On the role of lichens in vegetation-climate interactions

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Cladonia arbuscula

Contents

Summary

Current climate change is amplified over northern high latitudes, affecting the biogeochemical interactions and feedback between vegetation and climate. One step towards a more complete understanding of vegetation-climate interactions at high latitudes is to study the contribution from nonvascular photoautotrophs (NVPs), that is lichens, bryophytes, and biological soil crust communities. While NVPs have received less attention than their vascular counterparts, their contribution to boreo-arctic ecosystems is considerable. Mat-forming species often dominate vegetation and NVPs encompass great variation in physiology and adaptions that enables them to persist in a wide range of environmental conditions. This thesis focuses on the ecological and climatological interactions of the group of bright macrolichens commonly known as reindeer lichens. These relations are approached through three research objectives, where each objective is explored in a corresponding research paper.

The first objective was to quantify the effect of reindeer lichens on surface albedo, i.e., solar reflectance, and investigate how surface albedo varies between vegetation types and along environmental gradients. This was investigated through collecting and analysing field observations on a vegetation type scale.

The second objective was to estimate current and historic reindeer lichen volumes across the pan-Arctic and relate changes in lichen volumes to drivers of environmental change. This was investigated with a remote sensing approach on a landscape scale, looking at how lichen abundance varies spatially and temporally.

The last objective was to investigate the effects of winter heatwaves on growing season ecophysiology in lichen rich vegetation, and how the effects may differ between species and type of winter stress. This was done through a field experimental approach, studying the responses on a species scale.

The results show how albedo of bright reindeer lichens is likely the highest albedo of common, naturally occurring vegetation, approaching 0.4. The high albedo is significant for vegetation-climate interactions at high latitudes, especially as carbon sequestration rates are relatively low in these regions. Across the pan-Arctic, I found an overall decline in reindeer lichens in the last 40 years. The decline was largest in the first half of the study period (1984–2001) and driven by a rapid increase in *Rangifer* population. From 2001–2020, *Rangifer* herbivore pressure was released in many areas, but the increased competition from trees and shrubs likely halted the lichen's recovery. While excessive herbivory, increase in wildfires, and summer warming benefit herbs and shrubs at the expense of lichens, winter heatwaves represent an opposite effect. Lichens prove to be much more robust against the ecophysiological stress of ice encapsulation and midwinter thaw and freeze than vascular plants and bryophytes. However, two of the three lichen study species showed some susceptibility to ground icing, and this infers different ecophysiological responses depending on the characteristics of future winter climate change. The results presented here gives opportunities for better modelling of surface albedo regulation in lichen vegetation, updated knowledge on the state of pan-arctic lichen populations, and novel insight into the responses to winter stress in lichens.

Oppsummering

Pågående klimaendringer forsterkes over nordlige breddegrader, og påvirker de biogeokjemiske interaksjonene og tilbakekoblingene mellom vegetasjon og klima. Et skritt mot en mer fullstendig forståelse av interaksjoner mellom vegetasjon og klima på høye breddegrader er å studere bidraget fra ikke-vaskulære fotoautotrofer (NVP), det vil si lav, moser og skorpesamfunn. Mens NVP-er har fått mindre oppmerksomhet enn karplanter, er deres bidrag til boreo-arktiske økosystemer betydelig. Mattedannende arter kan dominerer vegetasjonen og NVP-enes diversitet i fysiologi og tilpasninger gjør dem i stand til å trives i et bredt spekter av miljøforhold. Denne avhandlingen setter søkelys på økologiske og klimatologiske interaksjoner hos gruppen av lyse makrolav vanligvis kjent som reinlav. Disse forholdene undersøkes gjennom tre forskningsmål, hvor hvert mål utforskes i en tilhørende forskningsstudie.

Det første målet var å kvantifisere effekten av reinlav på overflatealbedo, dvs. solreflektans, og undersøke hvordan overflatealbedo varierer mellom vegetasjonstyper og langs miljøgradienter. Dette ble undersøkt gjennom innsamling og analyse av feltobservasjoner på en vegetasjonstypeskala.

Det andre målet var å estimere nåværende og historiske reinlavvolumer over hele den panarktiske regionen og relatere endringer i lavvolumer til ulike miljømessige drivere. Dette ble undersøkt med bruk av fjernmåling på en landskapsskala, for å anslå romlig og tidsmessig variasjon i lavmengde.

Det siste målet var å beskrive økofysiologiske effekter av vinterlige hetebølger på lavrik vegetasjon, og hvordan påvirkningen gjennom vekstsesongen varierer mellom arter og ulike typer vinterstress. Dette ble gjort med en felteksperimentell tilnærming, og ved å studere effekter på en artsskala.

Albedo av lyse reinlav ble målt oppimot 0,4, som sannsynligvis er den høyeste kjente overflatealbedoen fra naturlig forekommende vegetasjon. Den høye albedoen er spesielt viktig for interaksjoner mellom vegetasjon og klima på høye breddegrader, ettersom karbonbinding går relativt sakte i kalde områder. Over hele den panarktiske regionen fant jeg en generell nedgang i reinlav de siste 40 årene. Nedgangen var størst i første halvdel av studieperioden (1984–2001) og drevet av en rask økning i *Rangifer*-populasjoner. Fra 2001–2020 ble beitetrykket fra *Rangifer* kraftig redusert i mange områder, mens økt konkurranse fra trær og busker sannsynligvis reduserte gjenvekst av lav. Mens ekstensiv herbivori, økt brannfrekvens og lengre somre gagner karplanter på bekostning av lav, representerer vinterlige hetebølger en motsatt effekt. Lav viser seg å være mye mer hardføre mot det økofysiologiske stresset ved isinnkapsling og gjentatt tining og frysing om vinteren enn karplanter og moser. Imidlertid viste to av de tre lavartene en viss sårbarhet for isinnkapsling, og karakteristikkene til fremtidige vinterklimaendringer vil dermed diktere de økofysiologiske responsene i vegetasjonen. Resultatene presentert her gir muligheter for bedre modellering av overflatealbedoregulering i lavrik vegetasjon, oppdatert kunnskap om tilstanden til panarktiske lavbestander, og ny innsikt i respons på vinterstress hos lav.

List of papers

Paper I

Finne EA, Bjerke JW, Erlandsson R, Tømmervik H, Stordal F, Tallaksen LM (2023). Variation in albedo and other vegetation characteristics in non-forested northern ecosystems: the role of lichens and mosses. Environ Res Lett 18:074038. https://doi.org/10.1088/1748-9326/ace06d

Paper II

Finne EA, Erlandsson R, Tømmervik H, Stordal F, Tallaksen LM, Bjerke JW. Decadal decline in pan-arctic lichens: climate change supersedes herbivory as the main driver. Manuscript in preparation.

Paper III

Finne EA, Bjerke JW, Stordal F, Tallaksen LM. Lichens more tolerant than plants to winter heatwaves: insights from an alpine field experiment. Manuscript submitted.

1 Introduction

Anthropogenic climate change is now a ubiquitous driver of change in virtually all ecosystems (IPCC 2023). The effects are particularly visible in the Arctic, where the warming has occurred at a rate four times the global average, amplified by loss of snow and ice (Previdi et al. 2021; Rantanen et al. 2022). Less snow and ice reduce surface albedo, i.e., the ratio of outgoing to incoming solar radiation, and this is a major positive feedback mechanisms that amplifies the warming (Yu et al. 2022). Not only is climate change affecting the biosphere, but changes to the biosphere affect climate in return through alteration of biogeochemical and physical processes between the surface and atmosphere (Bonan 2015a). A major undertaking is to improve our understanding of the interactions and feedback between climate and vegetation, which is a prerequisite to study historic, current, and future changes to both climate and vegetation.

1.1 Roles of NVPs in biochemical, water and energy cycles

The contribution of non-vascular photoautotrophs (NVPs) to vegetation functioning generally increases towards high latitudes and altitudes. NVPs, replacing the obsolete term cryptogams, includes lichens, bryophytes, and biological soil crust assemblages of microlichens, bacteria and algae (BSC) (Porada et al. 2023). In sum they contribute significantly to the total terrestrial biomass, ground cover, and affect hydrology processes, carbon cycling, and nitrogen economy (Figure 1). NVPs are estimated to sequester 3.9 Pg carbon annually, corresponding to 7 % of the global terrestrial net primary production (NPP) (Elbert et al. 2012). Well known is the vast amount of carbon stored in northern peatlands, where carbon accumulation over thousands of years possibly equate to 20-30 % of the global terrestrial carbon storage (Yu et al. 2010). Still, NVPs are often overlooked in ecosystem service assessments and modelling of vegetation-atmosphere interactions, potentially leading to an underestimation of their ecological significance (Wullschleger et al. 2014).

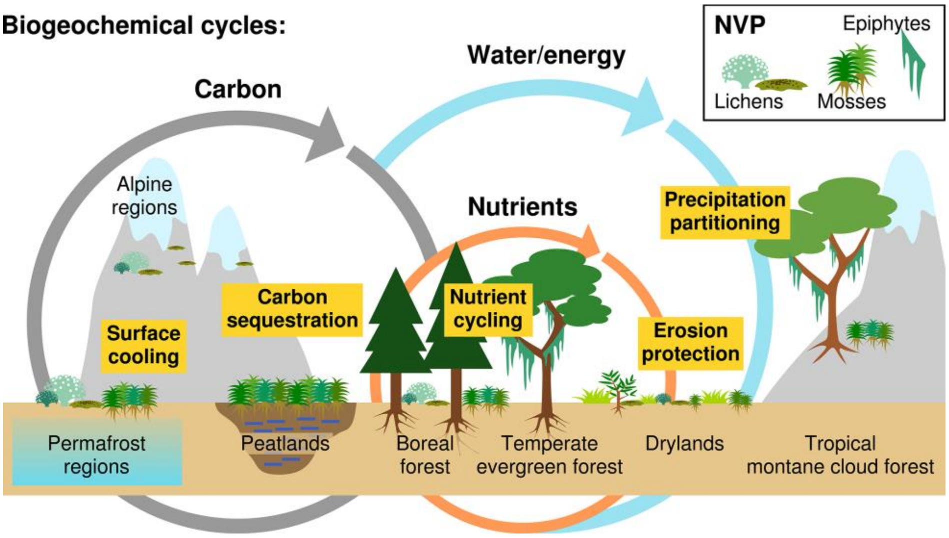

Fig. 1: Schematic overview of the contributions from non-vascular photoautotrophs (NVPs) to terrestrial ecosystem functioning (yellow boxes) and the associated biogeochemical cycles of carbon (grey arrow), nitrogen and phosphorus (orange arrow), and water and energy (blue arrow). These are placed to correspond with the biomes where the regulating effect of NVPs on the respective functions and cycles are presumed to be most important. The impacts to alpine regions, permafrost regions, and boreal forest are essential to this thesis. Reproduced from Porada et al. (2023).

Central to the ecological differences between NVPs and vascular plants (VPs) is their water relations. In contrast to most VPs, NVPs are poikilohydric, meaning they lack mechanisms to maintain constant internal hydration. Their metabolic activity depends on the internal water content, and alternates from inactive periods when desiccated, to quickly regaining physiological activity when rehydrated. This rapid adaption to fluctuations in water availability is in contrast with the activity patterns in the homoiohydric VPs, which generally follow slower seasonal and diurnal rhythms (Lange et al. 2001). This leads to ecological differences, such as the annual peak in NVP photosynthetic activity occurring at the shoulder seasons of the typical peak VP growing season, and the maximum daily photosynthetic activity occurring in the morning when the thallus is still hydrated by dewfall (Proctor 2012). Thus, the ecophysiological differences between NVPs and VPs infers different interactions with climate and climate change.

This thesis focuses on the mat-forming terricolous (ground-dwelling) lichens due to their distinct traits, key ecosystem functions, and wide distribution. Fruticose (shrubby growth form) species of the genera *Cladonia, Cetraria,* and *Nephromopis* dominate vast boreo-arctic areas and are often referred to as *reindeer lichens* due to their importance as winter forage item for reindeer and caribou (*Rangifer tarandus* L.). The most common species (*Cladonia stellaris* (Opiz) Pouzar & Vězda*, C. arbuscula* (Wallr.) Flot*., Nephromopsis nivalis* (L.) Divakar, A.Crespo & Lumbsch) are bright, having the citric yellow usnic acid as a main secondary metabolite, and form near-continuous mats with thicknesses of 20 cm or more. These mats act as a barrier for seeds and hamper establishment of faster growing shrubs and herbs when intact. In addition to being a physical barrier, lichens can both reduce growth of other species through allelopathy and, contrastingly, facilitate seedling growth by stabilising the microclimate (Nystuen et al. 2019). The bright colouration makes the reindeer lichen mats appear very distinct from other vegetation types. At the core of this thesis is the exploration of ecological and climatological relations in lichens ecosystems at high latitudes and altitudes, and how these are changing with time.

1.2 Surface albedo regulation in NVP-dominated ecosystems.

The characteristics of vegetation-climate interactions and feedback differ spatially and among vegetation types. NVPs participate in fluxes of water and energy, nutrients, carbon, with surface cooling as a principal effect in high latitude and altitude ecosystems (Figure 1). Surface cooling includes both the insulating effect vegetation has on the ground, crucial for permafrost, and surface albedo. As albedo is the ratio of outgoing to incoming solar radiation, it regulates the amount of energy available for the surface energy balance. The large differences in surface albedo between snow, forest and open vegetation makes this a key component of vegetation-climate interactions in high latitude and altitude ecosystems (Table 1). Comparably, carbon fluxes, transpiration, and release of biogenic volatile organic compounds (BVOCs) are typically slower in cooler ecosystems, meaning the albedo effect is of higher relative importance for vegetation-climate interactions at high latitudes (Bonan 2008). Furthermore, albedo properties of natural surfaces are not constant. Vegetation change caused by land use change, climate change, or grazing intensification, have strong impacts on surface albedo, and across the northern hemisphere, the land surface albedo is in a declining trend driven by reduced snow cover, vegetation greening and moisture change (Yuan et al. 2022).

Table 1: Reference broadband albedo values for natural surfaces (Bonan 2015, reproduced from Oke 1987).

Surface	***Albedo***
Fresh snow	0.80–0.95
Old snow	0.45–0.70
Desert	0.20–0.45
Glacier	0.20–0.40
Soil	0.05–0.40
Cropland	0.18–0.25
Grassland	0.16–0.26
Deciduous forest	0.15–0.20
Coniferous forest	0.05–0.15
Water	0.03–0.10

Compared with green vegetation (Table 1), bright reindeer lichen mats have high albedo and may play a considerable, though underappreciated, role in the surface energy balance (Davies 1963; Petzold and Rencz 1975; Beringer et al. 2005). Both the high reflectivity of lichen thalli, and the low height of lichen vegetation result in a higher albedo than green, more complex vegetation during the snow-free season. The low stature of lichens also facilitates high snow surface albedo as few vegetation structures protrude the snowpack and, and in this way, reduce the albedo (Cohen et al. 2013). Considering the large changes that are taking place in high latitude ecosystems (Bjorkman et al. 2020; Rixen et al. 2022), there is a need to understand more about the albedo properties of vegetation and how it varies with environmental gradients.

1.3 Vegetation-herbivore interactions

Besides climate change, an essential driver of boreo-arctic vegetation change is herbivory, especially from reindeer and caribou, hereafter referred to as *Rangifer.* This is the main pan-arctic large terrestrial herbivore, in terms of population size, importance to humans, and interaction with vegetation. Herbivory from *Rangifer* can maintain an open, treeless landscape and change plant community composition, and in this way substantially impact surface albedo (e.g. te Beest et al. 2016). Specifically, *Rangifer* exert herbivore pressure on vegetation through three main mechanisms: fertilisation, trampling and selective feeding (Stark et al. 2023). How vegetation respond to this pressure is complex and dependent on vegetation type, interactions with the effects of climate change and other disturbances, and vary with by *Rangifer*'s heterogenous spatial use of the landscape (Bråthen and Oksanen 2001; Rees et al. 2003; Tømmervik et al. 2012; Biuw et al. 2014). Changes to vegetation will also necessarily feedback to *Rangifer*'s continued use of the vegetation. In general, the non-palatable species or species resistant to repeated grazing and trampling, and vegetation benefiting from fertilisation stimulating to increased microbial activity and increased nitrogen availability will be favoured under high herbivore pressure. Thus, the potential for vegetation dominated by lichens occur on the lower end of the gradient in herbivore pressure (Figure 2, Stark et al. 2023). With increasing herbivore pressure, the potential vegetation shifts towards dominance of bryophytes and finally to dominance of graminoids and other herbivore-tolerant vascular plants (Figure 2).

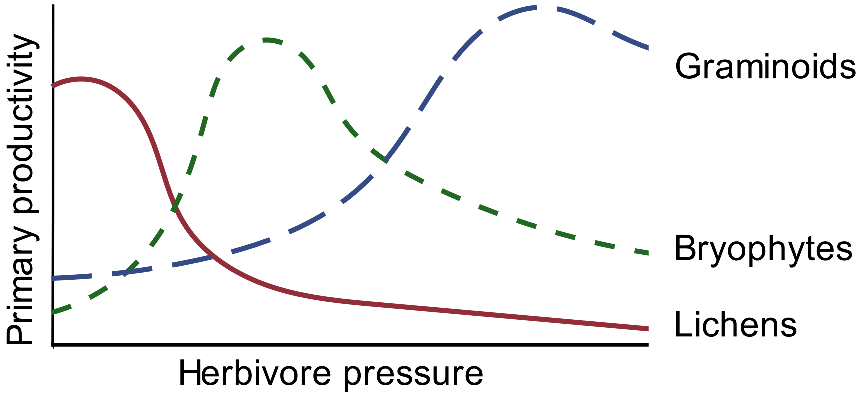

Fig. 2: Potential for biomass and primary productivity in graminoids (blue), bryophytes (green), and lichens (red) along an idealised *Rangifer* herbivore pressure gradient. Modified from van der Wal (2006).

However, the realised vegetation is also dependent on all other relevant environmental gradients and may deviate from the relationships depicted in Figure 2. Still, there is a clear reciprocal relationship between *Rangifer* and reindeer lichens due to the importance of lichens as winter fodder, and intense winter grazing can rapidly exhaust lichens where the snow depths are shallow. However, lichen populations can survive and thrive in lee sides in winter grazing areas where snow accumulation prevents reindeer access (Tømmervik et al. 2012; Cohen et al. 2013). In these winter pasture regions, lichen cover can vary greatly over short distances, from little abundance on exposed ridges to high abundance in leesides. Moreover, lichen mats are highly susceptible to trampling damage in summer, especially in the dry state. A high year-round grazing pressure in lichen heaths over well-drained soils can shift the vegetation to nearly monospecific heaths of the trampling resistant crowberry (*Empetrum nigrum* L.), common heather (*Calluna vulgaris* (L.) Hull), or dwarf birch (*Betula nana* L.) (Vowles et al. 2017; González et al. 2019). In areas with deeper soil with higher organic content, summer grazing suppresses lichen abundance and generally promotes dominance of herbaceous plants (Cohen et al. 2013).

