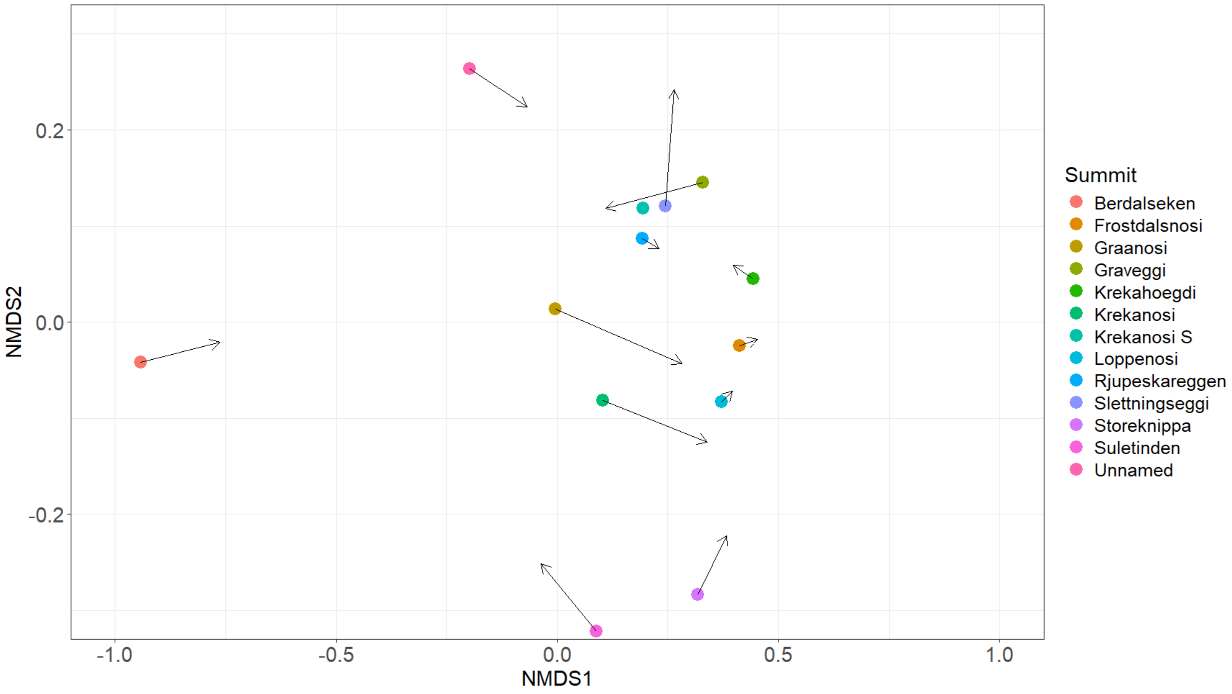

Fig. 7. *The NMDS of the vascular plant composition on the summits. The coloured dots represent vascular plant composition on the summits in 2010, while the arrows represent the direction of change on the same summits in 2024. The arrow heads represent the species composition in 2024. The turquoise dot without an arrow represents Krekanosi S, which was not visited in 2024*

Fig. 8. *The NMDS showing species composition and the species' functional groups represented as different colours. Species are presented as abbreviations, see table 4 in appendix C for the full species names.*

Table 8. *Results of the CCA analysis and the permutation test of the CCA, and RDA analysis and ANOVA permutation test of the RDA, where total = the total variance in the dataset, conditional = variance explained by summit, constrained = variance explained by year, unconstrained = variance not explained by year or summit, Inertia = variance, proportion = the amount of variance compared to the total variance, rank = number of variables. The results from the permutation test shows degrees of freedom (Df), variance (Inertia), F-value (F) and P-value and the results from the ANOVA test showing degrees of freedom (Df), variance, F-value (F) and P-value.*

CCA	Inertia	Proportion	Rank	
Total	1.12	1.00		
Conditional (summit)	0.77	0.69	12	
Constrained (year)	0.03	0.03	1	
Unconstrained	0.31	0.28	11	
Permutation test (Constrained)	Df	Inertia	F	P-value
Model	1	0.3	1.23	0.113
Residual	11	0.31		
RDA	Inertia	Proportion	Rank	
Total	17.27	1.00		
Conditional (summit)	13.19	0.76	12	
Constrained (year)	0.47	0.03	1	
Unconstrained	3.61	0.21	11	
ANOVA (Constrained)	Df	Variance	F	P-value
Year	1	0.47	1.43	0.120
	11	3.61		

Table 9. *Results of the permutation test from envfit, showing the correlation between the NMDS ordination and the environmental variables, explained by p-values and R^2-values (M.a.s.l. = meters above sea level, Size daa = size of the summits in decare from the highest point and down 32 meters in altitude).*

Environmental variable	R^2	P-value
M.a.s.l.	0.036	0.55
Size daa	0.002	0.96
Distance to nearest road (km)	0.094	0.21
Distance to nearest hiking trail (km)	0.014	0.81
Calcareousness	0.054	0.39
Sheep grazing	0.041	0.21
Reindeer grazing	0.018	0.48
Bedrock	0.185	0.12

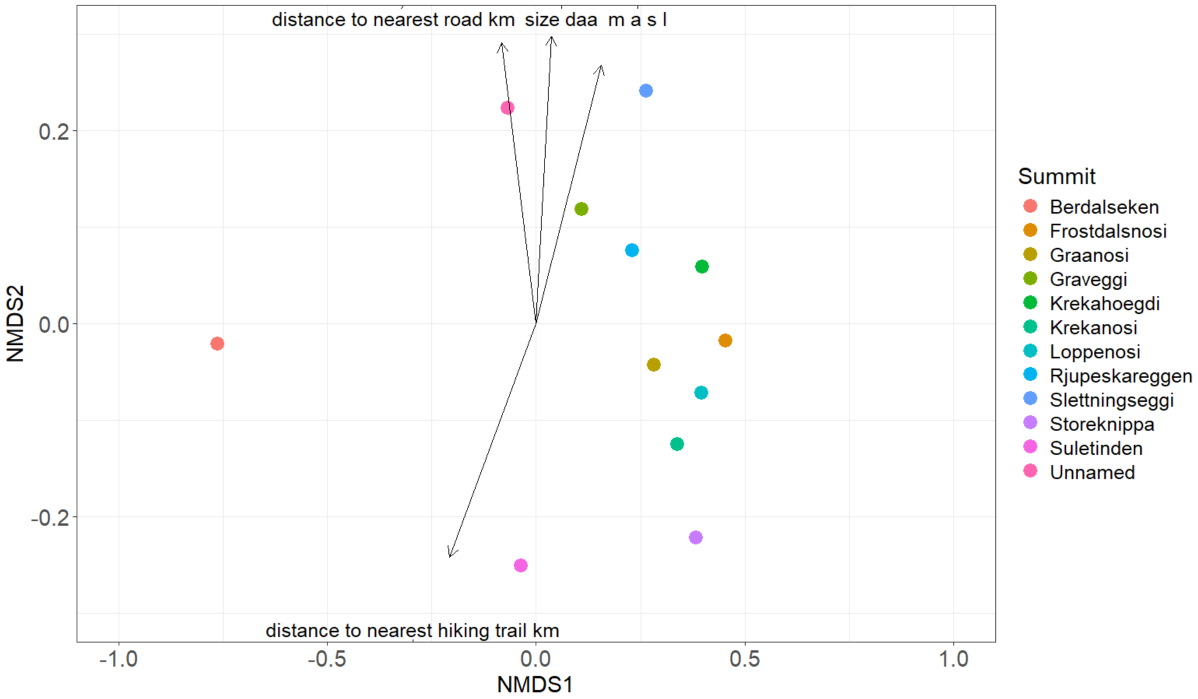

Fig. 9. *NMDS of the summits' species composition in 2024 and the correlation with the different environmental variables. The dots represent the different summits, while the arrows represent the direction and strength of correlation between environmental variables and the NMDS axes. Environmental variables include size in decare (size daa), distance to nearest road (km) and distance to nearest hiking trail (km).*

Table 10*. Results from the permutation test from envfit showing the correlation between the NMDS ordination and the mapping units, explained by P-values and* R^2 *values (* = significant, • = close to significant). The mapping units distribution is illustrated in fig. 10. See table 3 for description of the mapping units.*

Nature type	**R^2**	**P-value**
T1C1	0.043	0.556
T1C2	0.015	0.835
T1C4	0.027	0.680
T1C9	0.037	0.588
T3C2	0.075	0.330
T3C3	0.027	0.680
T7C1	0.025	0.714
T7C2	0.075	0.345
T7C4	0.045	0.555
T7C5	0.143	0.117
T13C1	0.272	* 0.028
T14C1	0.006	0.927
T22C3	0.044	0.542
T27C1	0.003	0.968
T27C2	0.016	0.820
T27C5	0.199	• 0.055
T27C6	0.147	• 0.098
V6C1	0.044	0.505