Reindeer lichen recovery after grazing and trampling damage necessitates sufficient fragments from which the lichens can propagate. Increasingly fragmented and discontinued lichen mats give more room for seeds of faster growing plants to establish, which then can outcompete the slower-growing lichens, resulting in a stable vegetation shift. The technological revolution in the reindeer husbandry of Scandinavia, which includes the introduction of snowmobiles and all-terrain vehicles (Rieseth et al. 2016), enabled increase in herd size and a more extensive land use resulting in declining lichen biomass. On Svalbard, grazing and trampling from the Svalbard subspecies (*R.t. platyrhynchus* Vrolik, 1829) has similar impacts as in mainland Scandinavia. The main difference is that the drier arctic winter weather and the predominant katabatic winds lead to shallow snow depths. Thus, fruticose lichens are therefore nearly absent in reindeer grazing areas, and for the same reason, several lichens grazed by reindeer are on the Svalbard Red List of threatened species (The Norwegian Biodiversity Information Centre 2021).

1.4 Lichen distribution change

While Larson (1987) estimated lichens to cover 8 % of Earth's land area, their global distribution and biomass is not well known. Furthermore, the biomass and cover of reindeer lichens are reported to decline in many parts of the pan-Arctic (Cornelissen et al. 2001; Joly et al. 2009; Sandström et al.

2016; Horstkotte and Moen 2019), raising concerns for the future of these ecosystems. Despite the ecological, climatological, and cultural importance of lichen, there is today inconsistent knowledge about general trends in global lichen abundance, and the relative importance of different drivers of change. In addition to the perspectives of *Rangifer* herbivore pressure and climate change, changes to lichen vegetation must be viewed in light of vegetation disturbances and human land use, including wildfires (Greuel et al. 2021), collapse of permafrost peat plateaus (Errington et al. 2022), and differences in forestry practices (Sandström et al. 2016; Tonteri et al. 2022).

Available studies have generally focused on local scales or specific events, and relied on locally optimized methods (Macander et al. 2020; Kennedy et al. 2020; Greuel et al. 2021; Orndahl et al. 2022). Despite some regional studies based on considerable field work efforts, empirical measurements are of limited use for extrapolation given the complexity and within-region differences in natural and anthropogenic factors driving changes in lichen abundance as well as in *Rangifer* management. Obtaining better methods and standardising estimation of reindeer lichen abundance is a necessary step for a better representation of lichens in vegetation models and to assess their contribution to vegetation-climate interaction. This is crucial information for monitoring lichen biomass change in response to climate change and other forms of environmental changes. Notably, estimates of lichen abundance on *Rangifer* winter pastures is needed for sustainable *Rangifer* management.

1.5 Climatic impacts on NVPs

Although the fundamental niche of lichens is climatically broad (Mallen-Cooper et al. 2023), increased shrub growth stimulated by an extended summer growing season, deepened permafrost thaw, and increased soil activity have been associated with a reduction in lichen abundance (Elmendorf et al. 2012; Fraser et al. 2014; Chagnon and Boudreau 2019; Errington et al. 2022). Paradoxically, recent increases in shrub biomass on North American caribou summer pastures have been accompanied by declines in caribou populations, as this shrub expansion involves species with strong anti-browsing defences (Fauchald et al. 2017).

In addition to warmer summer temperatures, changes in moisture and precipitation patterns can have great impact on the propagation of reindeer lichens and other NVPs, due to their dependence on rehydration by atmospheric water, either by precipitation or dewfall. Drier summer conditions and higher water vapour deficit (VPD) will both reduce the relative growth rate (RGR) and increase the amount of trampling damage from herbivores (Cooper et al. 2001). A key factor is the rewetting frequency. Heavy precipitation events will saturate the ability of NVPs to take up water and not be as beneficial as more frequent, smaller precipitation events.

Yet, a shift towards faster-growing vascular plants may be hampered by increased frequency and severity of extreme winter weather events. The acceleration of climate change has foremostly affected winter and fall climate in boreo-arctic ecosystems (Previdi et al. 2021). Particularly the effects of higher frequency and severity of winter warming events and mid-winter precipitation as rain are rapidly changing the winters (Rixen et al. 2022). Winter heatwaves are associated with increased shoot and leaf damage and a decline in gross primary production (GPP), and a coinciding shift in NPP towards respiration (Treharne et al. 2019). Evergreen plants such as *E. nigrum* are particularly susceptible to these events as green leaves and buds overwinter in the snowpack. When the snow melts and plant metabolism is reactivated, a following drop in temperature can lead to frost drought and vegetation damage (Bokhorst et al. 2010). Comparably, lichens may be more resistant against the negative effects of winter heatwaves due to their adaptions of rapid activation and inhibition to environmental change, even capitalising on the warm periods (Bokhorst et al. 2023).

While winter climate conditions represent a main constraint for species distribution in boreo-arctic ecosystems, the effects of winter climate change on vegetation are much less studied than summer climate change effects. This is particularly important for NVPs, which have their growing season not necessarily in sync with their vascular counterparts, and with physiological activity year-round if conditions allow (Arndt et al. 2023). Even during winter, there are windows of opportunity where lichens and bryophytes can reactivate and become physiologically active. The conditions are often favourable under a thin layer of snow. Snow melt starting at the bottom of the snowpack create pockets of air that are both moist and saturated in CO_2, therefore providing prime conditions for photosynthesis when the snowpack is thin enough to allow sufficient light to pass through (Kappen 1993). Hence, incorporating year-round vegetation ecology at high altitudes and latitudes is necessary to fully understand vegetation interactions and how they change.

2 Aims and objectives

The main aim of this thesis is to improve understanding of the role that reindeer lichens play in vegetation-climate interactions. I approached this through three perspectives: variation in climate relevant vegetation characteristics on a vegetation type scale, lichen distribution change on a landscape scale, and ecophysiological responses of climate extremes on a species scale (Figure 3). These perspectives were formulated as three corresponding objectives which are addressed in three research papers (numbered I-III).

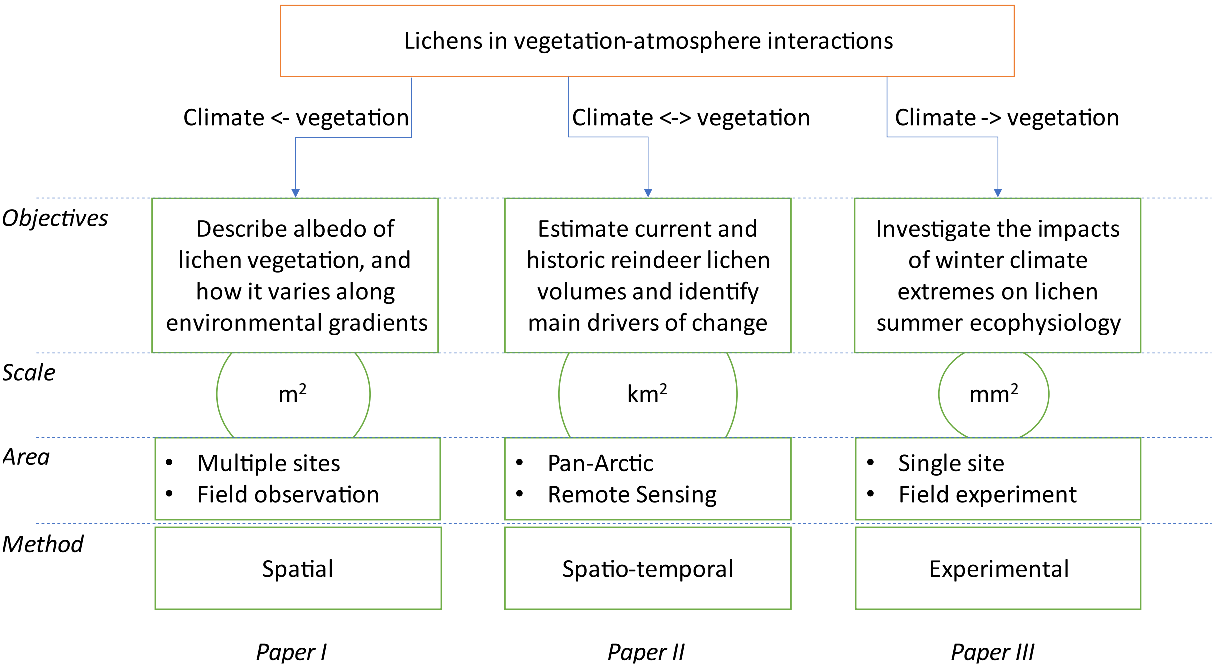

Fig. 3: Conceptual overview of the research, structured into three objectives and related papers (at three scales).

The three objectives are specified in the subsections below. Then, in the following sections, I will introduce the study sites and methodologies used to address the objectives, where the order follows the size of the study area (Figure 3) as the smaller study areas are nested within the larger. Then, returning to the paper order, the main results, and extended abstracts of the three papers are presented. Next follows a general discussion, conclusion and lastly an outlook.

2.1 Objective I: Quantify the effect of reindeer lichens on surface albedo, and how surface albedo varies between vegetation types and along environmental gradients.

To address this objective, we measured the surface albedo of common treeless boreo-arctic vegetation types through extensive fieldwork, emphasising on collecting data along large spatial scales and covering the full gradient in *Rangifer* herbivore pressure. Simultaneously, we collected key information on vegetation characteristics including species composition, height, greenness and carbon flux. We hypothesized that:

1. Vegetation cover is a strong regulator of albedo in northern non-forested ecosystems, mediated by bright lichen abundance.
2. Vegetation albedo is inversely related to biomass and carbon flux in our study area, describing a gradient from NVP-dominated to VP-dominated vegetation.
3. Reindeer grazing intensity and climate modulate vegetation albedo.

2.2 Objective II: Estimate current and historic reindeer lichen volumes across the pan-Arctic and relate changes in lichen volumes to drivers of environmental change.

Here, we estimated pan-arctic lichen volumes, which is convertible to lichen biomass (Tømmervik et al. 2009) from remote sensing products, in areas known to be historically abundant in bright reindeer lichens. The secondary aim of this study was to identify if patterns of change differed between regions and vegetation types and assess key drivers of vegetation change. Hence, the estimated lichen volumes were compared against trends in *Rangifer* population counts, vegetation indices and climate change indices.

2.3 Objective III: Investigate effects of winter heatwaves to lichen rich vegetation, and how the effects on growing season ecophysiology differ between species and type of winter stress.

Here, we explored the resilience to thaw-freeze (TF) and ice encasement (IE) events in widespread alpine vascular plants, lichens, and bryophytes through a field experiment, and evaluated the impacts on ecophysiological performance during the following summer growing seasons. We hypothesized that:

1. Warming events during winter causing thaw-freeze or ground-ice accumulation cause stress to alpine heath and ridge vegetation, manifesting as reduced ecophysiological activity and growth in the following summer.
2. Thaw-freeze events are more detrimental to vegetation than ground-ice formation, because of increased reactivation during the event and increased freezing stress after the event.
3. Lichens are more tolerant than bryophytes to full thaw-freeze and ground-ice accumulation.

3 Study sites and area

The three studies that form this thesis have three overlapping study areas (Figure 4). The field experiment (Paper III) was conducted adjacent to Finse Alpine Research Station on Hardangervidda mountain plateau (60.593° N, 07.524° E, 1200 meters above sea level). Finse has an annual mean temperature of −1.1 °C and annual precipitation of 970 mm (Tveito 2021). Lichen mats of *Nephromopsis nivalis, Cladonia mitis* Sandst.*, Alectoria ochroleuca* (Schrank) A.Massal.*,* and *Cetraria islandica* (L.) Ach. are common on convex terrain formations in the area, where they grow undisturbed from reindeer and direct human influence. Combined with the existing research facilities and climate and flux monitoring on Finse, this is an ideal location for conducting a field experiment on lichen ecophysiology. Locating the experiment here gave access to valuable surface temperature data during the experimental periods. Moreover, since installation of an eddy covariance tower in 2016, the surface energy balance, and fluxes of CO_2 and water vapor have been tracked.

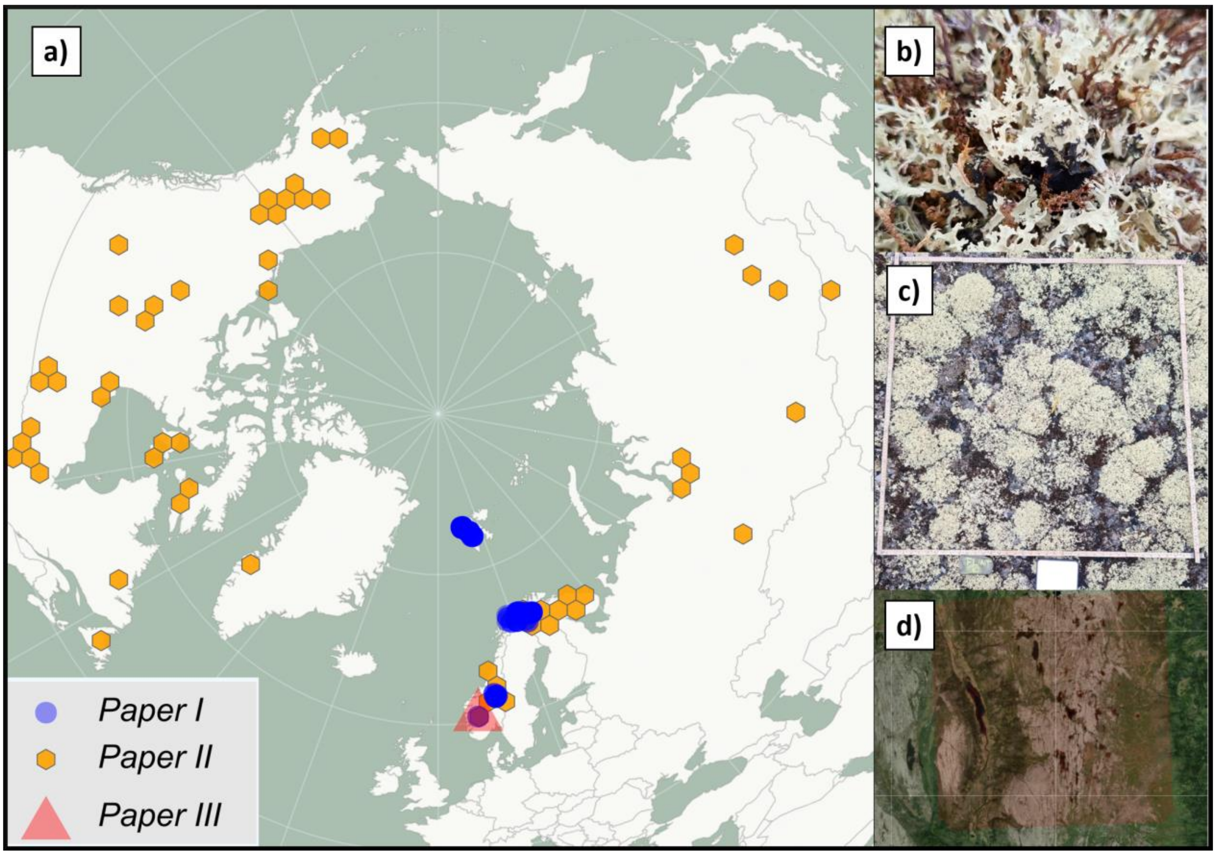

Fig. 4: a) The geographical distribution of study sites. Blue circles show the positions of the field sites used in Paper I (*N* = 135), yellow honeycombs cover the sites analysed using remote sensing (Paper II) (*N* = 121), and the field experimental site at Finse (Paper III) is marked with a red triangle. Note that the polygon size leads to overlap of sites used in Papers I and II. Images show **b)** *Nephromopsis nivalis* from the experimental site in Paper III, **c)** one of the field sites in Paper I where *N. nivalis* occur in mosaic with *Racomitrium lanuginosum*, *Alectoria nigricans* and *Cetraria islandica* (Flintholmen, Svalbard), and **d)** Sentinel 2A imagery of one of the study sites in Paper II (Fulufjellet, Norway and Sweden).

From Finse as the southernmost location to Krossfjorden, Svalbard, as the most northerly location (79.282° N), we established 136 field sites to capture albedo characteristics of common treeless vegetation types (Paper I). These sites were spread across four main regions; mountain region in southern Norway, Troms and central Finnmark in northern Norway, and Svalbard (Figure 4). The climate regimes were comparable, and occurrence of the same vegetation types and species could be identified across the whole study area. However, reindeer management differed between regions. Reindeer herbivore pressure at the sites in Southern Norway were generally low, whereas sites in Troms and central Finnmark were more intensely grazed. The sites in central Finnmark covered winter pastures, while Troms include sites that are grazed in the snow-free season. In Svalbard, field sites were distributed across areas with low to high reindeer herbivore pressure, as fjords and glaciers act as barriers for reindeer migration and creates high variation in grazing intensity over short distances.

Sites visited during own field work and sites obtained from sourcing the literature for areas with known present or historic occurrence of bright reindeer lichen were used to estimate changes in lichen volumes (Paper II). This resulted in a selection of 696 sites across the pan-Arctic. After merging nearby sites, using a 500 m buffer, and removing sites with incomplete Landsat satellite coverage during the study period, the final study area compromised 121 sites (Figure 4). These sites covered a total of 14,557 km^2 across seven countries and included variation in bioclimate from boreal forests to arctic tundra, variation in *Rangifer* management and human land use, and different wildfire regimes.

4 Methods and data

4.1 Field experiment

The field experiment was conducted close to Finse Alpine Research Station in 2021 and repeated in 2022. To my knowledge, this is the first field experiment simulating the effect of winter heatwaves to lichen dominated vegetation. The experiment had six replicates, blocks, each divided into three plots: thaw-freeze (TF), ice encapsulation (IE) and control (C) (Figure 5). The same experimental design was used in both years. We induced heatwaves using an array of infrared lamps hanging from wooden racks above the TF plots, following the methodology described in Bokhorst et al. (2008). As the plots became snow-free, the lamps were kept on for about a week to maintain temperatures in vegetation above freezing. Afterwards, the lamps were removed, and the plots were left to refreeze. The following cold shock is the main cause of the stress response in vegetation. The encapsulation of vegetation in ice that occurs after mid-winter rain was imitated by simply adding cold water to the IE plots. Wooden frames were installed around the plots to confine the wet snow in the plots while it froze. This methodology is similar to e.g. Milner et al. (2016). The main effect of this icing is related to the inhibition of gas exchange between vegetation and air, particularly making active cells unable to properly dispose of CO_2.