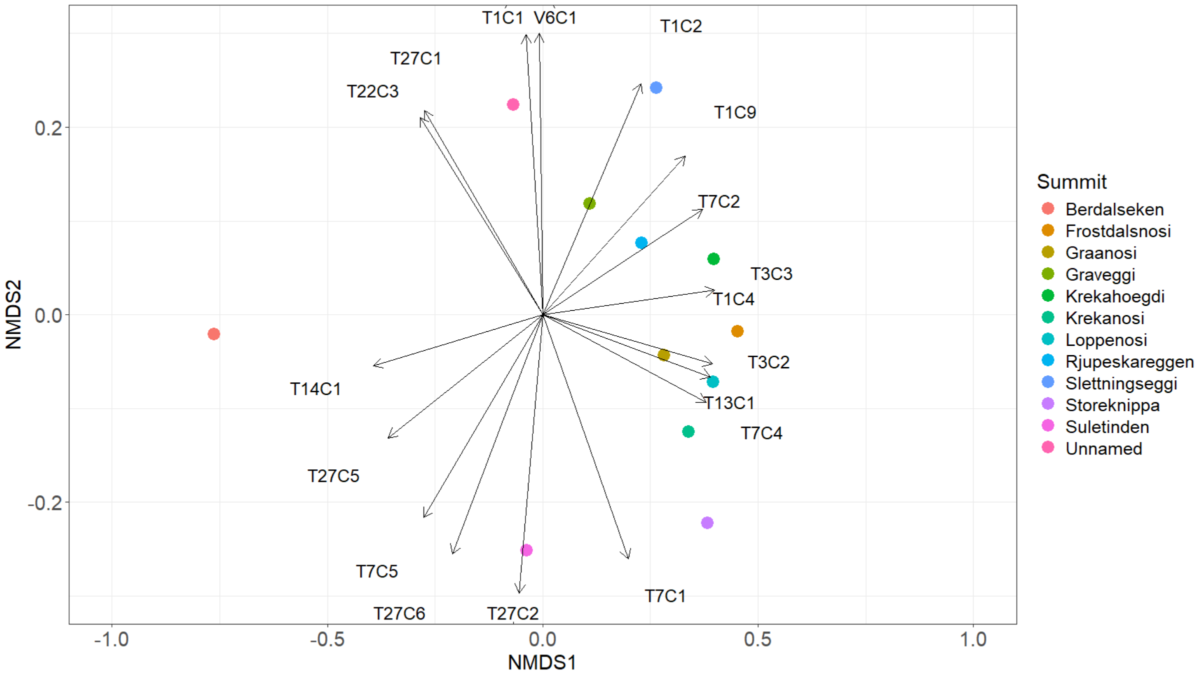

Fig 10. *NMDS with the species composition in 2024, illustrated by the coloured dots, and the correlation with different mapping units. The coloured dots represent the different summits, while the arrows represent the direction and strength of correlation between the mapping units and the NMDS axes. See table 3 for description of the mapping units.*

Remote sensing analysis

The unsupervised remote sensing analysis showed low accuracies for both mapping units and major habitat types (table 11). The No Information Rate (NIR) for both models exceeded their accuracies, indicating that the models failed to provide meaningful predictions and would not perform better than simply guessing the most common major habitat types or mapping units. This was also supported by the Kappa values for both models being close to zero, meaning the models would be equivalent to a random guess.

The models were struggling to identify the correct habitat classes (fig. 11 and 12). For instance, the major habitat type *snowbed* (T7) was often misclassified as *boulderfield* (T27) and *ridge* (T14) as *snowbed* (T7) (fig. 11). However, major habitat types classified as *boulderfield* (T27) and *ridge* (T14) were often correct. The mapping units *weakly intermediate to more calcareous windswept rock* (T1C9) was often misclassified as *high calcareous boulderfield* (T27C2), *low to intermediate calcareous ridge* (T14C1) as *low desiccation-exposed and very low to low calcareous bare rock* (T1C1) and *low to intermediate calcareous ridge* (T14C1) as *low desiccation-exposed and very low to low calcareous bare rock* (T1C1). *Low desiccation-exposed and very low to low calcareous bare rock* (T1C1) was, however, correctly classified quite often, as well as *low to intermediate calcareous ridge* (T14C1) (fig. 12). This indicates similarities in the pixels in the satellite images for many of the mapping units and major habitat types on the summits, making it difficult for the analysis to differentiate between them.

Table 11. *Overall statistics from the confusion matrix, showing model accuracy, 95% confidence interval (CI), No Information Rate (NIR), P-value and Kappa for both mapping units and major habitat types.*

	Accuracy	**95% CI**	**NIR**	**P-value**	**Kappa**
Mapping units	0.105	(0.059, 0,167)	0.147	0.943	0.015
Major habitat types	0.231	(0.165, 0.309)	0.315	0.989	0.437

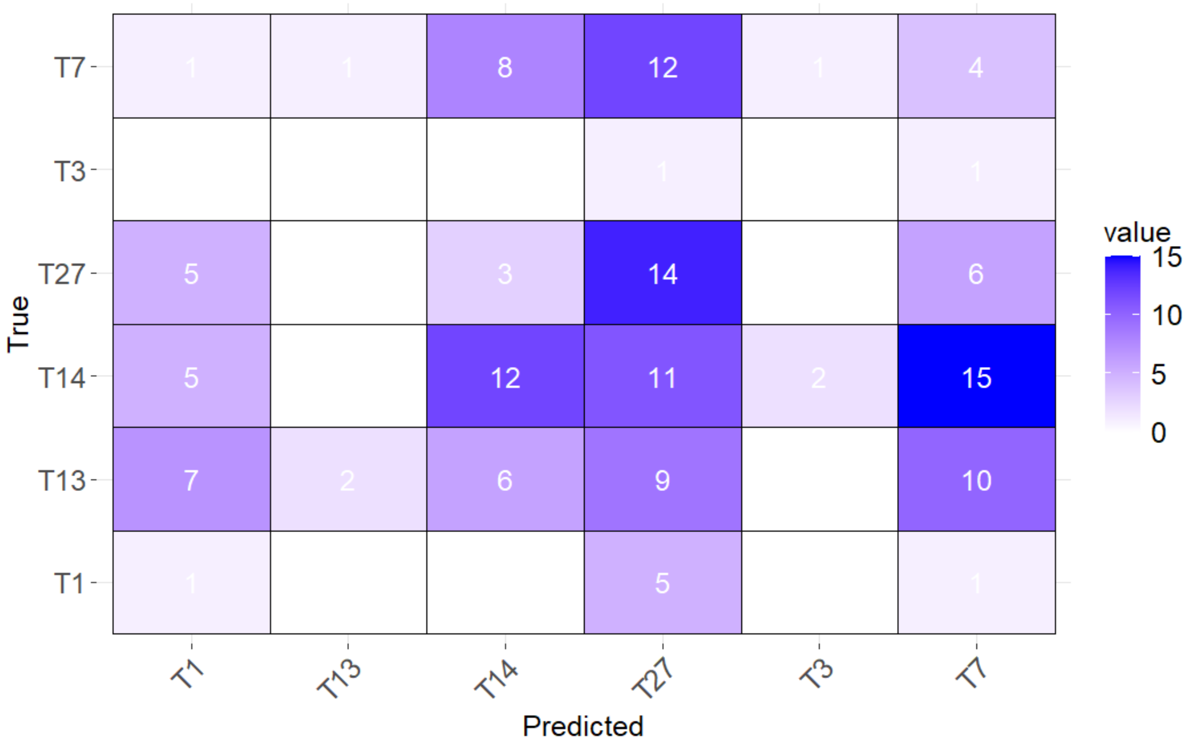

Fig. 11*. Heatmap of the confusion matrix with major habitat types. The y-axis represents the true data based on polygons made in the field, while the x-axis represents predicted data based on the majority of clusters within each polygon. The colours and numbers inside the cells indicate the frequency of the combination of true and predicted data, where darker colours indicate a higher frequency. The white cells are values = 0 See table 2 for description of the major habitat types.*

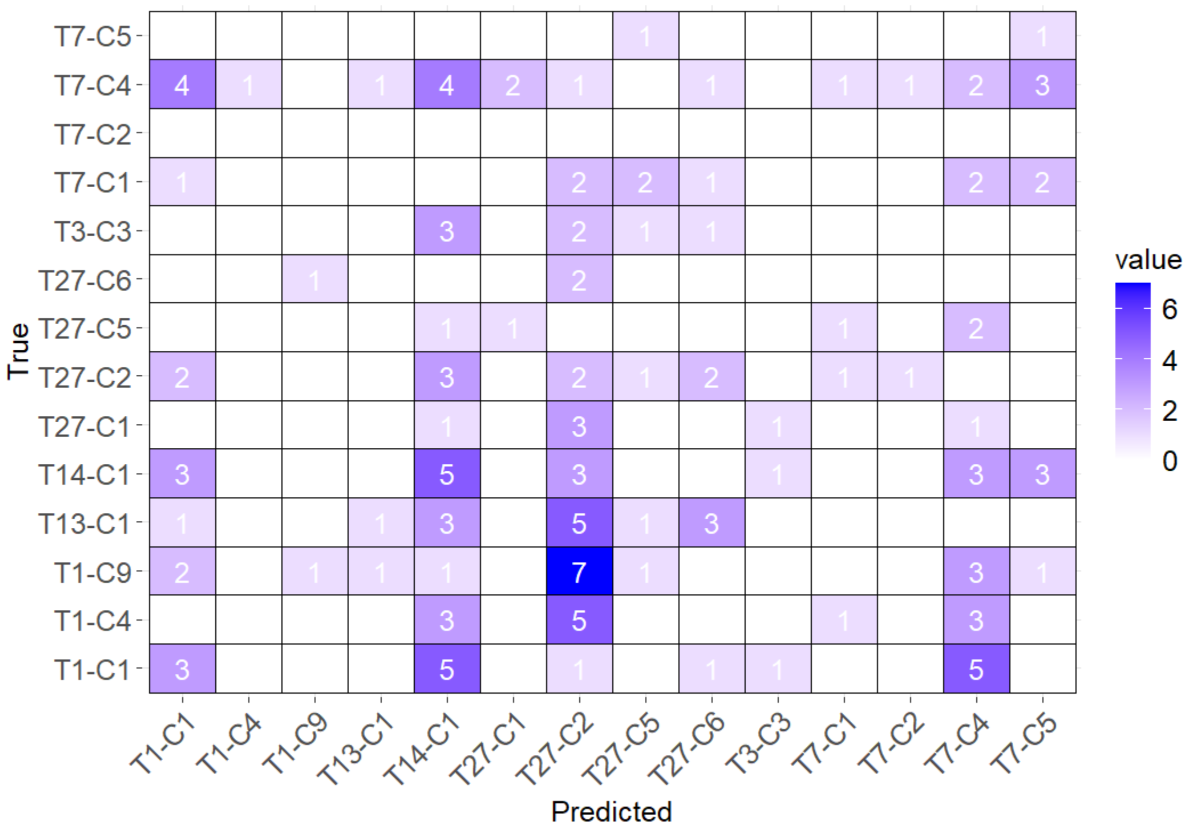

Fig. 12. *Heatmap of the confusion matrix with mapping units. The y-axis represents the true data based on polygons made in the field, while the x-axis represents predicted data based on the majority of clusters within each polygon. The colours and numbers inside the cells indicate the frequency of the combination of true and predicted data, where darker colours indicate a higher frequency. The white cells are values = 0. See table 3 for description of the mapping units.*