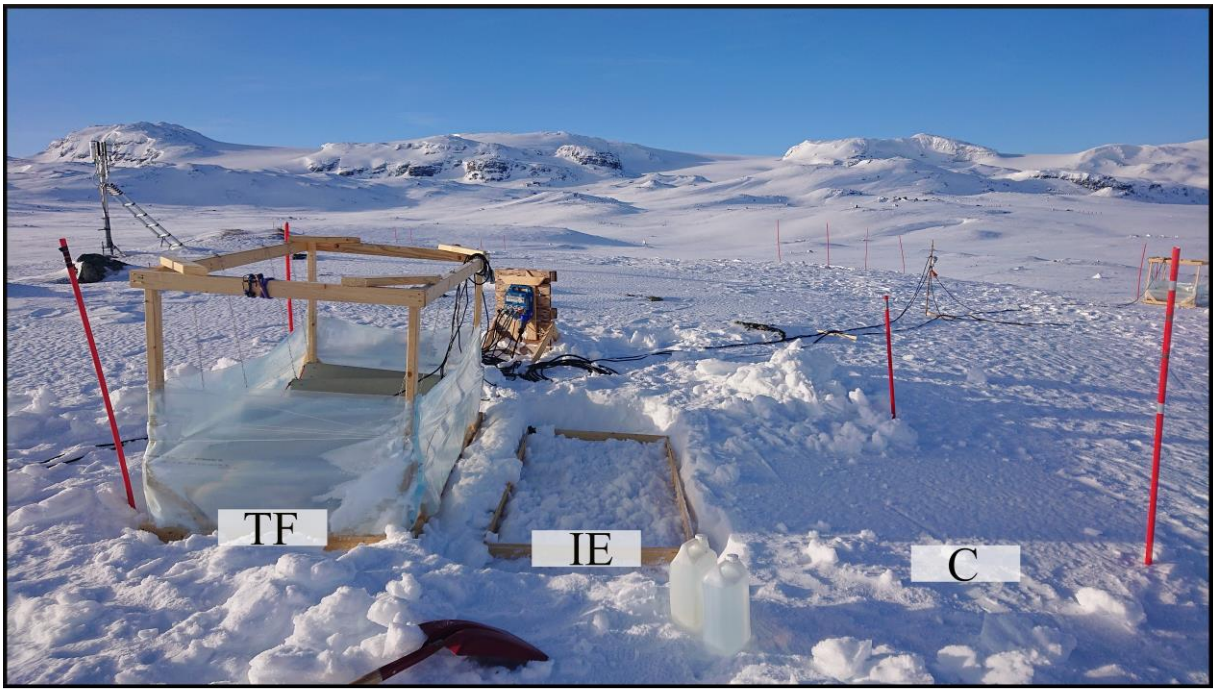

Fig. 5: Field experiment at Finse, showing one of six experimental blocks with its three plots. From left to right: Thaw-freeze treatment plot (TF), ice encapsulation treatment plot (IE), and control plot (C). The power supply, with a distribution box for the TF plots, can be seen placed next to the block. The other two blocks, marked with red sticks, are visible in the background.

The effects of the experimental treatments were assessed in the following summers, focusing on the dominant species and repeated measurements from early June to the peak vascular growing season by the end of July. Different methodology was used to identify any persistent effects, including frequency of visible vegetation damage, NDVI measurements, leaf chlorophyll, flavonol, and nitrogen content, CO_2 flux rates on species and plot level, and chlorophyll fluorescence. The main studied species were the lichens *Nephromopsis nivalis, Cetratia islandica,* and *Cladonia mitis*, the bryophytes

Polytrichum juniperinum Hedw., and *Ptilidium ciliare* (L.) Hampe, and the evergreen dwarf shrub *Empetrum nigrum.*

4.2 Field observations

The bulk of the fieldwork campaign for Paper I was completed in summer 2020, with supplementary measurement in 2021. Sites were selected to be as representative as possible of the local variation in vegetation and structure and classified into predefined vegetation types. Broadband surface albedo was measured at each site, as well as recordings of vegetation type and height, soil depth, instantaneous CO_2-flux, Normalised Vegetation Index (NDVI), photography, and species composition using the point-intercept method.

Fig. 6: Albedo measurements on Flintholmen, Svalbard. Research collaborator Rasmus Erlandsson, Norwegian Institute for Nature Research, controls that the albedometer instrument is stable.

We used two pyranometers mounted back-to-back for the albedo measurements (Figure 6), which was moved from site to site. To account for albedo variance due to solar position and the ratio of diffuse to direct radiation, the albedometer was installed at fixed locations over several days at Finse, capturing diurnal albedo variation under different cloud conditions. This information was used to standardise all values to a solar zenith angle (SZA) of 60° and cloud free conditions. Instantaneous CO_2-flux was measured using the chamber method, switching between illuminated and dark condition to obtain gross primary production and respiration rates, which were then used to estimate net primary production (NPP). These recordings give only a snapshot of the CO_2-flux, but with the number of replicates and by recording ambient photosynthetic active radiation (PAR), and temperature, this provided a valuable data set to compare against the albedo values. Furthermore, the vegetation was lightly watered prior to measurements when dry, as to not limit activity rates of

NVPs. NDVI was measured with a handheld device originally developed for agriculture. As NDVI is a ratio between infrared and red wavelengths, the amount of green biomass, especially for low vegetation heights, is well correlated with NDVI values, and correspondingly negatively correlated with lichen cover (Erlandsson et al. 2023). Thus, NDVI provided a measure of green biomass, complementing measurements of vegetation heights and species composition.

4.3 Remote sensing

Mats of bright reindeer lichens can be observed from satellite and aerial photos as bright-yellowish patches. However, there are considerable challenges to accurately estimate lichen cover and biomass from remote sensed products. Lichens have spectral properties distinct from those of green plants, but there is large variability in properties between dominating lichen thallus colours and forms (e.g., bright vs. dark, fruticose vs. foliose), and moisture level. The spectral signal is also influenced by the vegetations that grows together with the lichens and vegetation that grows above the lichen layer can mask the signal. Furthermore, it can be difficult to distinguish lichens from sand, pebbles, and rocks and the signal can be disturbed by complex terrain. Earlier attempts to create spectral indices to estimate lichen biomass have had some success, such as the development of the Lichen Volume Estimator, LVE (Falldorf et al. 2014). However, newly developed techniques have facilitated better opportunities to monitor lichens with remote sensing based on artificial intelligence, neural networks, and random forest (Richardson et al. 2023).

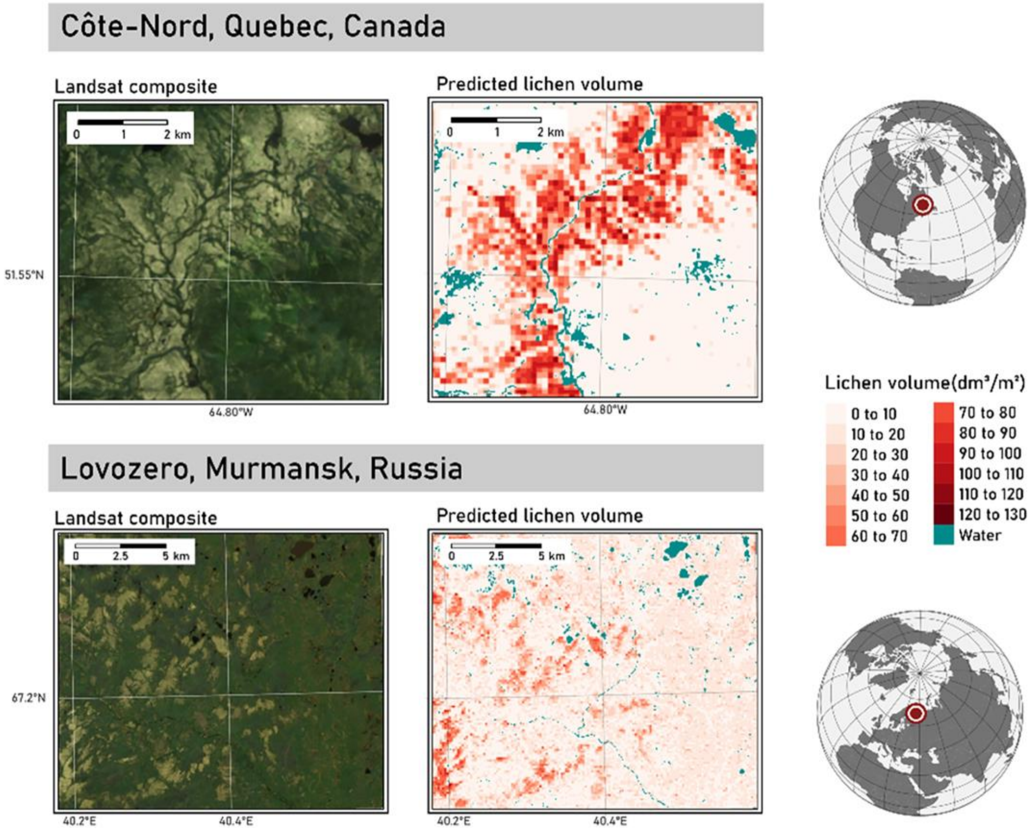

Fig. 7: Lichen volume estimates for sites in Canada and Russia, compared with RGB Landsat imagery. Reproduced from Erlandsson et al. (2022).

Erlandsson et al. (2022) constructed a model based on neural network in the artificial intelligence platform of Peltarion AB, Stockholm, Sweden (Figure 7). For an in-depth description of the modelling construction, see Erlandsson et al. (2022). The final model applied seven Landsat bands (red, green, blue, NIR, SWIR1, SWIR2, TIR), three indices based on the same bands (NDVI, Tucker 1979), normalised difference lichen index (NDLI) (Nordberg and Allard 2002) and a moisture index (MI) (Wilson and Sader 2002), and a locally normalised elevation variable. These bands have been continued throughout the Landsat satellite generations 4, 5, 7, and 8, enabling estimation of historic lichen volumes back to 1982. In training the data, 8,914 field records were used, where the field data collected for Paper I made up a part of this dataset.

Using this method and by limiting the scope of the study to areas with known occurrence of lichen vegetation from ground truthing, accurate estimation of lichen volumes across large spatiotemporal scales are possible. To obtain trends in lichen volumes, satellite imagery between 1984 (when Landsat 5 became operational) and 2020 were used. As the quality of images differs between years, and for the data processing to be manageable, the study period was divided into three focus years: the start in 1984, the intermittent year 2001, and the final year of 2020. Assuming small changes in lichen volumes from year to year, two-year Landsat mosaics (1984-1985, 2001-2002, and 2020-2021) were compiled for each timepoint to ensure sufficient snow- and cloudless coverage. Note that the midpoint was shifted from the actual midpoint of 2002-2003 due to known Landsat sensor quality issues in 2003 (Zhang et al. 2007).

The final model outputs of lichen volumes were compared against available data which could explain the observed trends, namely vegetation type, *Rangifer* population trends, NDVI change, wildfire severity, and change in days with frozen soil. Trends in population numbers of the herds grazing at each study site was compiled from all available sources. Due to the many uncertainties with the population estimates, the population trends were classified as either increasing, decreasing, stable or no reindeer (see Paper II SI). Vegetation type cover and the cover of shrubs and trees were obtained from Copernicus Sentinel classification (Buchhorn et al. 2020). NDVI was obtained as the average trend in July at each site and interval, using the AVHRR GIMMS data consolidated with MODIS NDVI (Li et al. 2023). For fire severity, the change in the normalised burn ration (dNBR) between timepoints was used, calculated using Landsat imagery (López García and Caselles 1991). Lastly, the trends in the ratio of annual days with frozen ground to thawed ground were calculated for each site and interval, from satellite passive microwave remote sensing (Kim et al. 2017).

5 Main results

5.1 *Quantifying the effect of reindeer lichens on surface albedo*

We report a 10-fold variation in surface albedo where biomass of bright, fruticose lichens was the single most important predictor for albedo values. This is in accordance with hypothesis I on the effect vegetation cover has on surface albedo in northern ecosystems. Intact mats of *Cladonia stellaris* had a maximum albedo of 0.389 under clear sky conditions and 60° solar zenith angle (SZA). To our knowledge, this is the highest broadband surface albedo recorded for any naturally occurring vegetated surface.

NDVI was negatively correlated to lichen biomass and weakly negatively correlated with albedo. However, the relationship stated in hypothesis II was not found between carbon flux and albedo. Instead, the instantaneous gross primary production (GPP) rates of moist, well-developed lichen mats were comparable to GPP in dwarf shrub and graminoid tundra. Furthermore, GPP and ecosystem respiration (ER) varied considerably less between plots and vegetation types than albedo.

An ordination analysis revealed that the data set could be structured along two main axes: a latitudinal gradient which explained a shift from moss tundra and corticate lichen tundra towards ecorticate lichens, and a NDVI gradient explaining a shift from NVP vegetation types to forbs and graminoid tundra. The latitudinal gradient covaried with a decrease in max temperature of warmest month and a decrease in albedo. This reduction in albedo was mainly driven by more diverse and darker lichen communities at higher latitudes, while vegetation types dominated by vascular plants had minimal latitudinal variation. The variation in *Rangifer* densities formed a potential third axis, which covaried with soil depth and a shift from woolly moss and corticate lichen vegetation towards shrubs. These relationships and the importance of lichens for vegetation albedo support the final hypothesis, that *Rangifer* herbivore pressure and climate modulate albedo.

5.2 *Estimating current and historic reindeer lichen volumes across the pan-Arctic*

Average lichen volume decreased by 15.3 % between 1984 and 2020, from 18.2 dm^3 m^{-2} (SD = 16.6) to 15.5 dm^3 m^{-2} (SD = 17.1). The trends were negative in 41 % of the study sites, 16 % showed an increase and 43 % had no significant change in lichen volumes. The largest decrease occurred in the sites with the most lichens during the first interval (1984-2001), whereas there was a non-significant decreasing trend in the second interval (2001-2020). Sites in Scandinavia decreased more on average than sites in Russia and Mongolia, while North American sites had intermediate decreases, albeit with the most variation.

Open vegetation, meaning no forest and no shrubs, had higher lichen volumes than shrublands and forests. The lichen volumes were also stable in the open vegetation during the study period, while volumes decreased in shrublands and forest. The decrease was largest in closed needle leaf forest, or taiga, where lichen volumes decreased by 19.7 %.

Rangifer population increase was the best explanatory variable for the decrease in lichens across the whole study period. *Rangifer* population increase was also the best performing variable during the first study interval (1984-2001), while vegetation regrowth after wildfires (negative dNBR) was the best explanatory variable in the second interval (2001-2020). NDVI change was both positively (first interval) and negatively (full period) insignificantly correlated with lichen volume change, while change in the number of days with frozen soil had low predictive power across both intervals.

5.3 Investigating ecophysiological effects of winter heatwaves in lichen vegetation

In winter, the thaw-freeze (TF) experiment stimulated to a gradual increase in photosynthetic activity in *Polytrichum juniperinum* and *Empetrum nigrum* while respiration remained constant, resembling a false spring response and loss of winter hardening. In contrast, the lichens (*Cladonia mitis*, *Cetraria islandica* and *Nephromopsis nivalis*) had constant GPP rates throughout the experimental period, and respiration decreased. After the ice encasement (IE) was completed, these plots had a dense ground-ice layer with thickness between 1 and 10 cm.

Contrary to our first hypothesis, that winter heatwaves would reduce ecophysiological activity and growth in the following summer, no significant effects on lichen ecophysiology were found after the TF events. Furthermore, the IE events had minor negative effects on the lichens, with the most wind-tolerant species *N. nivalis* reducing peak photosynthetic and respiration rates and *C. mitis* reducing peak photosynthetic rate. However, *P. juniperinum*, *E. nigrum* and *Carex bigelowii* Torr. ex Schwein. all had severely reduced photosynthetic efficiency and lowered seasonal growth in both TF and IE treatments. Overall, the vascular plants were more susceptible to IE, and IE led to reduced NDVI, while bryophytes appeared more susceptible to TF. Thus, our second hypothesis, that TF would be more detrimental than IE was only partially confirmed. Our last hypothesis was confirmed for our study species as the lichens were more tolerant to winter heatwaves than bryophytes.

6 Discussion

6.1 Quantifying the effect of reindeer lichens on surface albedo

The cover of bright reindeer lichen was found to be the variable with the largest effect on vegetation albedo in the assessed treeless boreo-arctic vegetation types (Paper I). This contrasts with the lacking and inconsistent representation of lichens and NVPs in Earth System Models (Porada et al. 2023). Including variation in vegetation beyond broad, global plant functional types (e.g. Table 1) can greatly improve representation of vegetation-climate interactions, especially at higher latitudes and altitudes, (Sulman et al. 2021), ecosystems currently not well represented in land surface models. The inclusion of NVPs aligns with the continued improvements to models, remote sensors and data processing which enables more sophisticated representation of the biosphere (Fisher et al. 2018).

In the widely used Community Land Model 5 (CLM5.0, Lawrence et al. 2019), broadband albedo (wavelengths 0.3-3.0 µm) is separated into visible (VIS), i.e., wavelengths below 0.7 µm, and near infrared (NIR), i.e., wavelengths above 0.7 µm (Lawrence et al. 2018). With this categorisation, ultraviolet radiation (UV) between 0.3 and 0.4 µm is included in VIS. Although the fieldwork in 2020 was done with pyranometers measuring global radiation (GR), it is possible to estimate a parametrisation suitable for CLM5.0 using the additional measurements from Finse in 2021 which also included a PAR albedometer recording in the VIS band (measuring photosynthetic active radiation, PAR, in µmol m^{-2} s^{-1}). Keeping in mind the dependence on atmospheric conditions for partitioning incoming radiation into different wavelengths, GR is comprised of about 46 % VIS and 54 % NIR (Zheng et al. 2017). Given that 2.02 µmol m^{-2} s^{-1} PAR equals 1.00 W m^{-2} (Reis and Ribeiro 2020) and by applying the median broadband albedo values for the different vegetation types published in Paper I, it is possible to estimate VIS and NIR albedo of the three main lichen groups (Table 2).

Table 2: Albedo values for three main lichen vegetation types; bright corticate lichen (CL), bright ecorticate lichen (EL), and dark lichen (DL), as mean values, values from Svalbard (Arctic), and the Norwegian mainland (boreal). Albedo values for 60° SZA are included, as global radiation albedo (0.3-3 um), visible albedo (<700 nm), and NIR albedo (>700 nm), for both clear sky and cloudy sky conditions.

	Clear sky			***Cloudy***		
	α_{GR}	α_{VIS}	α_{NIR}	α_{GR}	α_{VIS}	α_{NIR}
CL	0.220	0.127	0.301	0.200	0.123	0.301
EL	0.246	0.142	0.336	0.224	0.138	0.336
DL	0.127	0.052	0.190	0.125	0.052	0.190
Arctic CL	0.209	0.121	0.286	0.190	0.117	0.286
Arctic EL	0.212	0.123	0.290	0.193	0.119	0.290
Arctic DL	0.125	0.052	0.188	0.123	0.052	0.187
Boreal CL	0.253	0.147	0.346	0.231	0.142	0.346
Boreal EL	0.314	0.182	0.429	0.286	0.176	0.401
Boreal DL	0.134	0.055	0.201	0.132	0.055	0.200

A higher albedo during clear sky (Table 2), when there is more direct radiation, is expected in any uneven and complex surface, as discussed in Paper I. Another external factor leading to differences is water saturation. Lichen mats were slightly more water-saturated under cloudy conditions than during clear-sky conditions, and the increase in saturation lead to slightly reduced surface albedo. It is notable that lichens, the bright species in particular, have a higher VIS:NIR ratio than common for plant foliage. This follows from the spectral signature of lichens (Kuusinen et al. 2020), and this is also why NDVI can be used to differentiate between vascular plants and lichens (Erlandsson et al. 2023).

Values collected from Svalbard (Arctic) and the Norwegian mainland (boreal and alpine) are separated in Table 2 due to the generally lower values on Svalbard (see Paper I). Prostate growth forms dominate there, and the bright lichen communities typically grow more intermixed with rocks and dark lichens. As a rule, dark lichen species become more frequent with increasing latitude (Rikkinen 1995), and this was also evident in our data samples (Paper I). The difference was particularly large between ecorticate lichen-type (EL) on Svalbard (where *Cladonia arbuscula* and *C. mitis* are the most frequent) and on the mainland (where *C. stellaris* make up most of the biomass). EL had 48 % higher median albedo values on the mainland than on Svalbard, in contrast with the 7 % difference in albedo values of the dark lichen-type (DL) (Table 2). Although the albedo and vegetation composition differ between arctic and boreal representations of the same lichen vegetation types, the reflective properties of the species are constant and the relationship between albedo and biomass of different lichen species were constant across latitudes. In addition to the albedo differences between arctic and boreal EL, the bright EL type represented by *C. stellaris* had generally higher albedo than the bright CL type, typically represented by *Nephromopsis nivalis*. The EL often has higher growth rates and a more boreal distribution than the slower growing CL (den Herder et al. 2003; Solhaug et al. 2024), often found on alpine-arctic bioclimatic zone. The difference between these groups were found to be considerable, and larger than previously thought (Aartsma et al. 2020).

The reduction in bright lichens can accelerate albedo reduction. Especially in the sub-Arctic, transformation from the well-developed EL-vegetation to shrubs can have a considerable effect on the annual surface energy budget (see Paper I). Comparably, vegetation shifts from the lower albedo of lichen vegetation in the high-Arctic have less of an effect on the surface energy balance. In fact, the greening of vegetation can lead to increased albedo if the green foliage replaces dark lichens, BSC and rocks. This is also in agreement with the increasing trend in mid-summer albedo across the Arctic (Plekhanova et al. 2022).

6.2 Estimation of current and historic reindeer lichen volumes across the pan-Arctic

Elevated *Rangifer* grazing was the leading driver of lichen decrease since 1984 (Paper II). While many *Rangifer* populations declined from 2001 to 2020, the recovery was slow after the released herbivore pressure. This can be attributed to increased competition from vascular plants, particularly shrubs and trees, promoted by longer summer growing seasons, as discussed in Paper II. Reduced recovery after herbivory and other disturbances is concerning for the future of lichens as a dominant vegetation component in the boreo-arctic region, and the relationship between *Rangifer* and lichens. *Rangifer* herds will generally follow cyclic fluctuations in population numbers and thus cyclic variation in their herbivore pressure on lichen vegetation (Ferguson et al. 1998; Moen et al. 2022). Failure for the lichens to recover to previous volumes will reduce the potential to support numerous *Rangifer* herds, both for wild and (semi-) domesticated animals.

Winter survival is a key constraint for *Rangifer* population sizes, and the availability of, and access to, reindeer lichens is of utmost importance. Reduction of intact lichen pastures combined with winters when ground-icing and excessive snowfall blocks the access to the remaining lichen resources have already forced reindeer herders in Northern Scandinavia to purchase supplementary feeding for the animals during winter, a practice that is neither traditional nor cheap (Kater and Baxter 2022). Moreover, the dominance of clear-cutting in the forestry industry has led to severely declining abundance of arboreal lichens (traditionally also an important winter forage resource), further exacerbating the need for supplementary feeding (Kivinen et al. 2012). To preserve ecosystems characterized by mat-forming lichens, including all their provisioning and regulating ecosystem services, sustainable management of both *Rangifer* and vegetation is key. With the increased sensibility to damage and slower recovery time in a warmer climate, conservation of areas with intact lichen mats increases in importance.

The results of Paper II indicate that the effects of vegetation greening and climate change will become increasingly more important as regulators of lichen abundance. The rapid change in the Arctic of longer and warmer growing seasons, deeper permafrost thaw, increased VPD and wildfires are expected to contribute to lichens being outcompeted. This applies mostly to forested areas, shrub vegetation, and leesides where winter conditions are not as extreme as on ridges. Lichen abundance on the latter sites, where winter snow cover is irregular and snow depths shallow, would likely continue to be mainly controlled by grazing pressure rather than climate change (as discussed in Paper III).

Northwards range shifts are an alternative for lichens to maintain their bioclimatic niche under increased growth of shrubs and trees (Mallen-Cooper et al. 2023). However, the fast rate of migration to keep an equilibrium may not be realistic. Naturally, migration takes time, with average growth rate of mat-forming reindeer lichens being 4.9 mm yr^{-1}. (McMullin and Rapai 2020). Importantly, early colonisation is characterised by much lower growth rates as the small fragments are vulnerable to desiccation and competition from other species. Instead, actively assisting regeneration of mat-forming lichen ecosystems by transplanting lichen fragments has been suggested as a viable possibility (Rapai et al. 2023). However, this require considerable effort and resources to be successful at scale.

6.3 Investigating ecophysiological effects of winter heatwaves in lichen vegetation

The effects of winter climate change and summer climate change can have opposing effects on vegetation, as shown in Paper III. The low competitiveness of lichens during the summer growing season is in stark contrast with their high resilience to winter heatwaves. It was clear that the effects differed between species and the characteristics of the extreme events. Despite being active during rapid temperature drop from above zero to negative, none of the lichen species suffered persistent damage from the thaw-freeze events (Paper III). The ability of rapid alternation between an activate and a dormant state in synchrony with change in conditions offers a likely explanation for this robustness (Kappen 1993).

The combination of toxic metabolite build-up, carbon depletion and physical damage from intracellular ice likely caused the negative effects of ice encapsulation (IE) in the lichens (Benedict 1991; Bjerke 2011). The three species showed different resilience and ability to recover. *Nephromopsis nivalis,* which has an affinity to the most wind-swept habitats, was the least resilient and the disparity between IE and controls even increased throughout the season. The reduction in both photosynthetic rate and respiration rate suggest damage to both the fungal partner (mycobiont) and the algal partner (photobiont) of *N. nivalis*. The larger effect in late summer may suggest an asynchronous effect on the photobiont and the mycobiont. In comparison, *Cladonia mitis* showed only damaged to the photobiont, and the more snow tolerant *Cetraria islandica* showed no effects of the IE.

These species-specific differences in responses to the different effects of winter heatwaves infers different vegetation response depending on whether changed temperature or precipitation regime dominates. Climate predictions are unequivocal on an increase in heavy precipitation and rain-on-snow events over most of the Arctic (McCrystall et al. 2021). With frequent IE events, one would expect more negative effects on lichens and vascular plants, and reduced carbon uptake in alpine lichen vegetation. Contrastingly, TF dominance will have more severe effects on bryophytes and vascular plants, and likely less impact on carbon cycling in lichen vegetation.

How future winter climate change will change alpine lichen vegetation is also dependent on the topology and the heterogeneous wind deposition of snow (Yu et al. 2022). The effects observed here were considerably smaller than in similar experiments with deeper and more stable winter snow (Bokhorst et al. 2011). Species inhabiting the snow-swept alpine ridges are already adapted to unstable winter snow conditions, and therefore more resilient. Here, winter climate change represents relatively less environmental change than in lee-sides where stable snow cover is the norm (Niittynen et al. 2020).

7 Conclusions

The results from Paper I identify albedo properties to be the principal climate-regulatory function of lichens at high latitudes. The close coupling between lichens and *Rangifer* was explored both in Paper I and Paper II. Elevated *Rangifer* herbivore pressure in Scandinavia at the end of the 20th century was identified as the driver of the largest pan-arctic lichen decline during the last 40 years. Paper II also identifies that recent lichen regrowth after herbivory and wildfires has been very slow, likely due to increased competition from green vegetation promoted by longer growing seasons, a deeper active layer, and higher nutrient turnover. Lastly, Paper III documented high resilience in mat-forming lichens against unstable winter weather and snow cover conditions. This study also confirms previous research in showing that a single winter heatwave can have persistent long-term effects on alpine vascular plants. This prove that lichens can maintain competitiveness against vascular plant invasiveness also with increasing climate change. The effects of winter stress are likely to be more important in ridge ecosystems, where winter snow cover is already thinner and more unstable than in protected leesides.

8 Outlook

Lichens have a long history of being used as bioindicators of environmental change. Notably, lichens are susceptible to air pollution, sulphur dioxide in particular, and have been applied in pollution monitoring for more than 100 years (Nash 2008). Due to the wide distribution of lichens and their relatively fast response to environmental change, lichens can also be considered bioindicators for climate change (Aptroot 2009). With the presented distribution maps in Paper II and the response to winter climate change in Paper III, this provides a better foundation for the use of lichens as bioindicators, and to further assess their role in land-atmosphere interactions (Paper I).

Besides their role for surface albedo and carbon cycle, future research should focus on the role of NVPs as contributors to the hydrologic and nitrogen cycles. For example, arboreal lichens considerably increase global precipitation interception (Porada et al. 2018). Furthermore, cyanobacteria and other nitrogen-fixing bacteria are often found in association with NVPs, and this can be an important source of nitrogen mineralisation, especially in at the often nitrogen-limited high latitudes. Not only does this apply to the cyanolichens, which have cyanobacteria as a photobiont, but nitrogen-fixing bacterial communities are also found in association with chlorolichens, including the mat-forming lichens treated in this thesis (Alonso-García and Villarreal 2022). The ecological effects of NVPs on nitrogen cycling is still understudied, but it is likely that they provide a significant contribution to growth of other vegetation that depend on external nitrogen input (Henry and Svoboda 1986; Solheim et al. 2006).

Until recently, the role of lichens and other NVPs in vegetation-climate interactions have received disproportionally less focus than vascular plants, despite the ecological and cultural importance of NVPs at high latitudes. Going forward, a better representation of lichens in model and management frameworks is needed. Central in this work is the development of schemes analogous to plant functional types where the effects lichens and other NVPs have on surface albedo, carbon flux and other ecological and biogeochemical processes. This includes also a better representation of winter processes and how this impact different vegetation (Lambert et al. 2022). Continuing on the lichen volume estimations presented here, there are still considerable improvements to be made on the remote sensing techniques for lichen abundance (Richardson et al. 2023), which will improve the knowledge base.

Finally, to maintain the climate-regulating service and ecosystem function of lichens, increased conservation management actions is called for. The close association between abundance of bright lichen vegetation, *Rangifer* grazing, local and indigenous arctic communities further emphasize the pressing need for targeted management actions in light of environmental change and the observed declines in lichen volumes. The lichen declines add risk of population collapse in *Rangifer* already threatened by climate change, which in turn, will put further pressure on arctic indigenous communities whose livelihoods depend on *Rangifer*.

9 References

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10 Appendix

PAPER I

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Variation in albedo and other vegetation characteristics in non-forested northern ecosystems: the role of lichens and mosses

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Supplementary material for this article is available online

Abstract

Vegetation has a profound impact on climate through complex interactions and feedback loops, where especially regulation of albedo, the ratio of reflected to incoming solar radiation, is important at high latitudes. How vegetation albedo varies along environmental gradients in tundra ecosystems is still not well understood, particularly for ecosystems dominated by nonvascular vegetation. We studied broadband shortwave albedo of open boreal, arctic, and alpine ecosystems over a 2000 km long latitudinal gradient (60° N–79° N) and contrasted this against species composition, vegetation greenness (normalised difference vegetation index—NDVI), momentary ecosystem CO_2 fluxes and reindeer (*Rangifer tarandus*) grazing pressure. High cover of pale terricolous fruticose lichens was the single most important predictor for vegetation albedo, which had a maximum value of 0.389 under clear sky conditions and solar zenith angle 60°. To our knowledge, this is the highest broadband albedo recorded for a vegetated surface. NDVI was negatively correlated to lichen biomass ($r_s = -0.56$), and albedo ($r_s = -0.19$). Gross primary production and ecosystem respiration varied considerably less between plots and vegetation types than albedo. While it is well-known that *Rangifer* affects climate-relevant aboveground biomass, we here show that its regulation of surface albedo in northern ecosystems may also be of high importance for land-atmosphere interactions. The data presented here thus advocate for an increased understanding of the important and complex role of herbivores and lichen cover in climate-vegetation interactions.

1. Introduction

The biosphere is a key component of the climate system (Chapin *et al* 2000, Levis 2010). Terrestrial vegetation impacts albedo (the ratio of reflected to incoming solar radiation), heat and moisture fluxes, and cycling of carbon and nitrogen (Houldcroft *et al* 2009, Keenan *et al* 2016, Lara *et al* 2017, Rydsaa *et al* 2017). Nonvascular photoautotrophs (NVPs), which include bryophytes, lichens and biological soil crusts, sustain about 7% of terrestrial global net primary production and half of the terrestrial nitrogen fixation (Elbert *et al* 2012, Porada *et al* 2023). Locally, NVPs can be the dominant vegetation cover in areas exceeding 1000 km^2 (Johansen and Karlsen 2005, Tømmervik *et al* 2021). Despite this importance for terrestrial ecosystems, NVPs are often overlooked in vegetation-climate interactions and earth system modelling (Shaver and Chapin 1991, Elbert *et al* 2012, Wullschleger *et al* 2014, Porada *et al* 2023).

The importance of NVPs for terrestrial ecosystems generally increases poleward. Here, the effect of vegetation on surface albedo is particularly important for land-atmosphere interactions (Eugster *et al* 2000, Chapin 2005). For example, the warming effect of lowered albedo may outweigh the cooling effect of increased biomass as forest expands into tundra (de Wit *et al* 2014).

Pale fruticose ground lichens (shrubby growth form) have distinguishingly high albedo and can cover substantial areas (Davies 1963, Petzold and Rencz 1975, Beringer *et al* 2005, Reinhardt *et al* 2021), but research is needed to assess the influence of lichens on the surface energy balance on large scale and how this relationship may change with environmental factors (Bjordal 2018, Aartsma *et al* 2021, Mallen-Cooper *et al* 2021). A better understanding is also warranted by current declining trends of fruticose lichens (Joly *et al* 2009, Fraser *et al* 2014, Maliniemi *et al* 2018).

The most common fruticose lichens are important winter forage for reindeer (*Rangifer tarandus*) and susceptible to trampling damage in summer (van der Wal *et al* 2001, Tømmervik *et al* 2012, Ricca *et al* 2016). Indeed, the selective feeding, trampling and fertilisation from wild and domesticated reindeer shape vegetation and soil throughout the circumarctic region (Rickbeil *et al* 2015, Tuomi *et al* 2021, Stark *et al* 2023). The influence of reindeer on vegetation can hence strongly modify the climate-vegetation interactions of non-forested vegetation types in boreal, alpine, and Arctic areas (Maliniemi *et al* 2018, Post *et al* 2021, Dearborn and Danby 2022), including changes in albedo (te Beest *et al* 2016) and photosynthetic biomass (Ylänne *et al* 2018). As most reindeer in Eurasia are herded by Sámi and other indigenous arctic people, the interactions between vegetation, climate and reindeer are also essential for the livelihood of the reindeer herders (Tyler *et al* 2021).

In this study, we compare broadband shortwave albedo characteristics from high-latitude treeless habitats, paying particular attention to similarities and differences between habitats naturally rich in NVPs (lichens and bryophytes) and dominated by short-stature vascular plants (VP). We associate these characteristics with vegetation greenness (normalised difference vegetation index—NDVI), momentary ecosystem CO_2 fluxes and environmental properties including soil depth, local climate (i.e. temperature, precipitation), and reindeer grazing intensity. We hypothesize that: (1) vegetation cover is a strong regulator of albedo in northern non-forested ecosystems, mediated by pale lichen abundance; (2) vegetation albedo is inversely related to biomass and carbon flux in our study area, describing a gradient from NVP-dominated to VP-dominated vegetation; and (3) reindeer grazing intensity and climate modulate vegetation albedo.

2. Methods

2.1. Study sites

To capture the gradients in environmental variables, field plots were distributed across Norway including Svalbard, covering a north-south gradient of 2000 km (19 latitudinal degrees), a west-east gradient of 700 km (18 longitudinal degrees) and an elevation gradient from sea level to 1200 m a.s.l. (figure 1, see figure S1 and table S2 for additional information). Only sites with non-forested vegetation were included in the analyses, from climatically controlled non-forested ecosystems in arctic and alpine environments, to open landscapes shaped by historic land use (grazing, logging) or soil conditions.

2.2. Vegetation composition and reindeer grazing

Study sites were selected to capture the most widespread arctic-alpine and boreal non-forested, terrestrial vegetation types (table 1). The vegetation classification builds on the Norwegian vegetation classification systems, including the EcoSyst framework (Halvorsen *et al* 2020), but broadened to be applicable on large spatial scales and to include albedo differences. We differentiated between lichen vegetation dominated by three functional groups, pale ecorticate species (podetia without cortex, abbreviated EL), pale corticate (with cortex, CL) and dark species (DL). Meadow type vegetation was assigned to 'forbs and graminoids' (FG), and vegetation dominated by low-growth, deciduous shrubs and/or evergreen prostate shrubs was assigned to 'shrubs' (SH). Bryophyte rich vegetation was separated in green moss tundra (GM) and vegetation dominated by woolly mosses (*Racomitrium* spp.) (WM). Plots characterised by mechanically removed vegetation (by trampling or other disturbances) were classified as 'disturbed vegetation' (DV).