Discussion

This study aimed to investigate changes in vascular plant species richness, composition, altitudinal distribution and climatic indicator values on mountain summits in Norway over a 14-year period, seen in the light of climate change. The results showed small and non-significant changes in vascular plant species richness, composition and altitudinal distribution. However, there were significant increases in Dahl-R climatic indicator values on the summits. New species showed a tendency of more frequently colonizing boulderfields than ridges on the summits. Mapping units and environmental variables did not correlate well with the trends of change in the species composition. Lastly, the unsupervised remote sensing analysis failed to provide well adapted classifications of both mapping units and major habitat types on the summits.

Small responses in plant species richness, composition and altitudinal range

The study by Odland et al. (2010), conducted on the same summits as the present study, documented pronounced changes in species richness, composition and altitudinal shifts over a 40-year study period. Although my study spans over a shorter timeframe, previous research has shown that significant ecological changes in alpine plant communities can occur over both short and long periods (e.g., Steinbauer et al., 2018; Gottfried, 2012; Odland et al., 2010; Klanderud et al., 2003; Goff et al., 2025), showing increases in species richness, shifts in altitudinal distribution of species and changes in species composition over time, and similar changes were therefore expected here. Therefore, the results suggest that the response to climate change on these summits may have slowed. Several explanations for these delayed responses are possible, with lags in community responses being a likely factor (Alexander et al., 2018). The rate of species' range shifts are influenced by the extent to which species experience lags in dispersal, establishment, and local extinction (Alexander et al., 2018), which will be further discussed below.

Dispersal lags

A key trait influencing a species' ability to colonize new areas is seed dispersal capacity, which is closely linked to functional traits (Alexander et al., 2018). Dispersal traits adapted to wind and animal dispersal are particularly important for colonization on mountain summits to facilitate movement (Matteodo et al., 2013). For instance, in a long-term study, Parolo et al. (2008) investigated changes in altitudinal distribution of alpine plant species on mountain summits in the Alps, finding significant range shifts towards higher altitudes. To explain this upward migration, they examined dispersal traits and found that species with lighter seeds had the most pronounced altitudinal advance compared to the species with heavier seeds (Parolo et al., 2008). It is therefore plausible that small-seeded species in proximity to the mountain summits in this study rapidly colonized and shifted their altitudinal distribution on many summits in response to climate change during the study period of Odland et al. (2010), and that by 2024, few such species remained in the surrounding area that had not already reached the summits. Consequently, species with heavier seeds may now be expanding their ranges at a very low rate as the climate continues to change, creating a dispersal lag. Although this hypothesis was not tested in my study, it could be an interesting avenue for further research, especially considering that the rate of species richness increase appears to have slowed, as shown in this study.

Dispersal lags are also influenced by barriers to dispersal, such as landscape heterogeneity (Alexander et al., 2018). In mountainous regions, suitable habitat patches are often isolated due to the rugged topography, reducing the likelihood that even species with high dispersal potential will reach them (Alexander et al., 2018). This is emphasized by how long-distance winds dispersal of seeds is shown to have strong limitations, suggested by sharp genetic boundaries between regional populations of alpine plants (Schönswetter et al., 2005). Another example is the evidence of migration lags in post-glacial landscapes, where species with more isolated suitable habitat patches show more pronounced delays in colonization compared to others (Dullinger et al., 2012b). Furthermore, this may help explain the slow response to climate change observed in this study. The topographical heterogeneity of the Filefjell summits could restrict seed dispersal, contributing to slower-than-expected species turnover and altitudinal shifts in response to changing climatic conditions. Nevertheless, since a previous study have already reported significant changes in alpine plant communities in the same area (Odland et al., 2010), it is likely that topography alone cannot account for the lack of significant change found in this study. It is therefore important to consider other contributing factors alongside topographical constraints.

Establishment lags

Establishment lags may be another key factor behind the non-significant changes observed in the species communities on the summits. Many of the summit areas were extensively covered by boulderfields, which limit the availability of suitable habitats for establishment by plant species. Soil development in such environments is often poor, inhibiting species that require specific edaphic conditions (Chauvier et al., 2021). However, in this study, I found that the ratio of new species to total species was highest in boulderfields, meaning new species tended to establish in these areas. This could be due to the extent of boulderfields in the area, limiting the possibility of species to establish in other habitats, which may help explain the observed results with slower responses to climate change. Boulderfields are generally considered suboptimal for colonization, suggesting that there is a scarcity of other suitable habitats on the summits, especially the taller summits, as they consisted of fewer major habitat types and a high proportion of boulderfields. Additionally, ridges hosted the highest total number of species on the summits, suggesting that these habitats may be more saturated and thus less open to colonization. Moreover, ridges are typically characterized by harsh growing conditions, such as frequent drought, strong winds, and minimal snow insulation during winter (Bratli et al., 2022), which may further limit successful establishment. These findings suggest that both physical constraints and ecological saturation may contribute to establishment lags, collectively limiting the pace of community change in response to climate warming.

In addition to abiotic limitations, biotic interactions such as facilitation and competition may influence establishment dynamics (Alexander et al., 2018). For example, there is evidence of strong facilitative effects when comparing plant growth in the presence versus absence of facilitative species (Cavieres et al., 2014). This suggests that the presence of pioneer species may be necessary to pave the way for later arrivals, causing a delay in overall community response. Conversely, in already densely populated alpine communities, competition may become a more dominant force, especially under climate change (Olsen et al., 2016). Increased competition can reduce the establishment success of new species, which may be occurring on for instance ridges in this study as this habitat type hosted many species but had the fewest occurrences of new species. Taken together, these establishment constraints, both abiotic and biotic, may help explain the limited community-level changes observed over time.

Another plausible explanation for the limited changes observed in the species communities is the increasing frequency of extreme climatic events (Orlowsky et al., 2012). Events such as droughts and heatwaves may contribute to lags in establishment in alpine areas, as they can reduce plant species richness in the affected regions (He et al., 2022). For instance, record high temperatures during the summer months of 2014 and 2018 was registered in many regions in Norway (Skaland et al., 2019). This includes the region where Filefjell is located, with for instance a middle temperature in May to July of 2018 at 3.2 degrees Celsius above the normal in the area (Skaland et al., 2019). Additionally, the amount of precipitation was also very low for the same period, which together can cause unfavourable conditions for alpine plant species in the region. However, observations of extreme climatic events and their ecological effects in alpine areas remain scarce, especially over varying time scales (Wipf et al., 2013). Gaining a better understanding of how such events can lead to delayed ecological responses is essential (Wipf et al., 2013), and this factor should be integrated into future research on alpine plant species' responses to climate change.

Extinction lags

One could expect that endemic alpine plant species are disappearing from mountain summits due to climate change, seeing how climatic changes are contracting their habitats (Gottfried et al., 2012). However, my results showed no pronounced changes in species composition, which may be explained by extinction lags. One key explanation is the high environmental heterogeneity found in alpine ecosystems, which can buffer species against local extinction (Körner et al., 2021). Due to the fine-scale variation in topography, microclimate, and snowcover, species may be able to persist in local refugia even as regional climate conditions shift. This spatial complexity allows for species to migrate short distances and helps them survive in situ for longer than expected. In this context, extinction lags could arise because plants continue to find locally suitable conditions within the summit landscape, delaying the disappearance of species from the regional flora, resulting in minimal changes in species communities over time, as shown in this study.

Nevertheless, the findings on habitat preferences for colonization by new species, overall species richness and altitudinal shifts should be interpreted with caution. The analysis was based solely on the highest recorded elevation of each species per summit, offering limited insight into where species are increasing or decreasing in abundance. While the presence of new species can indicate colonization at higher elevations, it does not capture changes in species dominance or relative abundance in response to climate change. Patterns of relative abundance may reflect subtle ecological shifts that presence/absence data alone cannot detect. Previous research has shown that climate change can significantly alter the relative abundance of alpine plant species (Bhatta et al., 2018; Lamprecht et al., 2018; Rumpf et al., 2018; Steinbauer et al., 2020), highlighting abundance as a sensitive indicator of community-level change. Furthermore, the dataset used to assess major habitat types was relatively limited due to a lack of historical data on summit habitat conditions. Additionally, the vegetation data collected for this study only reflects the vegetation present at the time of fieldwork. Species that grow and bloom earlier or later in the growing season may therefore have gone undetected. By conducting fieldwork throughout the growing season, the reliability of the data may have been improved. Taken together, these limitations suggest that future research should incorporate abundance measures, habitat data and fieldwork throughout the growing season to better detect and understand ecological responses to climate change.