Species composition and biomass were assessed in the centre of the field plots using the point intercept (PI) method (Bråthen and Hagberg 2004). A metal rod (dia. 5 mm) was dropped $\geqslant$66 times inside a 30 cm × 30 cm frame placed in the centre of the field plots. Any vegetation structure touching the rod was recorded as one hit. Species identified in the frame but not hit were assigned a value of 0.1. Additionally, a relationship between PI measurements of *Cladonia stellaris* and biomass (g m^{-2}) was established experimentally (figure S2).

Information on reindeer densities (individuals km^{-2}) and seasonal use for domesticated reindeer areas in mainland Norway was retrieved from the Norwegian Agriculture Agency (2020). Reindeer densities in the rangelands of wild populations were extracted from assessments by Jordhøy *et al* (2010) and Strand *et al* (2015) (southern Norway) and from Le Moullec *et al* (2019) and Pedersen *et al* (2019) (Svalbard).

2.3. Albedo

We measured shortwave broadband albedo (wavelength 0.3–3 μm) using an albedometer consisting of two pyranometers (CMP11, Kipp & Zonen B.V., Delft, Netherlands) mounted back-to-back. The albedometer was mounted to an aluminium tube protruding 1.5 m horizontally out from a monopod towards the solar azimuthal position and stabilised by a person during measurements.

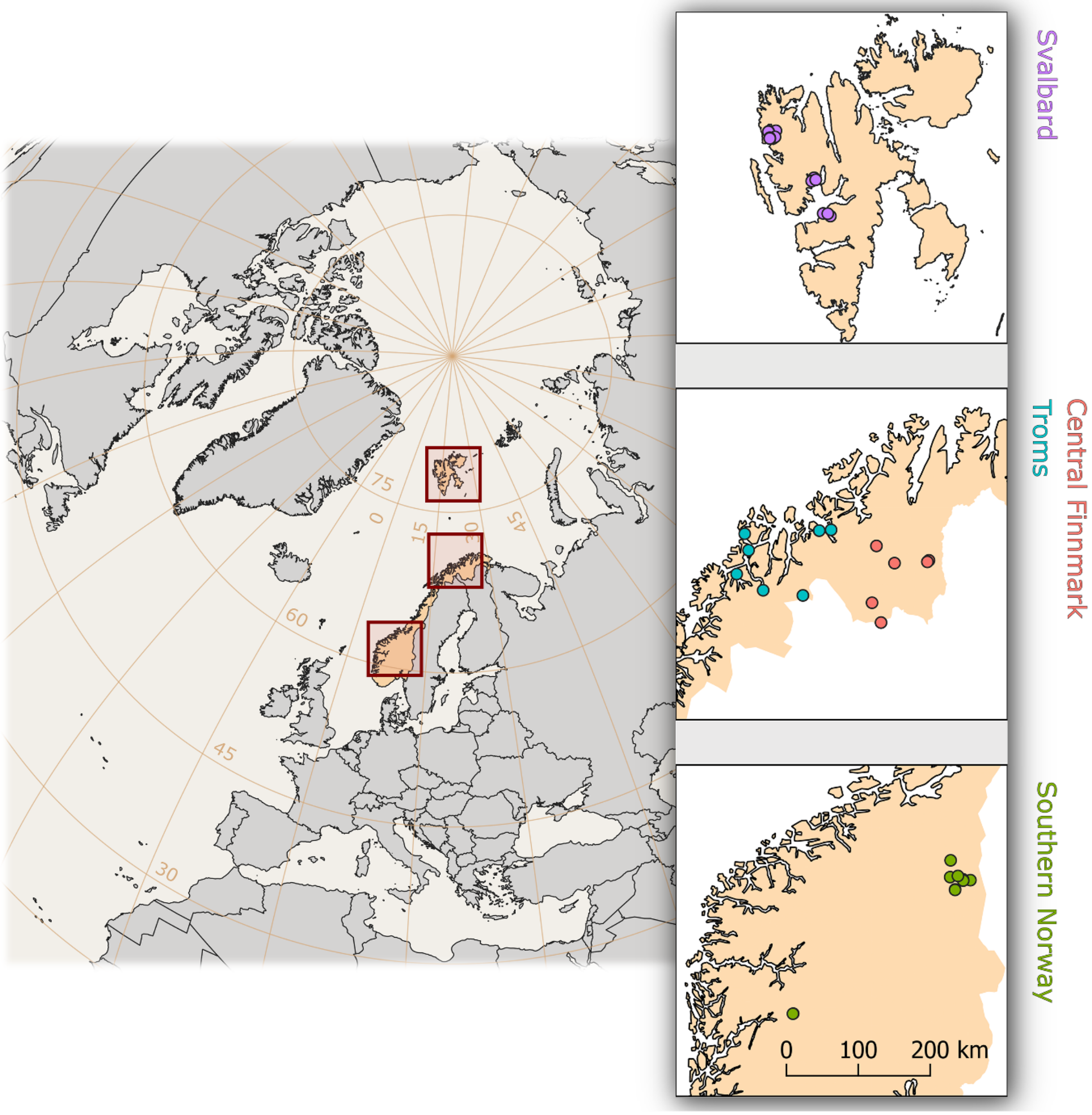

Figure 1. Overview map of field plots classified to four focal areas; Svalbard (purple), Central Finnmark (red), Troms (blue) and southern Norway (green).

Measurements from the upward- and downward-facing pyranometers were simultaneously recorded every 2 s, for at least 1 min (LOGBOX SE, Kipp & Zonen B.V., Delft, Netherlands). For each albedo measurement, a 20 s. running standard deviation (s.d.) was calculated and the most stable measurement period of 20 s. (i.e. the period with the lowest s.d.) was kept for further analyses. The influence of cloudiness and solar zenith angles (SZA) during sampling were corrected for as described in SI (c), and the presented albedo values represents clear sky conditions and 60° SZA.

The sampling footprint size depends on the measuring height and the instrument's field of view (FOV), following equation (1) (Levy *et al* 2018):

$$\text{Footprint diameter} = 2^{*}\text{height} \times \tan \times (\text{effective half FOV}). \quad (1)$$

FOV of the downward-facing pyranometer is 170°, and we sampled albedo from 0.5 m above the vegetation, giving a footprint with a diameter of 11.4 m and an area of 100 m^2. However, 50% of the sampled footprint equates to the inner 0.7 m^2 (FOV of 85°), as the relative contribution from vegetation quickly diminishes towards the periphery of the footprint. Furthermore, the effect of varying footprint sizes on the measured albedo was assessed by resampling at three additional heights: 0.3, 1.0, and 1.5 m (footprints from 37 to 920 m^2).

2.4. Albedo effect on the radiation budget

Hourly data on shortwave radiation were downloaded from four stations that overlaps with the study area. These are: Finse, Hisåsen, Iškoras and Adventdalen. (table S1). Average daily net shortwave radiation (SZA less than 80°) in the snow-free period

Table 1. Overview of vegetation types, their characteristic species, and the number of plots where these vegetation types occurred. BSC = biological soil crust. * = includes 3 plots lacking albedo measurements. ** = NDVI measurements not included.

No	Type	Description	Common species	Number of plots
EL	Ecorticate light-coloured lichens	Lichen tundra dominated by pale ecorticate fruticose lichens	Boreal, alpine *Cladonia arbuscula* *C. stellaris* Arctic *C. mitis*	20*
CL	Corticate light-coloured lichens	Lichen tundra dominated by pale corticate fruticose lichens	Boreal, alpine *Nephromopsis nivalis* *Alectoria ochroleuca* Arctic *N. nivalis*	16
DL	Dark lichens	Lichen tundra dominated by melanic fruticose lichens or BSC	Boreal, alpine *Cladonia gracilis* *Cetraria islandica* BSC Arctic *Cetrariella delisei* *Cladonia rangiferina* BSC	19
GM	Green Mosses	Dark green to dark brown moss tundra	Boreal, alpine *Polytrichum juniperinum* *P. piliferum* Arctic *Dicranum* spp. *Sanionia uncinata* *P. juniperinum*	15
WM	Woolly mosses	Colour-variable moss tundra dominated by species of *Racomitrium* which are light grey when dry and dark green when moist	Boreal, alpine *Racomitrium languniosum* Arctic *R. languniosum* *R. canescens*	19
FG	Forbs and graminoids	Strongly green graminoid-dominated tundra intermixed with forbs	Boreal, alpine *Luzula multiflora* Arctic *Dupontia fisheri*	14
SH	Shrubs	Green shrub tundra, dominated by deciduous, evergreen and/or semi-evergreen shrub species	Boreal, alpine *Betula nana* *Calluna vulgaris* *Empetrum nigrum* Arctic *Salix polaris* *Cassiope tetragona* *Dryas octopetala*	29
DV	Disturbed	Vegetation damaged from mechanical disturbances. Bare soil and exposed rocks	NA	4**

from 25 June to 26 September 2020 were budgeted for the common vegetation types identified in the vicinity of each station, using the observed albedo values and the same adjustments for cloudiness and SZA as described in SI (c).

2.5. NDVI and CO$_2$-flux

NDVI is a spectral vegetation index positively correlated with increasing green biomass (Tucker 1979, Myneni *et al* 1997, Raynolds *et al* 2012). NDVI was measured in the field with the active handheld GreenSeeker crop sensor (91500-00, Trimble Inc., Sunnyvale, California). The sensor emits and record light in wavelengths 660 ± 12 nm (red) and 770 ± 12 nm (near-infrared, NIR), and NDVI is calculated as (NIR-red)/(red + NIR). An average NDVI value for each plot was obtained by sweeping the instrument 1 m horizontally at 1 m above the ground, across the centre of the plot (Erlandsson *et al* 2023). The footprint of the sweeping average can be considered 0.8 m^2 according to the manufacturer's instructions. Brown, bare soil may display high NDVI values (Montandon and Small 2008) and plots with a considerable cover of bare soil (DV plots) were excluded from the NDVI analysis.

CO_2 flux was measured with an infrared gas analyser (EGM-4, PP Systems, Amesbury, MA, USA), connected to a 20 cm × 20 cm × 20 cm transparent poly-methyl methacrylate chamber. A collar with a plastic skirt weighted down with rock or chains was used to limit airflow between the chamber and the ground following standardised procedures (Bokhorst *et al* 2018). CO_2 concentrations were recorded at 10 s intervals for 2 min, first in ambient light, and subsequently in dark conditions. Photosynthetic active radiation (PAR), vapor pressure inside the chamber (mb), and air temperature both inside and outside the chamber were recorded simultaneously. A linear regression line was fitted to each light and dark measurement. For regressions with P-value less than 0.05 (Welch's t-test), the change in CO_2 concentrations (ppm s^{-1}) was used to calculate CO_2 assimilation rates following the methods and equations provided in the operators' manual (Doyle 2012). Otherwise, CO_2 flux was set to 0. Flux rates were square-root transformed to reduce heteroskedasticity and non-normality.

2.6. Statistical analyses

All analyses were done in the R environment (R Core Team 2022). Tukey's Honest Significant Difference test was used for multiple comparisons of vegetation type means of albedo, NDVI and CO_2-flux based on a studentised range distribution, using the R-package 'agricolae' (Mendiburu 2021). The point-intercept species data were visualised in a Non-Metric Multidimensional Scaling (NMDS) ordination diagram as there were considerable outliers and skewness in the data. NMDS utilises a rank-based dissimilarity method (Oksanen *et al* 2019). Ordination was constructed using 'metaMDS' with a square-root data transformation from the R package 'vegan' (Oksanen *et al* 2019). Euclidian distance was used as the dissimilarity index after an assessment with the 'rankindex' function. However, different indices were tested in both ordinations to reveal any incongruences. Ellipses around the mean position of sites for each vegetation type were drawn using 'veganCovEllipse' (Oksanen *et al* 2019), where the ellipse shapes depend on the covariation within sites with the corresponding vegetation type. Environmental variables were fitted to the ordination diagrams using the 'envfit' function. This included bioclimatic variables (1970–2000 at 30 arcsecond resolution, Fick and Hijmans 2017), aspect, slope and topographic position index (TPI) derived from digital elevation models provided by the Norwegian Polar Institute (Svalbard, 20 m resolution) and the Norwegian Mapping Authority (mainland Norway, 20 m resolution). Stress values in the different dimensions and Shepard diagram of ordination distances against original dissimilarities were used for ordination diagnostics.

3. Results

3.1. Albedo

Albedo values ranged from 0.036 in the dark lichens (DL) vegetation type to 0.389 in pale ecorticate lichens (EL) (figure 2). On average, EL had 20.5% higher albedo than pale corticate lichens (CL) (0.264 ± 0.066 and 0.210 ± 0.045, respectively; t-test, $t_{29.8} = 2.88$, $P = 0.007$). Furthermore, there was a positive relationship between albedo and biomass for both EL species ($r_s = 0.69$, $P < 0.001$, $n = 64$) and CL species ($r_s = 0.37$, $P < 0.001$, $n = 79$), estimated from the point-intercept (PI) analysis (figure 2). The relationship with albedo was more robust for EL than CL, and the difference between the linear regression coefficients of these relationships was significant (ANCOVA, $F_{1,139} = 3.969$, $P = 0.048$). In contrast, DL biomass showed a weak, negative correlation with albedo (figure 2, $r_s = -0.3$, $P = 0.002$, $n = 106$). The PI estimated lichen biomass of EL was converted to actual dry weight (see SI for details), rendering a linear relationship between albedo and EL biomass where albedo $= 0.16 + 0.13^*$(kg m^{-2} dry EL lichen biomass).

EL plots were recorded with up to 97% cover of *Cladonia stellaris*, while plots with CL dominance had at least 33% of other species, in particular DL species (e.g. *Alectoria nigricans* and *Cetraria islandica*) and dark bryophytes (e.g. *Polytrichum* spp. and *Ptilidium ciliare*). Extrapolating the regressions to 100% cover of EL, CL and DL lichens gives theoretical albedo values of 0.34, 0.30 and 0.06, respectively (figure S4).

There were no significant differences in mean albedo values among the vegetation types dominated by VPs and bryophytes (figure 2). However, 2 woolly moss plots in Troms with very dry and homogenous *Racomitrium lanuginosum* mats displayed notably high albedo (0.293 and 0.227). Contrastingly, woolly moss plots from Svalbard had a mean albedo of 0.143 ± 0.029 ($n = 14$).

Shortwave radiation absorption was 15.6% and 16.0% higher for dwarf shrub than pale ecorticate lichens at Hisåsen (southern Norway) and Iškoras (Central Finnmark), respectively, representing differences of 1.61 and 1.28 MJ m^{-2} d^{-1} in radiative forcing (figure 3). Green moss tundra was 8.5% higher than corticate lichen at Finse (southern Norway) and 6.4% higher in Adventdalen (Svalbard), while the radiative forcing differences were 0.98 and 0.44 MJ m^{-2} d^{-1}, respectively. Differences between e.g. dark lichens and woolly mosses, or shrubs and forbs and graminoids were not significant (figure 3).

Generally, albedo from the four differently sized footprints showed a slight increase in variability with smaller size (figure S5). Overcast and clear sky albedo differed distinctly during the continuous albedo measurements at Finse (figure S3). In comparison to clear sky conditions at 60° SZA, albedo

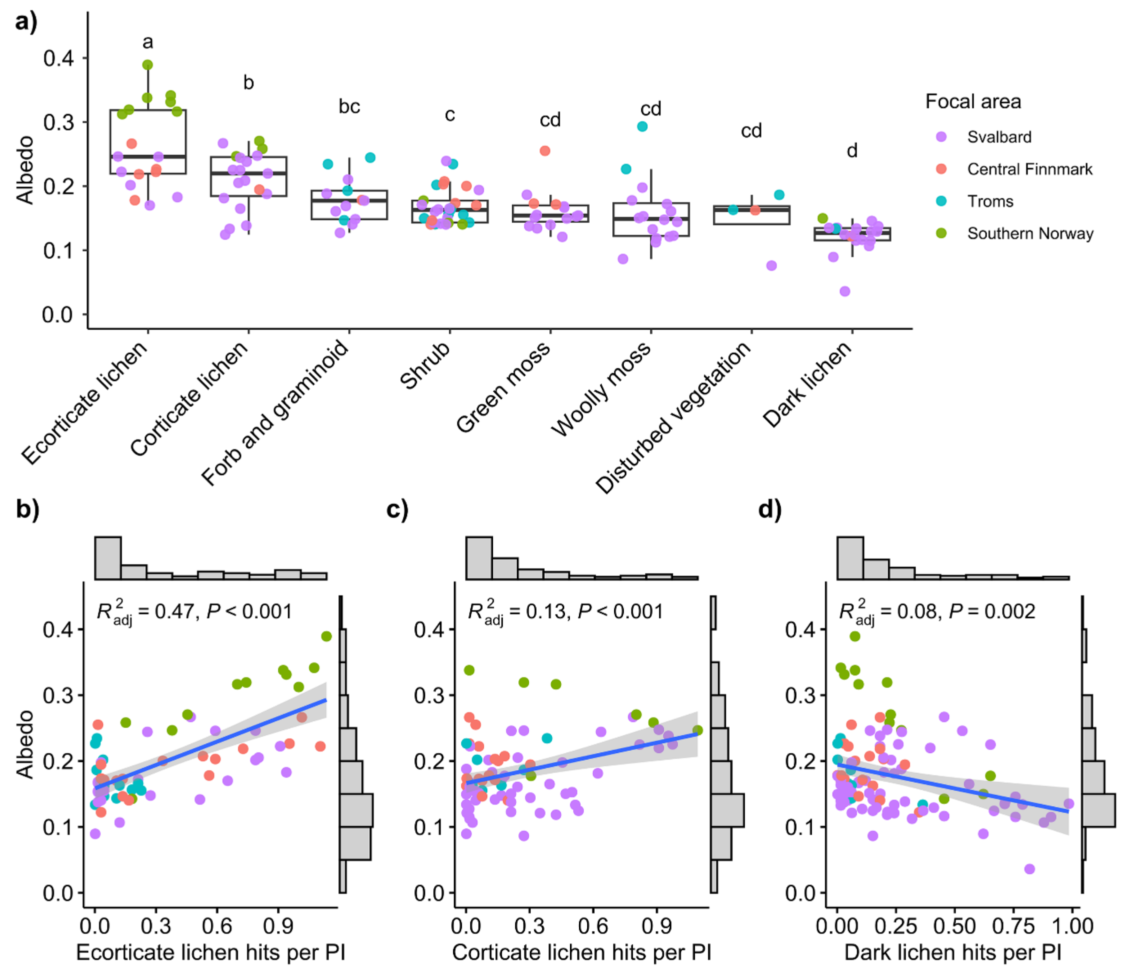

Figure 2. (a) Albedo characteristics of the vegetation types studied (see table 1 for full type names). The boxplots display the range from the first to the third quartile with mean value as the horizontal line, and the minimum and maximum values excluding outliers as the length of the whiskers. Each scatter point represents a field plot, and the colours indicate the focal area of each plot (see legend). Letters above boxes indicate significant differences between vegetation types. (b)–(c) Plot-level albedo explained by the ratio of point-intercept (PI) hits on lichen species to the total number of intercepts for the three lichen groups. (b) EL (pale ecorticate lichens), (c) CL (pale corticate lichens), and (d) DL (dark lichens). Species included in this analysis are the EL species *Cladonia arbuscula* and *C. stellaris*, the CL species *Alectoria ochroleuca, C. uncialis, Nephromopsis cucullata* and *N. nivalis*, and the DL species *A. nigricans, Bryocaulon divergens, Cetraria aculeata, Cet. islandica, Cet. ericetorum, Cetrariella delisei, C. gracilis, C. rangiferina* and *C. stygia*, as well as dark biological soil crust (BSC) species. Density distribution of plots are shown on the margins.

decreased by 7% under partly cloudy conditions and 9% at full overcast.

3.2. NDVI and CO_2 flux

The highest recorded rates of gross primary production (GPP) were from forbs and graminoids-dominated plots (FG), which averaged significantly higher than shrubs, corticate and dark lichens, and woolly mosses vegetation types (figure 4). Most plots dominated by NVPs had comparably lower rates at the time of sampling (figure 4), although fluxes in certain ecorticate lichen plots (EL) were comparable to FG-plots under optimal conditions. Vegetation moisture, as relative humidity inside the CO_2 chamber, had a slight positive correlation with GPP in lichen dominated plots (lm, R^2 *adj.* $= 0.23$, $P = 0.020$, figure S6). Ambient PAR during measurement was a poor predictor of flux rates, both in lichen dominated plots (lm, R^2 *adj.* $= 0$, $P = 0.386$) and across all plots (lm, R^2 *adj.* $= 0.03$, $P = 0.060$). The variation in ecosystem respiration (ER) behaved similarly to GPP, but there was a larger discrepancy between ER rates in FG and EL. Woolly mosses had also significantly lower ER values than green mosses plots, while this was non-significant for GPP. Both GPP and ER increased with abundance of green VPs and mosses, however there was no relationship with abundance of lichens (figure 4). Thus, albedo was poorly correlated to GPP and ER ($r_s = 0.16$, $P = 0.147$ and $r_s = 0.08$, $P = 0.504$ respectively, figure S7).

In congruence with the CO_2 flux rates, plots dominated by green vegetation had the highest NDVI values, where the three 'green vegetation types' FG, SH and GM had significantly higher values than

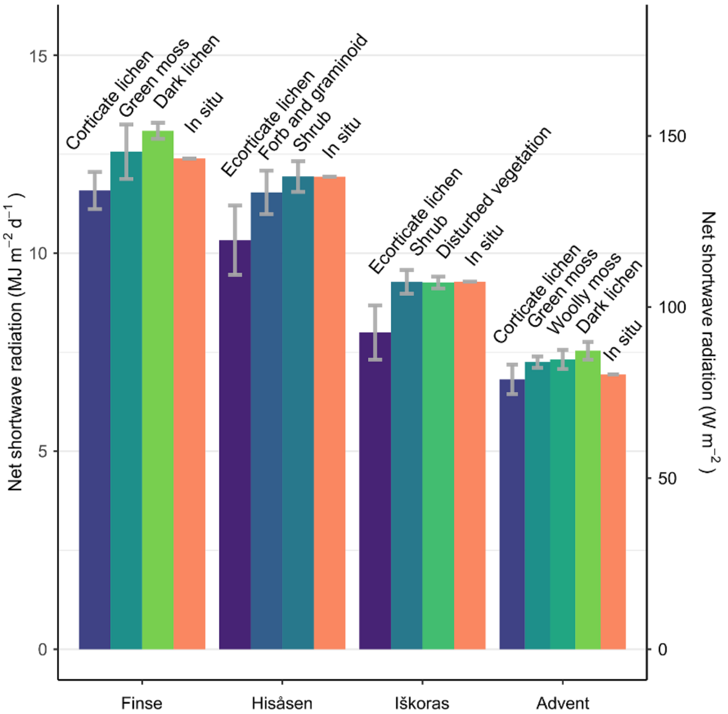

Figure 3. Average daily net shortwave radiation (solar zenith angle less than 80°) in the snow-free period from 25 June to 26 September 2020 at four sites with solar radiation measurements (orange bars) and potential net radiation given the albedo of the studied vegetation types that are native to each station (bars with blue to green colours). The error bars correspond the standard deviation in albedo for each vegetation type. The sites Finse and Hisåsen are located in the southern Norwegian focal area, Iškoras in the focal area Troms and Central Finnmark, and Adventdalen (in the figure abbreviated to 'Advent') is in the focal area Svalbard.

WM and the lichen vegetation types DL, EL and CL (figure 4). Across all vegetation types, higher NDVI values were strongly correlated with increased abundance of green plants (figure 4). In contrast, NDVI was negatively correlated with increased biomass of EL, CL and DL species ($r_s = -0.56, P < 0.001, n = 96$, figure 4). This contributed to a weak negative correlation between albedo and NDVI ($r_s = -0.19$, $p = 0.034$, figure S7).

3.3. Variation along environmental gradients

The NMDS ordination of species PI data (figure 5) revealed several structures in the dataset. Woolly mosses, corticate and ecorticate lichen vegetation types showed separation from a cluster consisting of green mosses, dark lichens, shrubs, forbs and graminoids, with the first group being predominantly reindeer winter pastures and year-round sites with low reindeer grazing pressure, and the second group mainly year-round and spring-summer pastures with more grazing. The bioclimatic variables that showed the best fit to the ordination, while not being strongly correlated, were BIO2 (mean diurnal air temperature range), BIO5 (max temperature of warmest month), BIO18 (precipitation of warmest quarter), see figure S8. These variables covaried with the latitudinal gradient and a shift from moss vegetation types (WM and GM) towards EL, thus also covarying with increased albedo. High NDVI values covaried with year-round and summer pasture plots with relatively high reindeer densities, particularly forb and graminoid-vegetation. Increasing soil depth and higher reindeer densities were closely associated, and negatively covarying with TPI. Hence, reindeer density had less covariation with albedo. ER was also a significant variable for the distribution in ordination space, mostly associated with increased NDVI and soil depth, while GPP was not (figure S8).

The stress value of the ordination was 0.247, and a Shepard stress plot showed that some of the original dissimilarity is lost in the NDMS (figure S8), thus inferring some caution in the interpretation of the ordination. By adding a third dimension to the diagram, the stress declines to 0.179 (figure S8). However, the 3D ordination did not change the main structure of the diagram nor provided any further insights, and it was generally more complex to interpret.

4. Discussion

We studied vegetation albedo of open boreal, arctic, and alpine ecosystems over a 2000 km long latitudinal gradient and contrasted this against species composition, NDVI, carbon flux and reindeer grazing

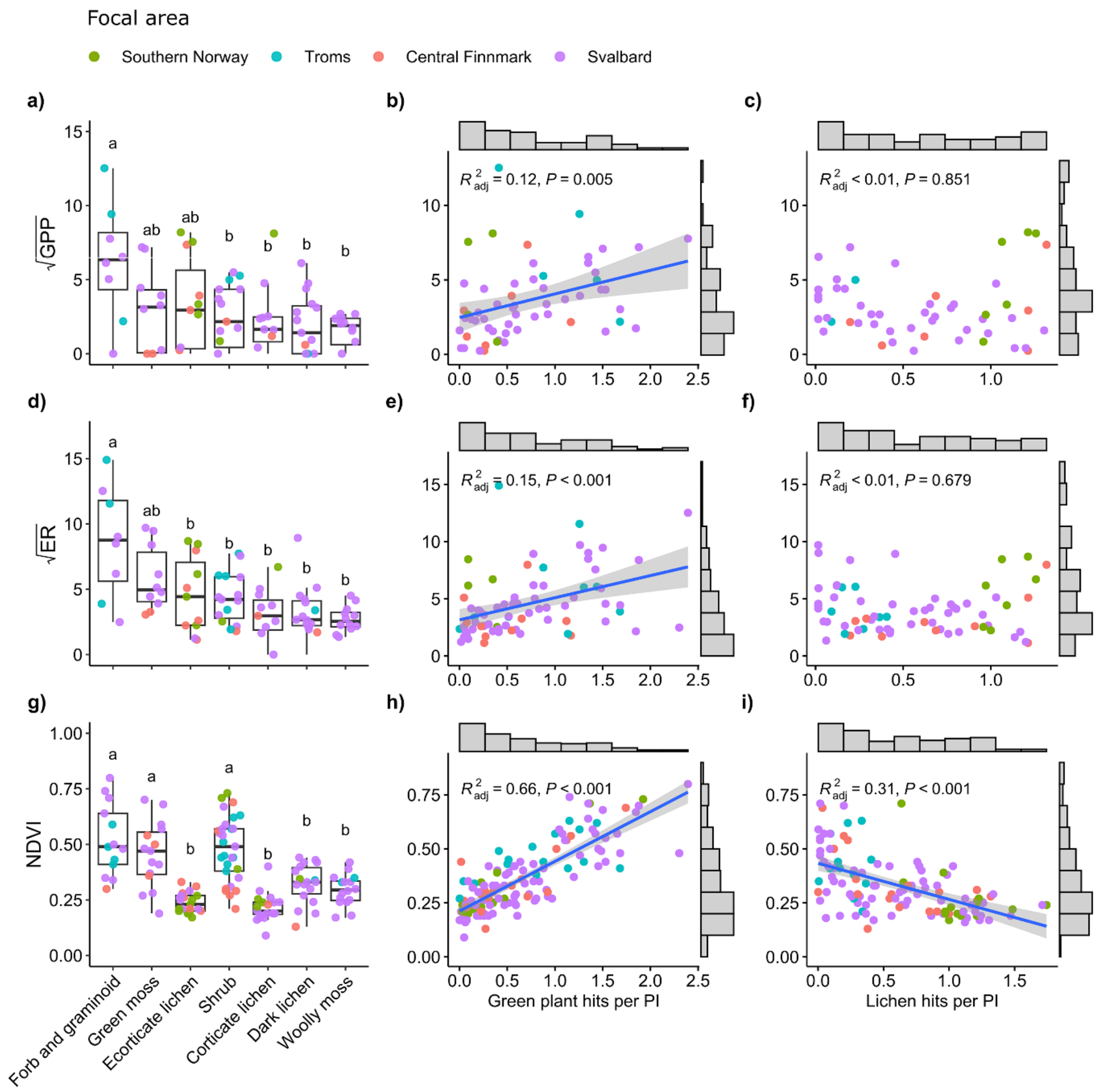

Figure 4. Variation in gross primary productivity ((a)–(b); GPP; mg C m^{-2} h^{-1}), ecosystem respiration ((d)–(f); ER; mg C m^{-2} h^{-1}) and normalized difference vegetation index (g)–(i); NDVI) across all field plots. (a), (d) and (g) displays the variation between and within the studied vegetation types (see table 1 for full names of vegetation types). The boxplots display the range from the first to the third quartile with mean value as the horizontal line, and the minimum and maximum values excluding outliers as the length of the whiskers. Each scatter point represents a field plot, and the colours indicate the focal area of each plot. Small letters above boxes indicate whether there are significant differences between vegetation types and the colours indicate the focal area of each field plot. (b), (e) and (h) show each parameter explained by intercept hits by green plants per point intercept (PI). (c), (f) and (i) show each parameter explained by intercept hits by green plants per point intercept (PI). Density of points are displayed along the axes. For a full species list, see table S2.

pressure. Our study area included a 10-fold variation in albedo where biomass of pale, fruticose lichens was the single most important predictor for albedo values. This confirms hypothesis 1, that vegetation is a strong regulator of albedo. GPP and ER values were generally low, and less variable between green plants and lichen vegetation than albedo. Thus, the negative correlation we observed for albedo and NDVI was not found for carbon flux and albedo, consequently contradicting hypothesis 2 which stated that albedo would be inversely related to biomass and carbon flux. The albedo variation in our study areas could be attributed both to climatic gradients and the gradient in reindeer grazing intensity. This supports hypothesis 3, that reindeer grazing intensity and climate modulate vegetation albedo.

4.1. Albedo characteristics of different vegetation

Broadband albedo values from plots dominated by pale lichens reached a maximum value of 0.389, possibly the highest recorded value for any naturally occurring vegetated ground. The maximum albedo was observed in a balanced winter grazing pasture for semi-domestic reindeer in southern Norway (Lyftingsmo 1974, Tømmervik *et al* 2021), and is slightly higher than 0.371 reported by Aartsma *et al* (2020) from an experimental setup with an idealised lichen mat. To our knowledge, the previously

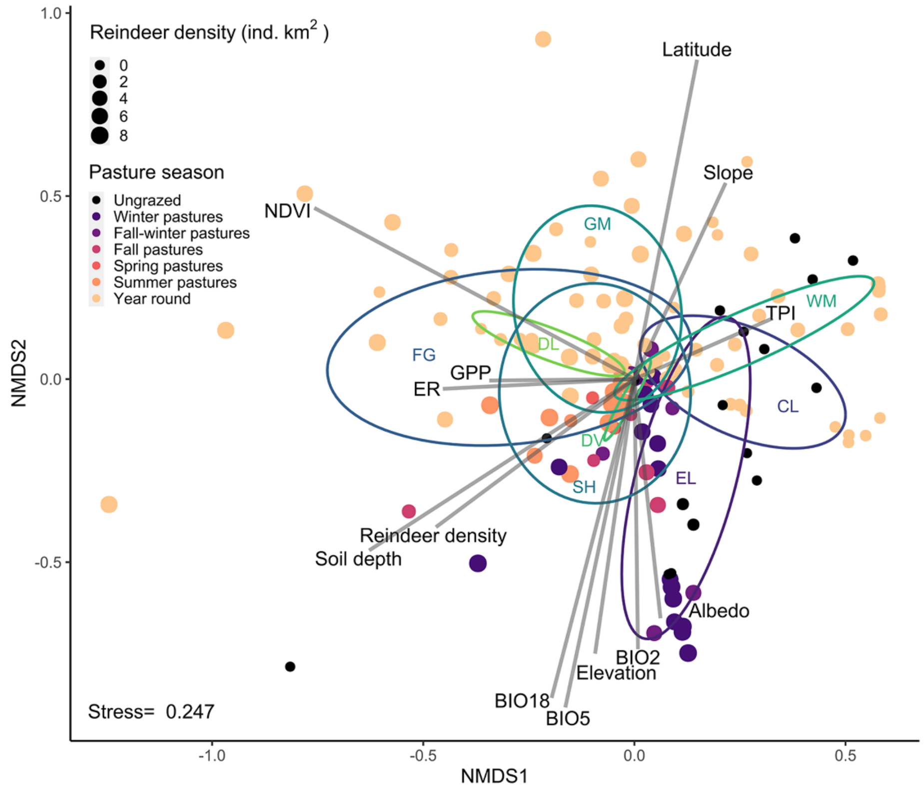

Figure 5. Non-metric multidimensional scaling (NMDS) diagram (Euclidean distance) depicting dissimilarity in species composition in the field plots. The point size of each field plot corresponds to reindeer density (number of individuals per km^2), and the colour refer to pasture usage as described in the inset legend. Vegetation type means are shown as ellipse centroids, and the shape of the ellipsoids is defined by the covariance within each vegetation type: green mosses (GM, blue-green), woolly mosses (WM, dark green), pale corticate lichens (CL, dark blue), pale ecorticate lichens (EL, purple), shrubs (SH, blue-green), forbs and graminoids (FG, blue), dark lichens (DL, light green) and disturbed (DV, green). The vectors point towards increased value of the variables soil depth, elevation, latitude, topographic position index (TPI), normalized difference vegetation index (NDVI), gross primary production (GPP), ecosystem respiration (ER) and albedo, as well as the BIOCLIM variables BIO2 (mean diurnal air temperature range), BIO5 (max temperature of warmest month), BIO18 (precipitation of warmest quarter).

highest albedo value of lichen dominated vegetation measured in unmanipulated plots in the field is 0.31 (Peltoniemi *et al* 2010).

We distinguished between pale corticate (CL) and pale ecorticate lichens (EL), where plots dominated by EL had, on average, higher albedo than the CL-dominated plots. This contrasts to Aartsma *et al* (2020) who concluded that the albedo difference between these two lichen groups were negligible. Although the species-wise albedo may be largely equivalent, the CL species included in our study (predominantly *Alectoria ochroleuca, Nephromopsis nivalis* and *N. cucullata*) are generally found in more exposed habitats than the EL species (predominantly *Cladonia stellaris* and *C. arbuscula*) (Hestmark *et al* 2005), and EL mats are generally much thicker and more homogenous than the CL mats. With the large geographical extent of the present study, as compared to that of Aartsma *et al* (2020), we covered more of the ecological gradients where pale lichens occur, and thus included more of the variation in lichen mat characteristics and species composition within these vegetation types.

Dark lichens (DL) had the lowest average albedo value of all studied vegetation types, although it did not differ from green moss tundra (GM) and woolly mosses (WM). The dark colour of DL is often attributed as an adaption to cold climates as it increases solar heat absorption and makes it possible for the lichens to drive photosynthesis even in late winter and early spring, e.g. in CO_2-rich air pockets under a thawing shallow snow cover (Sonesson 1989, Rikkinen 1995). However, DL rarely dominates the landscape in the same way as pale lichen vegetation does, and DL is often confined to areas where wind-transported snow accumulates (Bidussi *et al* 2016). Compared to EL and CL, the importance of DL for vegetation-climate interactions is thus small.

The high maximum albedo and the albedo range of woolly mosses stand out compared to other moss- and VP dominated vegetation types. This is largely attributed to the hyaline hair tips of WM that change the colour of the moss from light grey-green in a dry state to dark green when wet (Solheim 1998). In fact, the albedo characteristics of well-developed and dry WM mats approached the albedo of CL vegetation, similar to the values reported by Tanner and Vandewarker (2019). These are also, to the authors knowledge, the highest albedo values reported from bryophyte-dominated vegetation and emphasise the importance of humidity-mediated variability in albedo, e.g. in remotely assessed albedo from areas where WM constitutes an important part of the vegetation.