Lastly, no significant changes in species' altitudinal distributions were found, contrary to several studies (Lenoir et al., 2008; Odland et al., 2010; Pauli et al., 1996, 2012; Rumpf et al., 2018). This may reflect delayed responses in plant communities as discussed above, as well as methodological differences. For example, Rumpf et al. (2018) found upslope shifts in species limits, optima, and abundance by resampling historical plots, especially among low-elevation species. My study only considered the highest occurrences on the summits, not full altitudinal ranges, which may also explain the differences.

Moreover, range shifts may occur in other directions. For instance, He et al. (2019) documented projected northward and westward plant movements in the Himalayas. Considering such cardinal directional changes could offer a more complete picture of alpine vegetation responses to climate change.

Changes in Dahl-R indicator values

Although no significant changes were found in species richness, composition, or altitudinal distribution, this study revealed a significant increase in Dahl-R climatic indicator values. This suggests a shift in microclimatic conditions on the summits towards warmer habitats. Such a shift aligns with the small but consistent annual temperature increases observed during the study period (0.032°C per year; see 'Methods') and is further supported by findings from previous research (Gottfried et al., 2012; Odland et al., 2010; Rumpf et al., 2018; Steinbauer et al., 2020). For example, Rumpf et al. (2018) documented an upward expansion of warm-adapted species and a contraction of cold-adapted species in alpine areas in response to climate change. Similarly, Odland et al. (2010) reported significant increases in Dahl-R values over a 40-year period on the same summits as visited in this study, indicating an increase in warm-adapted species on the summits. Gottfried et al. (2012) also found significant increases in thermophilization indicator values (*D*-values) in European mountain regions. These increases were strongly correlated with climatic trends during the study period. Despite the study period being less than a decade, it showed substantial community changes and rapid ecosystem responses to climate warming, as evidenced by the rise in *D*-values (Gottfried et al., 2012). This indicates a progressive decrease of cold-adapted, high-elevation species, further suggesting contraction of suitable habitats that often support many range-restricted endemic species. Overall, the observed increase in climatic indicator values found in my study, despite stable species richness and composition, suggests that such indicators may serve as warning signals of ecosystem shifts in response to climate change.

Interestingly, summits with increased species richness in 2024 also tended to have higher Dahl-R values, suggesting that colonization by thermophilic species may be driving both increased richness and elevated climatic indicator values. Conversely, summits with reduced species richness exhibited lower Dahl-R values. This may be due to vegetation gaps resulting from the disappearance of warm-adapted species, possibly because the climate has not warmed sufficiently for them to thrive or due to extreme events, or because cold-adapted species have disappeared while warm-adapted species have yet to establish themselves (Steinbauer et al., 2020). When investigating the differences in Dahl-R values within new and lost species on the summits, there is a pattern of new species having somewhat higher Dahl-R values than the lost species in 2024. This pattern supports the interpretation that ongoing species turnover is contributing to the thermophilization of alpine plant communities.

However, this raises an important question: how can there be a significant increase in climatic indicator values on the summits without corresponding changes in species richness or species composition? One possible explanation is that species with higher Dahl-R values, typically lowland or thermophilic species, are colonizing more summits. While their presence may not yet be sufficient to change the overall composition or richness significantly, they still affect the average community-level Dahl-R values. Another consideration is that Dahl-R values were only available for around 70% of the species in this study. The absence of indicator values for the remaining 30% may mask additional ecological trends, potentially under - or overestimating the full extent of community change.

Environmental variables on the summits

Environmental variables did not contribute to explaining trends in species composition change on the summits in this study, which was not as expected. The chosen environmental variables in this study was bedrock, meters above sea level, size of the summits, calcareousness, hiking trails, mountain roads and grazing, where many of these variables has been shown to influence changes in species composition on mountain summits (Austrheim et al., 2001; Müllerová et al., 2011; Nicklas et al., 2021). The discrepancy between my findings and the findings of other studies could be due to the parameters used in this study. For instance, grazing pressure is important to take into account when studying changes in species composition, where reduced grazing pressure can explain downward shifts in species composition on mountain summits (Bhatta et al., 2018; Lenoir et al., 2010), and I did not consider grazing pressure in this study. The data on grazing used in this study accounts for presence/absence of grazing. The absence of a significant correlation with species composition ordination may reflect a relatively constant grazing pressure over the past 14 years, which would be unlikely to drive noticeable changes in community structure. However, species composition changes were not significant, making it difficult to identify environmental variables explaining the minor trends.

I found that bedrocks had some correlation with the species composition, but this was not statistically significant. This is in contrast to other findings that showed different responses to climate change with different types of bedrocks, with for instance increased richness in siliceous bedrocks and decreased richness in calcareous bedrocks (Nicklas et al., 2021). One explanation could be the absence of variation in bedrocks on the summits, meaning that most of the summits shared the same types of bedrocks. Another explanation could be that bedrock might have strong effects on some summits, but not all, making it difficult to find patterns in the effects of bedrock types.

In this study, only a handful of environmental variables was chosen for the analysis, and there are other variables that could be interesting to include, such as snowbed depth and snowcover duration on the summits over time (Huss et al., 2017), and other biotic (e.g., competition and facilitation) and abiotic (e.g., temperature, precipitation, soil moisture) factors.

Major habitat types and species composition

There were only weak correlations between major habitat types and species composition across the studied summits, but there are some patterns interesting to highlight. *Low calcareous coarse scree* (T13C1) showed a significant correlation with the species composition, despite its relatively low cover on the summits. This raises questions about its ecological role. It is possible that although this mapping unit is limited in extent, summits with even small amounts of T13C1 support species that are more strongly responding to climate-related factors, leading to a detectable influence in the species composition. However, it is important to consider that the significant correlation between T13C1 and the ordination may be driven by a single or a few summits where this habitat type is particularly dominant and where species composition differs from the rest. In a dataset with only 12 summits, such patterns can easily be influenced by outliers or unique summit characteristics, and in this study, T13C1 was only recorded on the summit Graveggi in very small amounts.

Snowbeds showed a weak and non-significant correlation with the trends of change in species composition, which was contrary to expectations. Given that previous studies have documented shifts in snowbed plant communities and predict continued changes due to climate-driven alterations in temperature and precipitation (Björk et al., 2007; Matteodo et al., 2016), a stronger relationship was anticipated. These climatic changes influence snowmelt timing and shorten the growing season by reducing the snow/rain ratio (Ernakovich et al., 2014; Rumpf et al., 2022). The weak correlation observed in this study may indicate that snowbed communities are either more resistant to recent climatic shifts, or that changes are occurring with a temporal lag. Alternatively, the result may reflect site-specific conditions that buffer snowbed habitats from broader trends. This highlights the complexity and variability of ecological responses in alpine systems, and underscores the importance of continued, long-term monitoring to capture these potentially delayed or localized patterns of change.

These results suggest that major habitat types may not be the main drivers of compositional changes during the study period. Moreover, the ordination is based on data of the highest recorded occurrence per species per summit, not full composition or abundance data, and the habitat data reflect total habitat cover per summit, not the specific habitats where species were observed. Thus, the analysis captures summit-level correlations rather than direct species–habitat associations. As the observed changes in species composition were not significant, it is also challenging to identify explanatory variables for such weak trends.

Unsupervised classification failed to distinguish mapping units and major habitat types

I found that remote sensing using unsupervised classification failed to accurately map mapping units or major habitat types according to the NiN classification system on the visited summits. To the best of my knowledge, there are not many studies that have used remote sensing in mapping of habitat types in the alpine zone in Scandinavia. However, many studies in other areas have investigated treeline shifts and dynamics in the treeline ecotones, as shown in this review by Chhetri & Thai (2019), where unsupervised classification techniques has been successfully used to investigate and predict treeline shifts due to climate change (Guo et al., 2014). It is plausible that the methods used in studying treeline ecotones can be further developed to fit the heterogeneity of habitats in the alpine zone.

Unsupervised classification is a commonly used approach in vegetation cover mapping. However, achieving high classification accuracy is critical for its effectiveness. In comparison, supervised classification can provide higher accuracies by relying on labelled training datasets with known classes, using ground-truth data and predictor variables to build a model that often results in high classification accuracies (Xie et al., 2008). For instance, a study by Rwanga et al. (2017) assessed the accuracy of land use and land cover classifications using supervised classification. Their study, which included land cover categories such as agricultural land, water bodies, shrubs, forest, and bare ground, achieved an overall accuracy of 81.7% and a Kappa coefficient of 0.722, indicating that the classification was reliable. Their analysis also revealed significant confusions between bare land and other land cover types (Rwanga et al., 2017). However, they demonstrated that classification accuracy could be improved by including additional, category-specific parameters, meaning they investigated which specific parameters caused confusions in the classification to further advance the model. These findings suggest that alternative remote sensing methods, such as supervised classification and parameter refinement, can yield more accurate results than the unsupervised approach used in this study.

Although the unsupervised classification performed poorly in identifying detailed mapping units, it showed somewhat better performance when distinguishing the less detailed major habitat types, such as boulderfields and ridges. This may be attributed to the extensive areas of ridges and boulderfields on the summits visited in this study, major habitat types that are easily distinguished due to their differences in colour and spectral differences. For instance, ridges are often dominated by bright coloured lichens which are easily observed in satellite images but are often absent from boulderfield areas. That said, different major habitat types may hold similar spectra, making it very difficult for both supervised and unsupervised classifications to obtain accurate results (Xie et al., 2008). These results highlight both the potential and limitations of remote sensing for habitat classification in alpine environments, emphasizing the need for refined methods in remote sensing techniques.

Using other types of input data and selecting classification techniques suited to each data type may enhance habitat mapping in alpine environments (Xie et al., 2008). For instance, the Normalized Difference Vegetation Index (NDVI) is widely used as a proxy for vegetation greenness and photosynthetic activity, enabling the detection of temporal vegetation dynamics and providing more detailed information on major habitat types and local vegetation (Geerken et al., 2005; Wang et al., 2004). Additionally, time series of vegetation indices throughout the growing season can be used as input to enhance classification accuracy by aligning spectral data with phenological stages (Bagan et al., 2005). Integrating such methods in remote sensing applications for alpine zones could enhance the ability, not only to monitoring vegetation changes, but also to predict future shifts in plant community composition, habitat distribution, and broader ecosystem dynamics.

Conclusions

This study found that changes in alpine plant communities on the summits in Filefjell, Norway, are occurring at a slower pace than reported in previous studies. One likely explanation is a lag in species' responses to climate change. Despite this, there is clear evidence of ongoing thermophilization, demonstrated by increasing climatic indicator values over the study period, pointing to shifts in microclimatic conditions that favour thermophilic species. Additionally, such indicator changes may serve as warning signals of ecosystem shifts in response to climate change.

Some major habitat types appear more susceptible to colonization than others. In Filefjell, boulderfields showed a tendency of being colonized more frequently by new species compared to other major habitat types. Even though the unsupervised classification method applied here did not succeed, the potential of remote sensing in ecological monitoring remains significant. Ongoing climate change makes it vital to monitor alpine ecosystems to understand their responses and anticipate future changes. Given the likelihood of delayed ecological responses, long-term research remains essential.

To truly understand how alpine ecosystems respond to climate change, we must look closely, think long-term, and act before the silence of change becomes irreversible.

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Appendix A - Maps

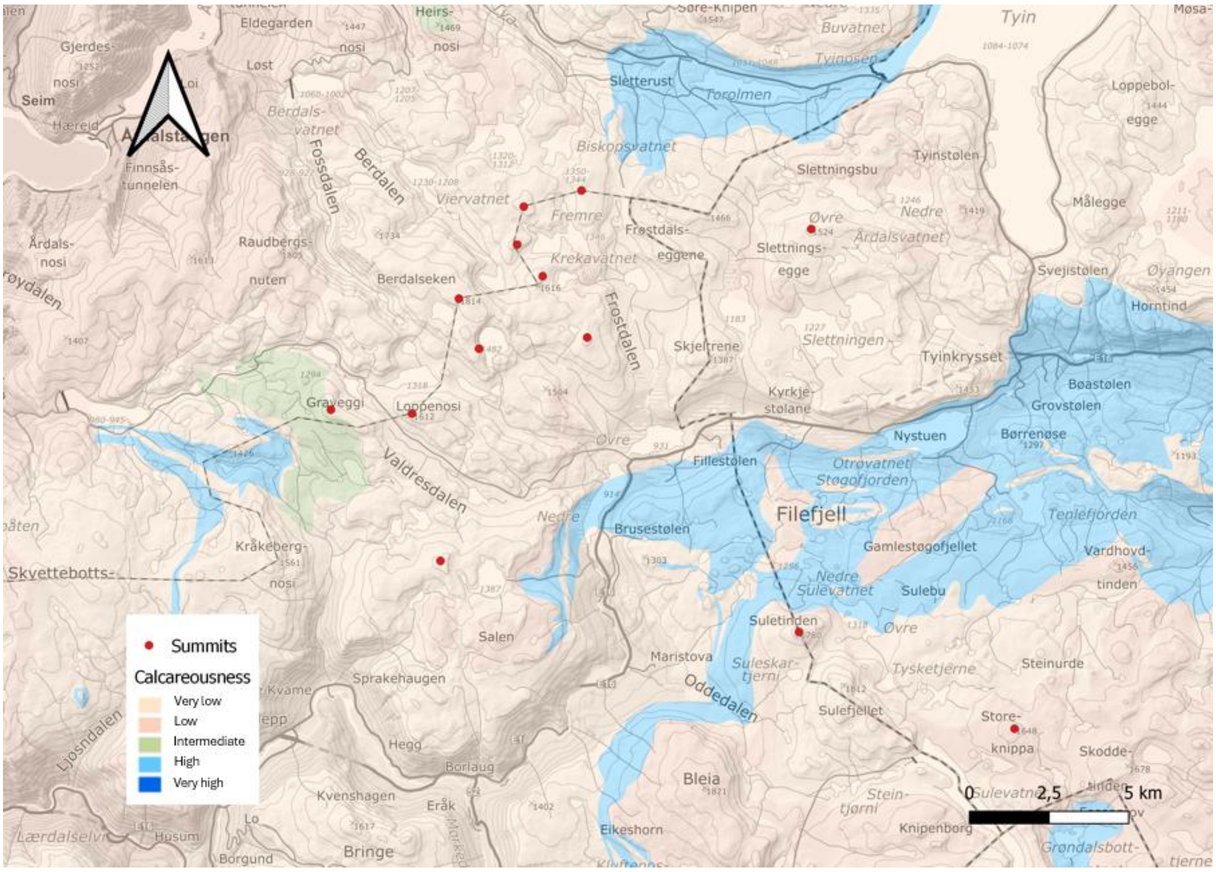

Fig. 1. *Map of Filefjell showing calcareousness in the bedrocks across the area. Made with QGIS version 3.26.3 (QGIS.org, 2025). Background map: Topographical map of Norway (Kartverket, n.d), map of calcareousness collected from Kartverket (2024).*

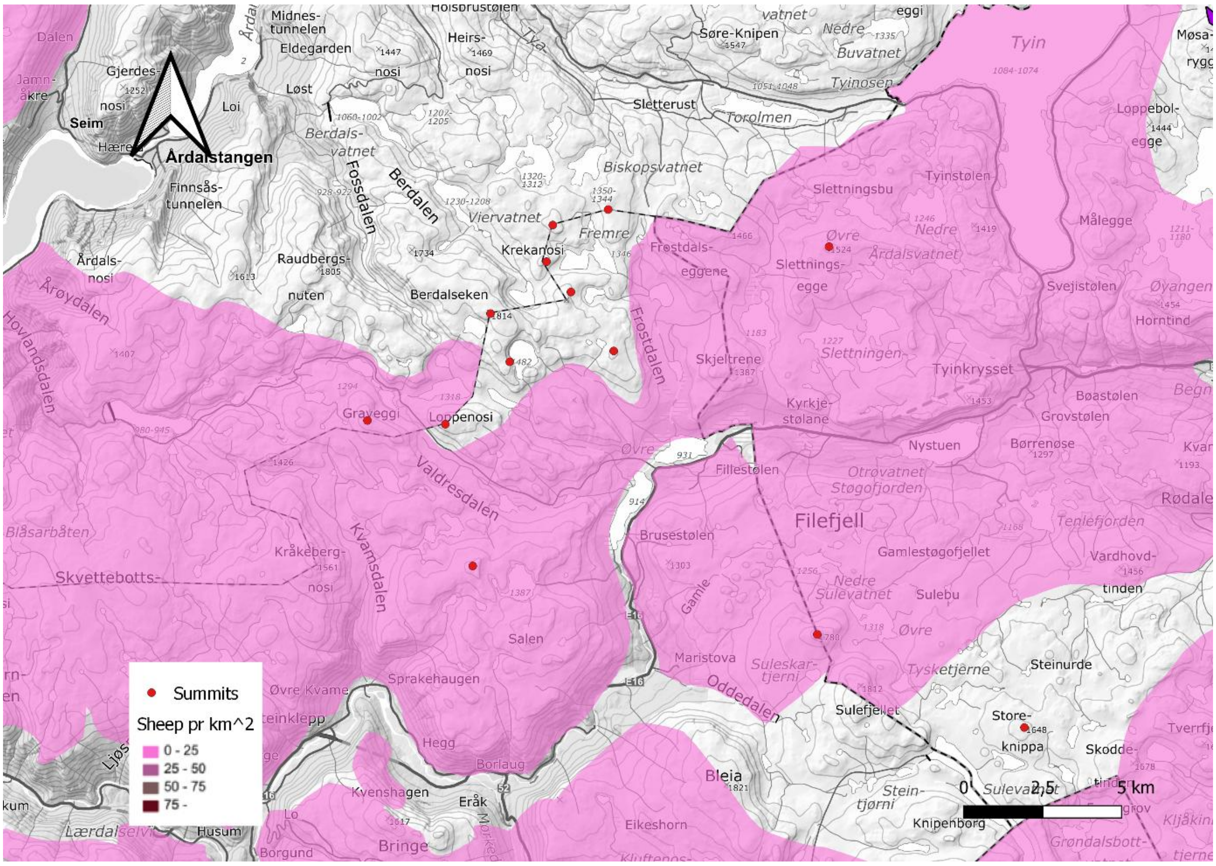

Fig. 2. *Map of Filefjell showing areas and density of sheep grazing, grey areas indicate areas with no grazing by sheep. Made with QGIS version 3.26.3 (QGIS.org, 2025). Background map: Topographical map of Norway (Kartverket, n.d), map of sheep grazing collected from Kartverket (2018).*