4.2. Relationships between albedo and other vegetation characteristics

Plots dominated by meadow vegetation were on average the most photosynthetically active, and both GPP and ER showed a weak positive relationship between biomass of green VP and mosses, however there was no correlation between lichen biomass and CO_2 flux rates. The weak relationship between VP and carbon flux rates, and the considerable contribution from NVPs to carbon flux rates, were partly contrary to hypothesis 2. Contrasting environmental conditions largely influence momentary carbon fluxes, both for VP (Street *et al* 2007, Le Moullec *et al* 2020) and NVP vegetation (Uchida *et al* 2006, Street *et al* 2013). As NVPs are poikilohydric (lacking ability to self-regulate water content), they experience peak photosynthesis early and late in the season, and after periods of dewfall or rain (Lange *et al* 1998). Carbon fixation from NVP-dominated vegetation, particularly at the shoulders of the growing season, can contribute significantly to ecosystem NPP (Campioli *et al* 2009). Here, maximal observed NVP photosynthetic rates were 67 and 65 mg C m^{-2} h^{-1} for plots dominated by *Nephromopsis nivalis* and *Cladonia stellaris*, measured when wet from dew or rain. In fact, of the nine plots with highest instantaneous GPP, four were lichen plots, suggesting that NVP vegetation cover under certain conditions can have a carbon uptake that is comparable to arctic and alpine VP vegetation types.

NDVI, as a measure of green biomass, better explained the shift from NVP-dominated to VP-dominated systems than carbon flux rates in our dataset. NDVI was negatively correlated with both albedo and increased lichen biomass, in congruence with previous studies (Nordberg and Allard 2002, Rees *et al* 2004, Erlandsson *et al* 2023). Further, NDVI variability within and between the three lichen types could largely be explained by a combination of differences in vegetation composition and spectral differences (Nelson *et al* 2013, Kuusinen *et al* 2020). By and large, the DL plots had lower lichen biomass and higher biomass of green prostate shrubs and mosses and therefore also higher NDVI than the pale lichen plots CL and EL.

4.3. Albedo characteristics across environmental gradients

The presented data encompass a wide latitudinal gradient and strong gradients in reindeer density and seasonal use. Those factors are known to be important for species distribution and ecosystem characteristics (van der Wal 2006, Lindén *et al* 2021, Simensen *et al* 2021). The temperature gradient was associated with a poleward decrease in albedo. While albedo variation was minimal between focal areas for vegetation types dominated by green plants, ecorticate and corticate lichen plots had the highest albedo values in the southernmost focal area. This was particularly pronounced for the ecorticate lichen vegetation type due to the immense lichen mats of southern Norway focal area, with a near-complete dominance of *Cladonia stellaris*.

Species richness in lichen vegetation types also increased poleward, which is in congruence with the findings of Chagnon *et al* (2021). There are several potential reasons for this pattern. The longer snow season modulates lichen distribution at high altitudes and latitudes (Odland *et al* 2018). At the same time, there is a strong latitudinal gradient in historical and current reindeer grazing impact, with very little to negligible grazing impact in the southernmost focal area (southern Norway), but moderate to high impact in the other focal areas. Lichens subject to a permanent grazing pressure accumulate less biomass and are hampered from developing into near-continuous mats (Gaare 1999, Tømmervik *et al* 2012, Ricca *et al* 2016). Furthermore, arctic winter weather with predominant katabatic winds lead to shallow snow depths at some locations (Førland *et al* 1997), potentially leading to more grazing in winter. Still, light reindeer grazing may even benefit lichens as shrubs and grasses protruding the lichen mats are thinned or grazed down (Lyftingsmo 1974, Andrejev 1977). Overall, these factors contribute to the spatial variation in lichen cover and thickness found in this study.

Grazing effects vary between lichen groups. Increased grazing of corticate lichen dominated areas, on ridges with shallow soil cover, would likely result in a shift towards even shorter vegetation, including increasing abundance of bryophytes, biocrust communities and exposed gravel and rocks (Haapasaari 1988, Øvstedal *et al* 2009, Pushkareva *et al* 2016). In contrast, increased grazing of ecorticate lichen dominated vegetation could promote increased VP vegetation (Nordhagen *et al* 1943, Odland *et al* 2018). The degree to which vegetation albedo affects the surface energy balance depends on latitude and climate. Shifts between a continuous cover of pale ecorticate lichens to shrubs in the boreal regions in the southern parts of the study area may represent the largest change in radiative forcing of the vegetation types assessed here, due to the extreme albedo differences between these two types, the high incoming solar radiation in the boreal, most southerly region (as compared to more northerly study areas), and the vast areas dominated by pale ecorticate lichen vegetation.

5. Concluding remarks

High-latitude environments are changing rapidly, leading to vegetation changes which affect both albedo and carbon dynamics (Rixen *et al* 2022, Yu *et al* 2022). Unravelling interactions and feedbacks between climate, herbivore grazing, and vegetation change becomes imperative to understand vegetation-climate interactions. Until recently, the role of lichens and mosses have been given less focus than VP-dominated vegetation, despite the large surface coverage of NVPs at high northern latitudes. The distinctively high importance of pale lichens for the surface energy balance calls for increased conservation management actions so that these ecosystems can continue to provide their climate-regulating services. The close association between abundance of pale lichen vegetation, reindeer grazing, local and indigenous arctic communities further emphasize the pressing need for targeted management actions, especially considering the pan-Arctic declining trends of lichens.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: 10.6084/m9.figshare.22718404. Data will be available from 1 September 2023.

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E A F, J W B, F S, L M T and H T conceived the study and planned the data collection. E A F, J W B and R E did the fieldwork. E A F analysed the data and wrote the first manuscript. E A F and J W B finalised the manuscript with contributions from all authors.

Conflict of interest

The authors declare that they have no conflict of interest.

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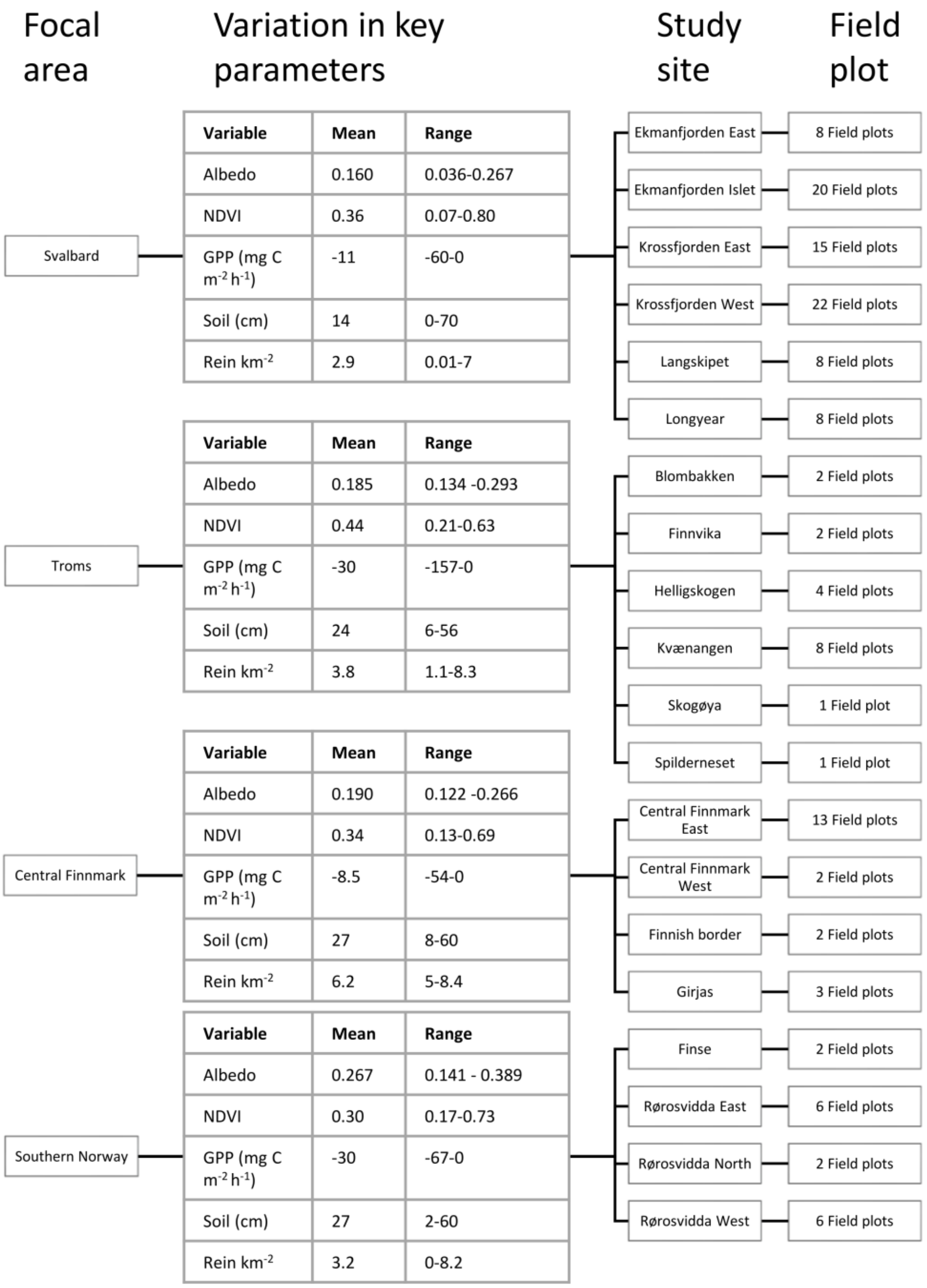
Supporting information (SI).

This supporting information document provides an overview of the following items:

(a) The field plot hierarchy and
(b) a correlation experiment applied to test the relationship between point-intercept data and dry weight biomass of the lichen *Cladonia stellaris*
(c) additional albedo data (diel variation, lichen cover-albedo relationship and variation with albedometer footprint size)
(d) Relationships between GPP, ER, humidity, NDVI and albedo
(e) plots of species abundance supporting the ordination analysis presented in the main document.
(f) Species list of study plots

(a) Field plot characteristics



Svalbard

Variable	Mean	Range
Albedo	0.160	0.036-0.267
NDVI	0.36	0.07-0.80
GPP (mg C $m^{-2} h^{-1}$)	-11	-60-0
Soil (cm)	14	0-70
Rein km^{-2}	2.9	0.01-7

Study site	Field plot
Ekmanfjorden East	8 Field plots
Ekmanfjorden Islet	20 Field plots
Krossfjorden East	15 Field plots
Krossfjorden West	22 Field plots
Langskipet	8 Field plots
Longyear	8 Field plots

Troms

Variable	Mean	Range
Albedo	0.185	0.134 -0.293
NDVI	0.44	0.21-0.63
GPP (mg C $m^{-2} h^{-1}$)	-30	-157-0
Soil (cm)	24	6-56
Rein km^{-2}	3.8	1.1-8.3

Study site	Field plot
Blombakken	2 Field plots
Finnvika	2 Field plots
Helligskogen	4 Field plots
Kvænangen	8 Field plots
Skogøya	1 Field plot
Spilderneset	1 Field plot

Central Finnmark

Variable	Mean	Range
Albedo	0.190	0.122 -0.266
NDVI	0.34	0.13-0.69
GPP (mg C $m^{-2} h^{-1}$)	-8.5	-54-0
Soil (cm)	27	8-60
Rein km^{-2}	6.2	5-8.4

Study site	Field plot
Central Finnmark East	13 Field plots
Central Finnmark West	2 Field plots
Finnish border	2 Field plots
Girjas	3 Field plots

Southern Norway

Variable	Mean	Range
Albedo	0.267	0.141 - 0.389
NDVI	0.30	0.17-0.73
GPP (mg C $m^{-2} h^{-1}$)	-30	-67-0
Soil (cm)	27	2-60
Rein km^{-2}	3.2	0-8.2

Study site	Field plot
Finse	2 Field plots
Rørosvidda East	6 Field plots
Rørosvidda North	2 Field plots
Rørosvidda West	6 Field plots

Figure S1: Field plot hierarchy. Parameters include albedo measured 100cm above ground, normalized to blue sky albedo at SZA 60°, Normalized Difference Vegetation Index (NDVI), measured in a sweeping motion 1 meter above ground, Ecosystem Gross Primary Productivity (g C m^{-2} h^{-1}), soil depth and reindeer density (estimated number of individuals per km^2). “Rein” = Reindeer.

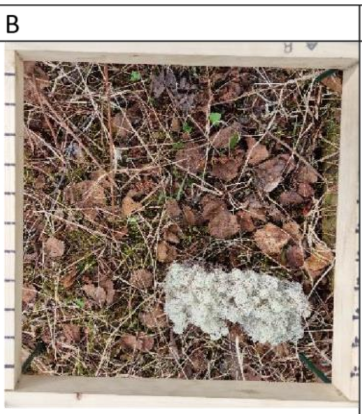
Table S1: Overview of the weather stations used for calculating shortwave radiation budget, including the 30-year climatic norm from 1991 to 2020 (Tveito 2021).

Station	**Focal area**	**Coordinates (Lat, long)**	**Vegetation**	**m.a.s.l.**	**Annual mean temperature (°C)**	**Annual precipitation (mm)**	**Owner**
Hisåsen	Southern Norway	61.11,12.26	Drained peatland regrown with dwarf birch (*Betula nana*).	680	+2.7	530	University of Oslo (UiO)
Finse	Southern Norway	60.59,07.52	Corticate lichen heath intermixed with shrub and graminoid heathlands and snow-beds dominated by dark lichens and mosses	1200	-1.1	970	UiO
Iškoras	Troms/Central Finnmark	69.34,25.30	Palsa mire consisting of a mosaic of dry fen and partly vegetated ponds.	591	-1.6	359	UiO
Adventdalen	Svalbard	78.25,15.49	Fluvial silt and finer sediments partially covered by graminoid and moss tundra	28	-3.9	220	The University Centre in Svalbard (UNIS)

(b) Estimating biomass from point intercept (PI) analysis

PI data are widely used to estimate vegetation biomass (Jonasson 1988, Röttgermann *et al* 2000). Still, to our knowledge, no relationship has been established for lichen biomass and point-intercept hits under variable water content. Moen *et al* (2007) showed regressions of lichen biomass against mean thallus height and volume on monocultures of four *Cladonia* species but did not state whether these measurements were done on dry or wetted lichens. We conducted a small experimental test where PI hits and lichen dry weight were measured at intervals of 100, 75, 50, 40, 30, 20, 10 and 0 % cover of the fruticose lichen *Cladonia stellaris*. Three replicates were made for lichens in water-saturated and dry state conditions (Figure S2).

a)

(%)	A	B	C
10			
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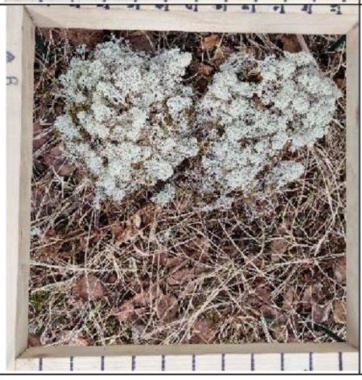
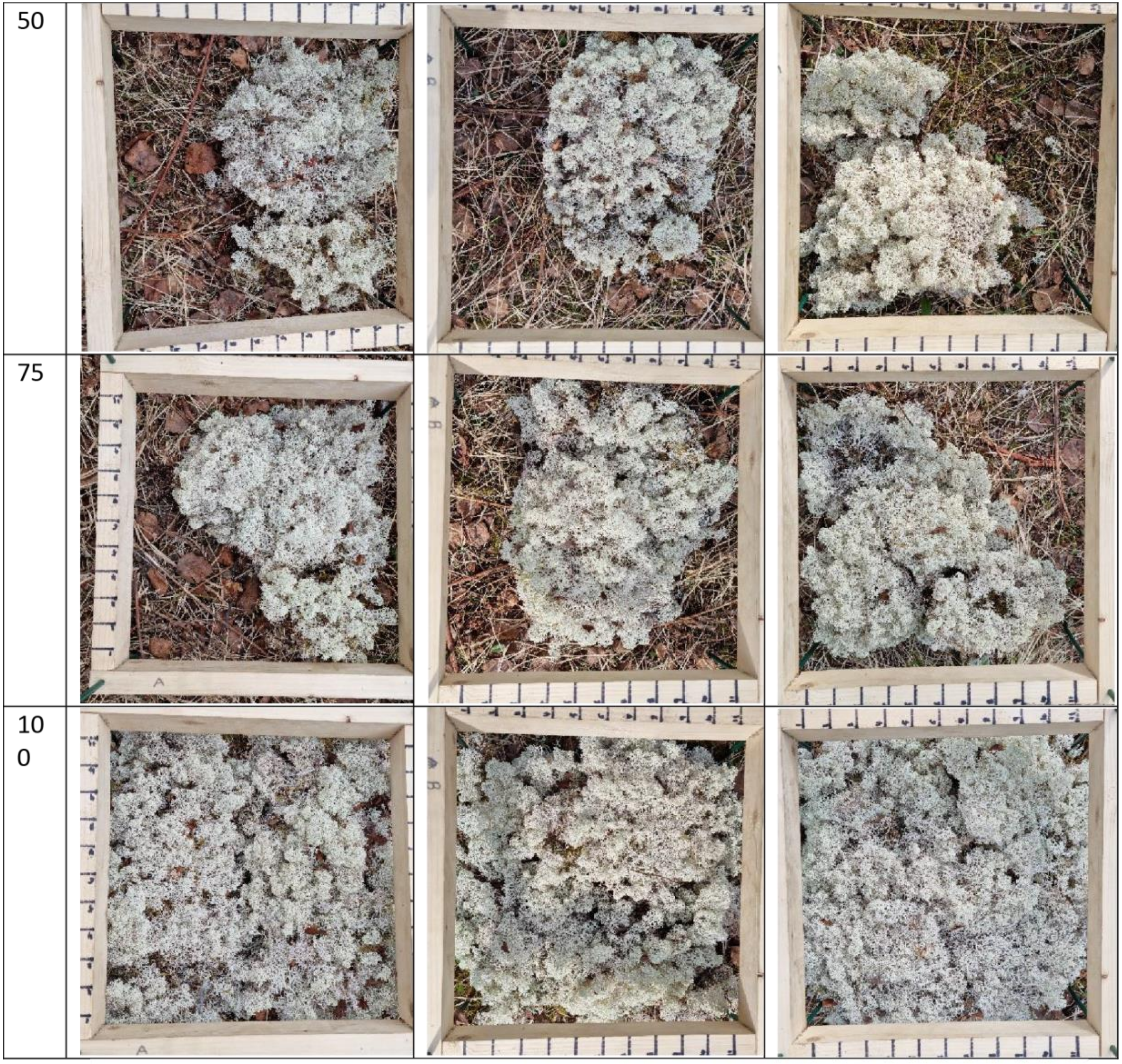
40			



b)

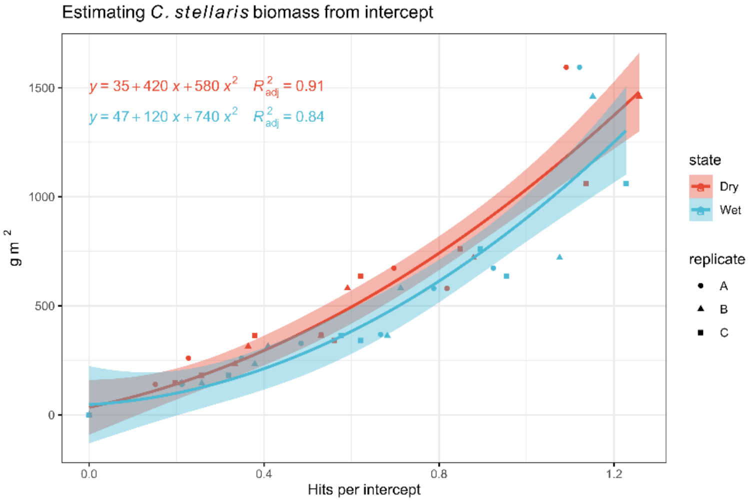


Figure S2 a) Photo series of the 3 replicates of correlating point-intercept data on *Cladonia stellaris* with biomass, from 100 % lichen cover to 0 %, collected both in dry and water-saturated state. The lichen samples were subsequently dried and weighted. b) Relationship between *Cladonia stellaris* biomass estimated from point-intercept hits in dry (red) and wet (blue) states. Replicates are identified by their point symbol.