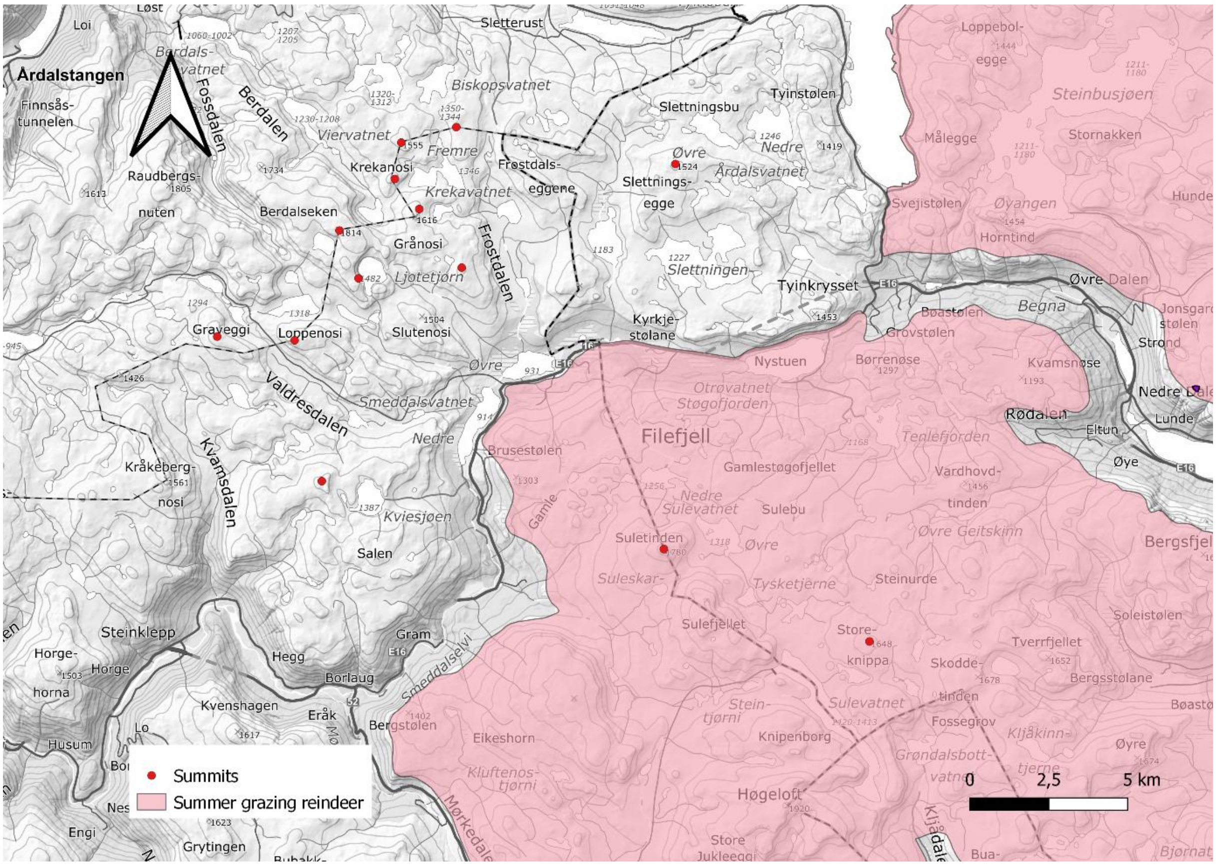

Fig. 3. *Map of Filefjell showing areas with summer grazing by reindeers, grey areas indicate areas with no grazing by reindeers. Made with QGIS version 3.26.3 (QGIS.org, 2025). Background map: Topographical map of Norway (Kartverket, n.d), map of reindeer grazing collected from Kartverket (2015).*

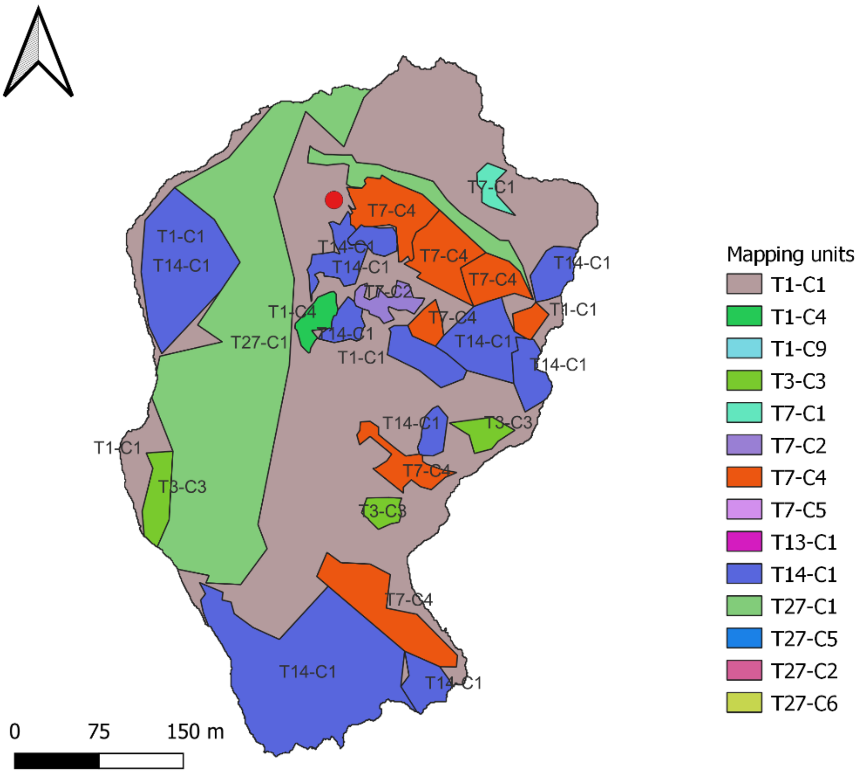

Fig 4. *Polygons of the different mapping units on the summit Frostdalsnosi. For descriptions of the different units, see table 3.*

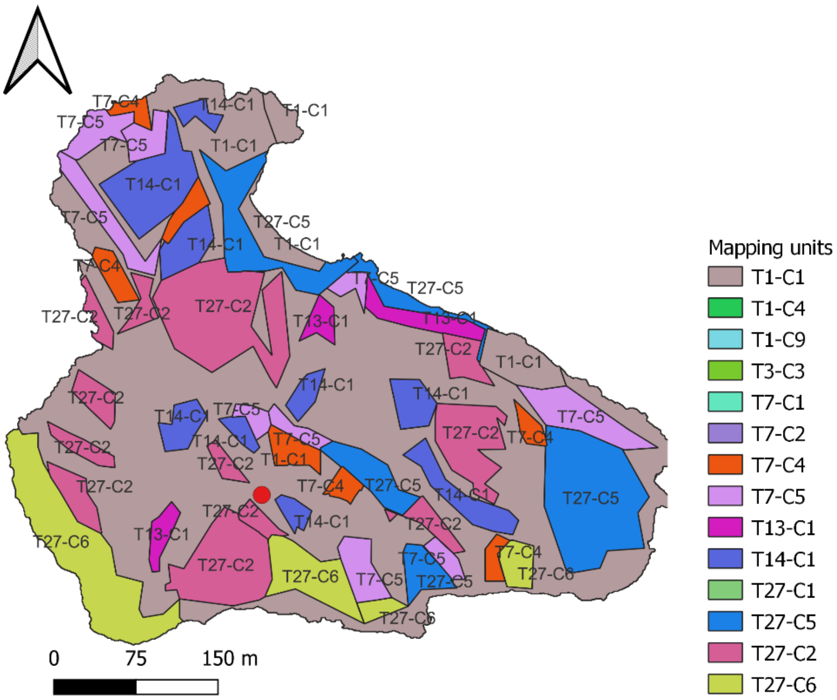

Fig 5. *Polygons of the different mapping units on the summit Graveggi. For descriptions of the different units, see table 3.*

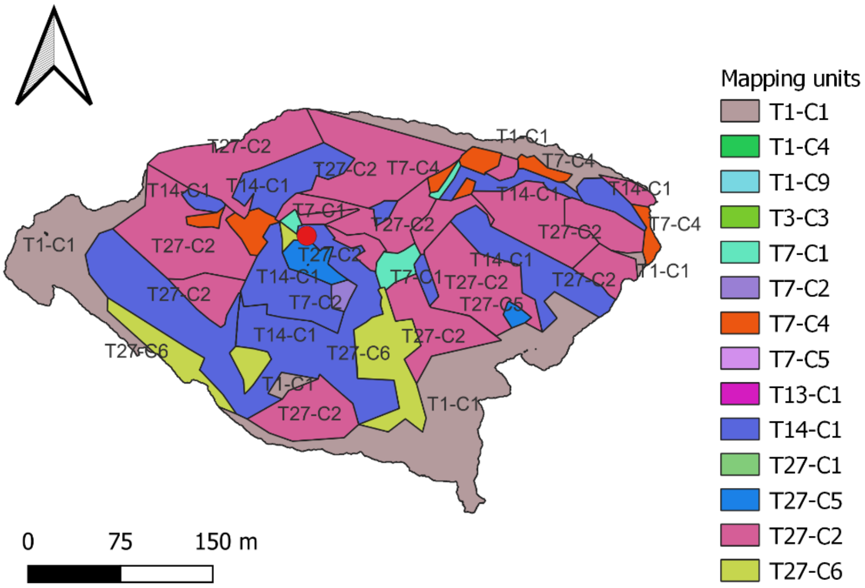

Fig 6. *Polygons of the different mapping units on the summit Slettningseggi. For descriptions of the different units, see table 3.*

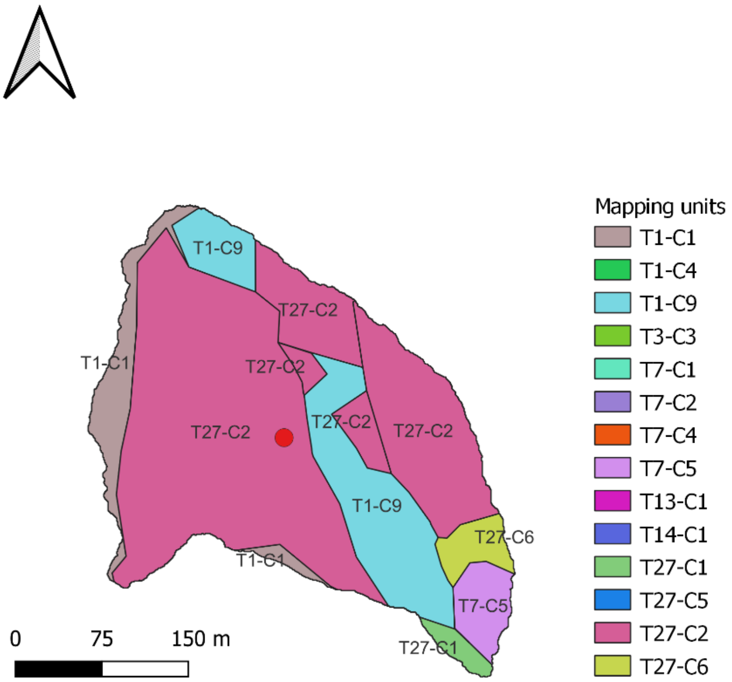

Fig 7. *Polygons of the different mapping units on the summit Suletinden. For descriptions of the different units, see table 3.*

Appendix B – Species altitudinal distribution on the summits

***Table 1**. The species and their corresponding distance to the summits' highest points in 2010 and 2024. Blank cells indicate that the species was not found on that summit in the given year. To see the species' full names, see table 4 in appendix C.*

	Berdalseken		Frostdalsnosi		Graanosi		Graveggi		Krekahoegdi		Krekanosi		Krekanosi S	Loppenosi		Rjupeskareggen		Slettningseggi		Storeknippa		Suletinden		Unnamed	
species	2010	2024	2010	2024	2010	2024	2010	2024	2010	2024	2010	2024	2010	2010	2024	2010	2024	2010	2024	2010	2024	2010	2024	2010	2024
ach_mil														13	22										
agr_cap																					10				
agr_mer			24	26								30			12					17	8				
alc_alp			23	21					10	13		15		24	20		19								
alc_sp												24		24											
ant_alp			8	4	13	1	30		8	17	1	3	30	2	6	28	19	23	3	17	4	9	14		
ant_dio		23				1				17	28	5	26			15	23	3	14	17	4	32	17		
ant_odo			13	6		21	10	18	5	3		7	2	8	12	9	9	3	2	17	14			18	31
ara_alp															29					19	32				
arc_alp			8	3	26				23	1							27								
arc_uva									23																
ath_dis			11	21		30	10	7	10	24		9	22		20	20	20	12	9		26				16
ave_fle		31	3	4	20	24	3	13	6	1	4	7	5	28	25	7	11	3	1	24	22	10	25	26	31
bar_alp			22	9	20	22			15	29		15		11	9					16	10				
bec_gla	5	5	3	4	1	1	0	21	1	0	1	1	2	1	0	13	25	2	2	0	0	18	28		
bet_pub			5	19		26			32				6	2	5	13	22								
bis_viv			8	7	13		32		10	19	3	5	15	7	10	30	30	24	24	3	3	32			
cal_phr				15																					
cam_rot			14	23		30	32		12	19	3	27		6	28			6		7	9				
car_atr			14	5		22			30	7	28	16		7	25					14	9				
car_bel		28	1	2		1	1	4	1	0	1	0	3	0	0	6	3	2	2	2	1	2	2	10	12
car_big			3	3	0	0	10	3	5	3	1	1	2	2	2	4	7	2	2	1	4	3	3	22	11

car_bru			10	10			9	10					7		6	30	27	3	5			22			28
car_lac			7	5	18	19	14	24	30	32	10	7	17	24	10	8	11	7	19	7	9	29	2	21	31
car_rup																				0	0				
car_sax															11										
car_vag																				13	3				
cer_alp			24	18			26	21	9			15		13	22	15	23	3	9	0	1	9	14		26
cer_alp_lan													29							25	0				
cer_cer			28	17			14	22	26	24	12		14	24	22	18	15	21	24	27	15	31	32		
cha_ang				26			32		11	12			26						15						
coe_vir												20													
cry_cri			30	14		12	3	24	10	23	15	20	12		25	13	2	16	21				28	21	31
cys_fra						13										24	25		19						
des_alp	10	11	11	13	3	3		20	7	6	7	7	5	21	8	13	9	16	17	7	9	2	1	20	23
dip_alp			16	6	18	7	4		5	10	1	5	6	7	12	10	17	3	3	15	8				
dra_fla																				1	22	32			
emp_nig			2	3	5	7	0	3	1	0	1	0	1	3	1	3	1	0	0	0	1	3	22	3	2
epi_ana			20	30					30					22	19	32	18				21				
equ_arv																				24					
eri_ang	10	21	29	13	2	1		1	30	30	1		5	25	2	3	4			4	4	9	2	5	7
eri_sch			29	18		12	32	2		32					10	7	8			10	16			26	9
eri_uni			22	8		9	9		25		3	3		3	1					8	8	9	14		
eri_vag	23	23		1	20			9					2	15	2	3	4	22	5	4	4		5	6	9
eup_wet									23	23					20					14	8				
fes_ovi												19						6	20						
fes_viv	18	12	2	1	1	0	0	7	1	0	0	0	1	0	0	2	1	0	0	0	0	0	0	9	5
gen_niv																					11				
ger_syl									32																
gym_dry										30									2					20	
har_hyp			19	13	18	12			10		4	5		8	12		29			10	9			27	
hie_alp			2	2	18	1	9	6	3	0	1	1	2	4	3	20	8	2	2	5	3			3	21

hie_sp																	17	24	2						
hup_sel	12	23	1	3	0	0	0	1	1	0	0	3	1	2	1	6	7	1	2	3	3	1	3	5	6
jun_big			27	13										28	24					11			25		
jun_com			11	10		27	31		8	8		20		21	26		19	2	17		10				
jun_tri			2	2	10	5	3	32	1	0	1	2	3	8	2	6	24	1	0	17	19				
leo_aut			17	19			28	22	1					23	24										
luz_arc	3	5	1	2	0	1	0	1	1	0	1	0	1	0	0	3	7	0	0	2	4	2	0	8	6
luz_fri																		24							
luz_spi		23	1	1	3	1	3	7	1	1	1	2	3	4	1	7	7	0	0	0	1	8	4	15	17
lyc_ann																			14		11				
lyc_cla						0											27								
min_bif			20	17							15			24	24	27		2	1	11		29			
oma_nor				23		21	21	20	7	31		15	12								16			27	22
oma_sup			5	4	30	30	1	6	7	8	5	4	5	7	3	6	14	2	2	8	6	10	14	18	16
oxy_dig			5	7		1	26	18	14	17	17	19	5	13	10	15	9	21	24	7	4	18	14		23
pet_fri				30		25																			
phe_con				18												32									
phi_alg						29		28												28	17				
phl_alp				30			28		15	33		24						29		28					
phy_cae			12	6	16	6	4	27	8	9	3	9	7	8	10	9	26	21	10	23	10			31	29
poa_alp_alp			28	18				28		30		20		21	5					25	11	32	8		
poa_alp_viv	19	32										28				12	18			28		32			
poa_arc				30	10	29				26						22	20	22		16	10	32	29		
poa_fle	5	3	0	0	0	1	0	1	1	0	0	0	1	0	0	2	1	0	0	0	0	1	1	3	4
poa_jem											4	23									10				
pot_cra			12	6		1			20		4	16		19	28					0	2	31			
pyr_min			30	29			32		21	27			26					29							
ran_acr									14	28				22						30					
ran_pyg			7	5		14		22	26				12	21	18	17	15	21	22	7	17	31	31		
rho_ros			6	5	18	4	21	20	10	26	4	1	20	0	0					1	2	19	14		

rub_cha			30	18									2			6	8	26	27						
rum_ace			17	9		30	13		5	13		23	3	15	23	6	8	5	7						
sag_sag															18					13	26				
sal_gla			16	21			30		11	18				24	27				26						
sal_her	19	4	2	3	0	1	1	2	1	0	1	0	1	1	0	3	3	0	0	0	0	2	5	6	6
sal_lan				23					20	28				29	32						24				
sal_lap			29	2	26	23	32		14	17		15	20	21	25	9									
sal_phy							3																		
sal_sp																									31
sau_alp			8	5	2	22	30		19	17	1	1	24	3	8	7	21	29	24	0	1	9	14		
sax_cer						13				24		9								11	4	14			
sax_ces			22	25						13		26		7	22					0	1	14			
sax_niv				25		13		22							17					1	11	14	14		
sax_opp			27	24					8	15		23		6	7					0	1	14	14		
sax_riv			7	5				19	30				10			19	15	21	22	10	1	14	16		
sax_ste		23	21	13		29	13	4	8	29		1	9	30	16	15	8	32	23		31	10		16	8
sax_ten																				17	18				
sel_sel			24	5																					
sib_pro	23	21	2	3	5	4	3	12	8	6	2	4	3	2	3	7	4	1	2	7	5	9	14	21	18
sil_aca			10		2	1	14				1	2		1	1					0	1				
sil_dio									15										30						
sil_wah			22																						
sol_vir			9	5	26	19	23		7	20			13	21	9	17	26		1						
tar_sp			12	11	26	12	21	22	5	15	10	5	14	10	12	18	9	26		10	7	22	15		31
tha_alp																				18					
tri_eur			30	7			32		17	11	30		25					28	22						
tri_spi	19		5	11	10	7	4	20	20	29	2	2	5	3	3	6	8	3	1	4	4	9	14	30	31
vac_myr			17	5	16	16	17	6	5	10	25	15	14	22	6	6	8	1	1						20
vac_uli			2	3		7	29	1	6	10		4		10	6		4	29	1		12				
vac_vit			1	2	2	1	1	32	1	0	1	0	1	3	1	3	4	0	0	0	1			13	20

vah_atr		19																				
ver_alp	16	11	20	21		20	13	28	5	6	14	8	10	18	19	31		16	7			
vio_pal	30	29										23					30					
vis_alp	2	4			14	32	8	26			7		11	13		21	26					29

Appendix C – Supplementary statistics and species abbreviations

Table 2. *Summary statistics from the Procrustes analysis comparing ordination configurations with 10 and 12 summits. The Procrustes sum of squares and root mean squared error indicate a good fit.*

Procrustes sum of squares:
0.015
Procrustes root mean squared error:
0.023

Table 3. *Results of the posthoc tukeys test from the linear mixed model (table 6), with the ratio of the number of new species and the total number of species as response variables and major habitat types as explanatory variables, showing estimate, standard error (Std. Error), degrees of freedom (Df), T-ratio and p-value (● = close to significant).*

Contrast	**Estimate**	**SE**	**Df**	**T-ratio**	**P - value**
T1 - T14	18.05	10.47	94.1	1.72	0.6721
T1 - T22	-16.61	11.20	98.3	-1.48	0.8143
T1 - T27	-20.67	10.37	97.9	-1.99	0.4913
T1 - T3	-8.21	12.38	99.8	-0.66	0.9978
T1 - T7	7.03	7.38	93.8	0.95	0.9797
T1 - V3	22.49	32.05	99.9	0.70	0.9968
T1 - V6	21.67	31.88	99.3	0.68	0.9974
T14 - T22	-34.66	13.53	96.8	-2.56	0.1831
T14 - T27	-38.72	12.71	94.3	-3.05	0.0578 ●
T14 - T3	-26.25	14.36	96.8	-1.83	0.6031
T14 - T7	-11.02	10.59	93.5	-1.04	0.9668
T14 - V3	4.45	32.73	98.9	0.14	1.0000
T14 - V6	3.62	33.01	99.9	0.11	1.0000
T22 - T27	-4.05	13.42	98.5	-0.30	1.0000
T22 - T3	8.41	14.94	98.9	0.56	0.9992
T22 - T7	23.64	11.28	97.4	2.10	0.4248
T22 - V3	39.12	32.94	99.0	1.19	0.9337
T22 - V6	38.28	32.94	99.0	1.16	0.9406
T27 - T3	12.46	14.27	98.4	0.87	0.9878
T27 - T7	27.70	10.44	96.5	2.65	0.1502
T27 - V3	43.16	32.70	99.1	1.32	0.8892
T27 - V6	42.34	32.97	100.2	1.28	0.9027
T3 - T7	15.24	12.37	98.5	1.23	0.9204
T3 - V3	30.70	33.24	98.7	0.92	0.9831
T3 - V6	29.88	33.64	100.3	0.89	0.9865
T7 - V3	15.47	31.98	99.4	0.48	0.9997
T7 - V6	14.64	31.89	99.2	0.46	0.9998
V3 - V6	-0.83	44.72	100.0	-0.02	1.0000

***Table 4**. Species' abbreviations, full names and functional groups.*

Species	Full name	Functional group
ach_mil	*Achillea millefolium*	Forb
agr_cap	*Agrostis capillaris*	Graminoid
agr_mer	*Agrostis mertensii*	Graminoid
alc_alp	*Alchemilla alpina*	Forb
alc_sp	*Alchemilla sp*	Forb
ant_alp	*Antennaria alpina*	Forb
ant_dio	*Antennaria dioica*	Forb
ant_odo	*Anthoxanthum odoratum*	Graminoid
ara_alp	*Arabis alpina*	Forb
arc_alp	*Arctous alpina*	Dwarf shrub
arc_uva	*Arctostaphylos uva-ursi*	Dwarf shrub
ath_dis	*Athyrium distentifolium*	Forb
ave_fle	*Avenella flexuosa*	Graminoid
bar_alp	*Bartsia alpina*	Forb
bec_gla	*Beckwithia glacialis*	Forb
bet_pub	*Betula pubescens*	Shrub
bis_viv	*Bistorta vivipara*	Forb
cal_phr	*Calamagrostis phragmitoides*	Graminoid
cam_rot	*Campanula rotundifolia*	Forb
car_atr	*Carex atrata*	Graminoid
car_bel	*Cardamine bellidifolia*	Forb
car_big	*Carex bigelowii*	Graminoid
car_bru	*Carex brunnescens*	Graminoid
car_lac	*Carex lachenalii*	Graminoid
car_rup	*Carex rupestris*	Graminoid
car_sax	*Carex saxatilis*	Graminoid
car_vag	*Carex vaginata*	Graminoid
cer_alp	*Cerastium alpinum*	Forb
cer_alp_lan	*Cerastium alpinum ssp. Lan*	Forb
cer_cer	*Cerastium cerastoides*	Forb
cha_ang	*Chamerion angustifolium*	Forb
coe_vir	*Coeloglossum viride*	Forb
cry_cri	*Cryptogramma crispa*	Forb
cys_fra	*Cystopteris fragilis*	Forb
des_alp	*Deschampsia alpina*	Graminoid
dip_alp	*Diphasiastrum alpinum*	Forb
dra_fla	*Draba fladnizensis*	Forb
emp_nig	*Empetrum nigrum*	Dwarf shrub
epi_ana	*Epilobium anagallidifolium*	Forb
equ_arv	*Equisetum arvense*	Forb
eri_ang	*Eriophorum angustifolium*	Graminoid
eri_sch	*Eriophorum scheuchzeri*	Graminoid
eri_uni	*Erigeron uniflorum*	Forb
eri_vag	*Eriophorum vaginatum*	Graminoid

eup_wet	*Euphrasia wettsteinii*	Forb
fes_ovi	*Festuca ovina*	Graminoid
fes_viv	*Festuca vivipara*	Graminoid
gen_niv	*Gentiana nivalis*	Forb
ger_syl	*Geranium sylvaticum*	Forb
gym_dry	*Gymnocarpium dryopteris*	Forb
har_hyp	*Harrimanella hypnoides*	Dwarf shrub
hie_alp	*Hieracium alpinum*	Forb
hie_sp	*Hieracium sp*	Forb
hup_sel	*Huperzia selago*	Forb
jun_big	*Juncus biglumis*	Graminoid
jun_com	*Juniperus communis*	Shrub
jun_tri	*Juncus trifidus*	Graminoid
leo_aut	*Leontodon autumnalis*	Forb
luz_arc	*Luzula arcuata*	Graminoid
luz_fri	*Luzula mult. Ssp. Frigida*	Graminoid
luz_spi	*Luzula spicata*	Graminoid
lyc_ann	*Lycopodium annotinum*	Forb
lyc_cla	*Lycopodium clavatum*	Forb
min_bif	*Minuartia biflora*	Forb
oma_nor	*Omalotheca norvegica*	Forb
oma_sup	*Omalotheca supina*	Forb
oxy_dig	*Oxyria digyna*	Forb
pet_fri	*Petasites frigidus*	Forb
phe_con	*Phegopteris connectilis*	Forb
phi_alg	*Phippsia algida*	Graminoid
phl_alp	*Phleum alpinum*	Graminoid
phy_cae	*Phyllodoce caerulea*	Dwarf shrub
poa_alp_alp	*Poa alpina var alpina*	Graminoid
poa_alp_viv	*Poa alpina var vivipara*	Graminoid
poa_arc	*Poa arctica*	Graminoid
poa_fle	*Poa flexuosa*	Graminoid
poa_jem	*Poa x jemtlandica*	Graminoid
pot_cra	*Potentilla crantzii*	Forb
pyr_min	*Pyrola minor*	Forb
ran_acr	*Ranunculus acris*	Forb
ran_pyg	*Ranunculus pygmaeus*	Forb
rho_ros	*Rhodiola rosea*	Forb
rub_cha	*Rubus chamaemorus*	Forb
rum_ace	*Rumex acetosa*	Forb
sag_sag	*Sagina saginoides*	Forb
sal_gla	*Salix glauca*	Shrub
sal_her	*Salix herbacea*	Dwarf shrub
sal_lan	*Salix lanata*	Shrub
sal_lap	*Salix lapponum*	Shrub
sal_phy	*Salix phylicifolia*	Shrub

sal_sp	*Salix sp*	Shrub
sau_alp	*Saussurea alpina*	Forb
sax_cer	*Saxifraga cernua*	Forb
sax_ces	*Saxifraga cespitosa*	Forb
sax_niv	*Saxifraga nivalis*	Forb
sax_opp	*Saxifraga oppositifolia*	Forb
sax_riv	*Saxifraga rivularis*	Forb
sax_ste	*Saxifraga stellaris*	Forb
sax_ten	*Saxifraga tenuis*	Forb
sel_sel	*Selaginella selaginoides*	Forb
sib_pro	*Sibbaldia procumbens*	Forb
sil_aca	*Silene acaulis*	Forb
sil_dio	*Silene dioica*	Forb
sil_wah	*Silene wahlbergella*	Forb
sol_vir	*Solidago virgaurea*	Forb
tar_sp	*Taraxacum sp.*	Forb
tha_alp	*Thalictrum alpinum*	Forb
tri_eur	*Trientalis europaea*	Forb
tri_spi	*Trisetum spicatum*	Graminoid
vac_myr	*Vaccinium myrtillus*	Dwarf shrub
vac_uli	*Vaccinium uliginosum*	Dwarf shrub
vac_vit	*Vaccinium vitis-idaea*	Dwarf shrub
vah_atr	*Vahlodea atropurpurea*	Graminoid
ver_alp	*Veronica alpina*	Forb
vio_pal	*Viola palustris*	Forb
vis_alp	*Viscaria alpina*	Forb

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