(c) Supplementary albedo data

Additional data on variation in albedo with cloudiness and solar zenith angle (SZA) were collected at Finse in July 2021. One site with predominately CL species (*Nephromopsis nivalis* (syn.: *Flavocetraria nivalis*) and *Alectoria ochroleuca*) and one site with dominance of DL species (*Cladonia gracilis* and *Cetrariella delisei*). The albedometer was installed 0.5 m above the ground and the setup was expanded with the addition of two photosynthetically active radiation (PAR) quantum sensors (PQS1, Kipp & Zonen B.V., Delft, Netherlands) mounted back-to-back (measuring at wavelengths 400-700 nm). The instruments were running for 6 days at the CL site and for 2.5 days at the DL site. Here, data points with 2 minutes running s.d. over 0.005 were removed. Data points from SZA larger than 80° were also removed. Due to a large water body located east of the DL site, which influenced albedo measurements, data points before solar noon were also omitted prior to further analysis at the DL site

Standardisation of albedo values

Variable cloud conditions and solar zenith angle (SZA) during albedo measurements were corrected for at each site (Rocha *et al* 2021). Potential solar insolation was acquired using the R package "insol" (Corripio 2019, R Core Team 2022), parametrised with an ozone layer thickness of 0.3 cm (GES DISC), a fixed relative humidity of 70 %, temperatures during sampling, albedo of the surrounding terrain equal to the average of all measurements and assuming unobstructed view. A cloud factor (cf) was calculated as 1 – (measured incoming radiation / potential radiation) and observations were classified to clear sky (cf > 0.70), partly clouded (cf ∈ 0.35, 0.70) and overcast (cf < 0.35), according to Juszak *et al* (2016). The partly clouded and overcast field observations were compensated with 5 % and 10 % increase in albedo respectively, following Juszak *et al* (2016). These values were also validated with the diel albedo measurements from Finse (southern Norway focal area) in 2021.

Measurements were standardised to 60° SZA using the compensation method described in Briegleb *et al* (1986), Dickinson (1983), Yang *et al* (2008) (Equation 2).

Eq. 2
$$\alpha_r = \frac{\alpha_\theta(1+2d*\cos\theta)}{1+d}$$

Here, α_r = clear sky albedo at 60° SZA, α_θ = clear sky albedo at θ degree SZA, and *d* is a constant dependent on the ground surface. We used a *d*-value of 0.304, estimated as the best fit to the diel albedo measurements from Finse using nonlinear least-square regression (Figure S3).

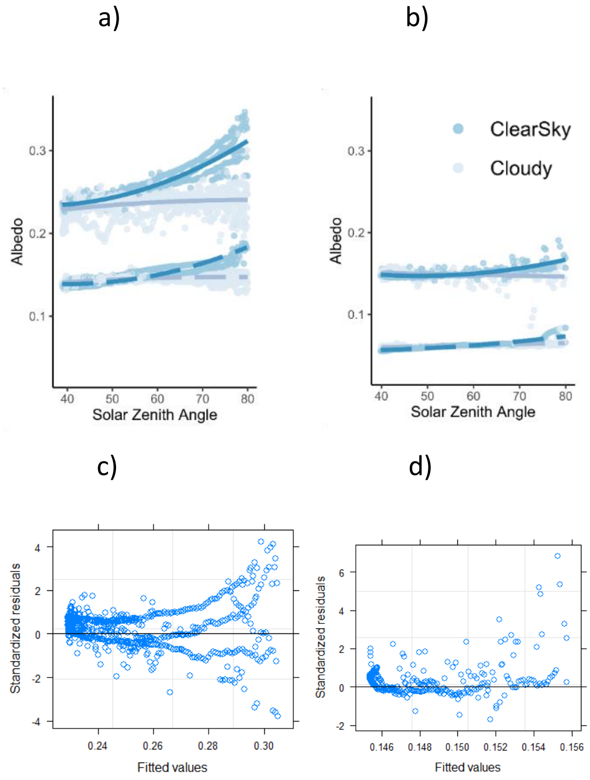


Figure S3 a) Broadband albedo (solid line) and photosynthetic active radiation (PAR) albedo (dashed line) as a function of solar zenith angle from the CL site at Finse, southern Norway. Blue scatter corresponds to clear sky conditions (~32 hours) and grey scatter is albedo under cloudy conditions (~54 hours). b) Broadband albedo (solid line) and photosynthetic active radiation (PAR) albedo (dashed line) as a function of solar zenith angle from the DL site at Finse, southern Norway. Blue scatter corresponds to clear sky conditions (~9 hours) and grey scatter is albedo under cloudy conditions (~6 hours). Due to a larger body of water east of the field site, before noon measurements have been removed. C) Fitting function to compensate for changed SZA at the two Finse sites using Nonlinear Least Squares. A *d* value of 0.304 was the best estimate for the CL plot, while 0.061 was a best fit for the DL plot. Residual standard errors were 0.0095 and 0.0052, respectively.

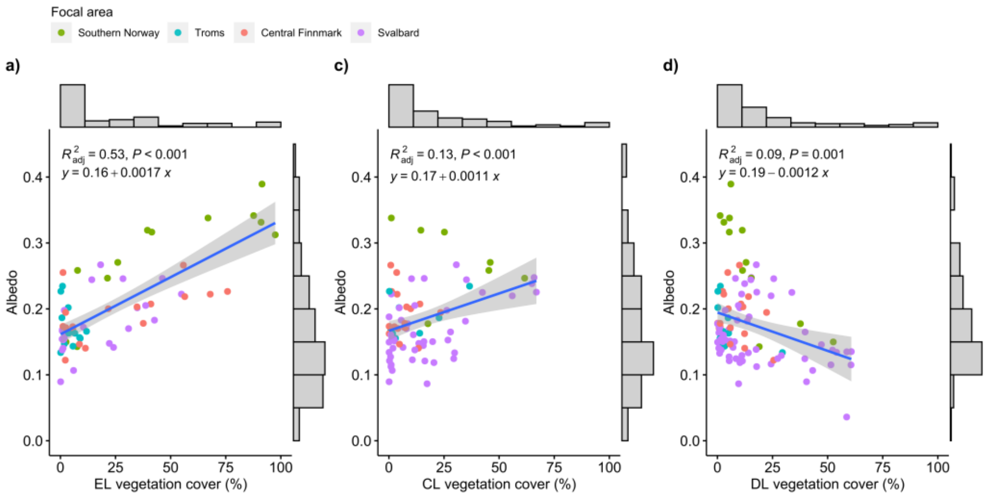


Figure S4: Site-level albedo explained by the lichen cover (% of point-intercept (PI) hits on lichen species to the total number of intercept hits at each study plot) for the three lichen groups a) EL (pale ecorticate lichens), b) CL (pale corticate lichens) and b) DL (dark lichens). Species included in this analysis is the EL species *Cladonia arbuscula* and *C. stellaris*, the CL species *Alectoria ochroleuca, C. uncialis, Nephromopsis cucullata* and *N. nivalis*) and the DL species (*A. nigricans, Bryocaulon* *divergens, Cetraria aculeata, Cet. islandica, Cet. ericetorum, Cetrariella delisei, C. gracilis, C. rangiferina* and *C. stygia*) as well as dark biological soil crust (BSC).

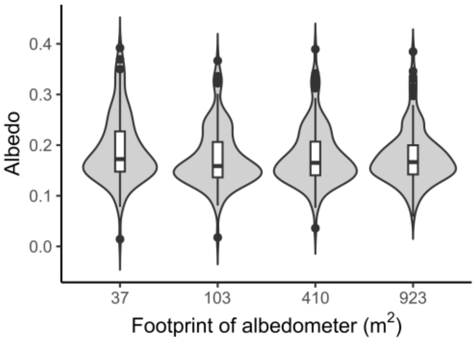


Figure S5: Violin- and boxplots of all albedo measurements at the four different footprint sizes. 1 standard deviation increases from 0.052 at 923 m^2 (mean value 0.17) to 0.062 at 37 m^2 (mean value 0.18) for all plots (*F* test of equality of variance, *p* = 0.042).

(d) Relationships; GPP, humidity, ER, NDVI and albedo

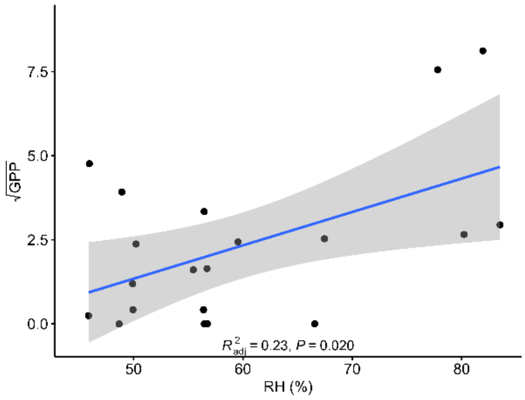


Figure S6: The relationship between square root GPP and relative humidity (RH) in the CO_2-chamber in ambient light for pale lichen plots. Only plots where more than 30% of the total intercepts hit on pale lichen thallus (EL and CL) are included.

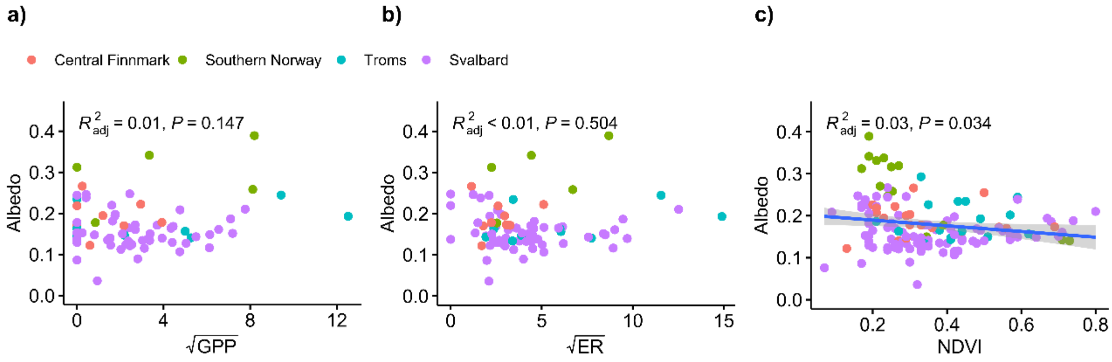


Figure S7: Field plot albedo explained by a) GPP; mg C m^{-2} h^{-1}), b) ER; g C m^{-2} h^{-1}), and c) and Normalized Difference Vegetation Index (NDVI). The point colours indicate the focal area of each field plot.

(e) Supporting material for the ordination analysis

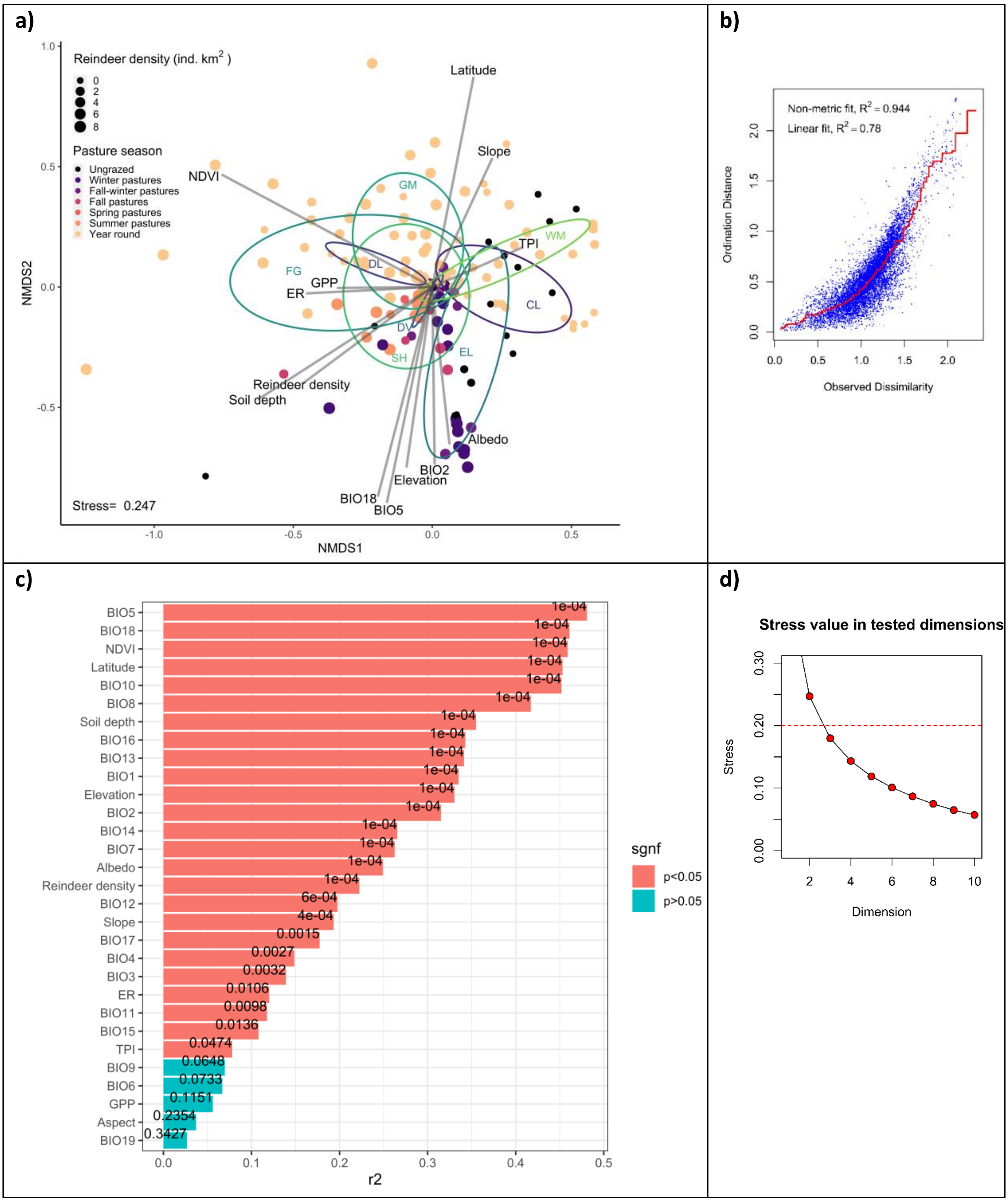


Figure S8: Evaluation of NMDS ordination of all sites (Figure 4), a) ordination diagram, b) Shepard's stress plot of the relationship between actual dissimilarities between sites from the original dissimilarity matrix and the dissimilarities in the ordination diagram, c) evaluation of explanatory power of each vector environmental variable, where red colour denotes significance (*p* < 0.05), and blue denotes non-significance (p>0.05). *p*-values are also given for each variable. d) stress values for increasing dimensions in the NMDS ordination. The dashed, red line marks a stress value of 0.20.

(f) Species list

Table S2: Species list from PI analysis in all field plots

Abbreviation	Full name	Author	Widely used synonyms
Abieabi	*Abietinella abietina*	(Hedw.) M.Fleisch.	
Agrocap	*Agrostis capillaris*	L.	
Alchalp	*Alchemilla alpina*	L.	
Alecoch	*Alectoria ochroleuca*	(Hoffm.) Massal.	
Alopova	*Alopecurus ovatus*	Knapp	
Andrpol	*Andromeda polifolia*	L.	
Anthnip	*Anthoxanthum nipponicum*	Honda	
Arctalp	*Arctostaphylos alpinus*	(L.) Spreng.	*Arctous alpina* (L.) Nied.
Arthcit	*Arthrorhaphis citrinella*	(Ach.) Poelt	
Aulapal	*Aulacomnium palustre*	Schwaegrichen	
Aulatur	*Aulacomnium turgidum*	Schwaegrichen	
Avenfle	*Avenella flexuosa*	(L.) Drejer	
Barblyc	*Barbilophozia lycopodioides*	(Wallr.) Loeske	
Bartalp	*Bartsia alpina*	L.	
Betunan	*Betula nana*	L.	
Bistviv	*Bistorta vivipara*	(L.) Delarbre	
Bleptric	*Blepharostoma trichophyllum*	L.	
Bryodiv	*Bryocaulon divergens*	(Ach.) Kärnefelt	
Callric	*Calliergon richardsonii*	Kindberg	
Callvul	*Calluna vulgaris*	(L.) Hull	
Carebig	*Carex bigelowii*	Torr. ex Schwein	
Carenig	*Carex nigra* subsp. *nigra*	(L.) Reichard	
Carerup	*Carex rupestris*	All.	
Caresp	*Carex sp.*	L.	
Casstet	*Cassiope tetragona*	(L.) D.Don	
Ceraarc	*Cerastium arcticum*	Lange	
Cerasp	*Cerastium sp.*	L.	
Cetracu	*Cetraria aculeata*	(Schreb.) Fr.	
Cetreri	*Cetraria ericetorum*	Opiz	
Cetrisl	*Cetraria islandica*	L.	
Cetrislcri	*Cetraria islandica* subsp. *crispiformis*	(Räsänen) Kärnefelt	
Cetrdel	*Cetrariella delisei*	(Bory ex Schaer.) Kärnefelt & A.Thell	
Cladama	*Cladonia amaurocraea*	(Flörke) Schaer.	
Cladarb	*Cladonia arbuscula*	(Wallr.) Flot.	
Cladbel	*Cladonia bellidiflora*	(Ach.) Schaer.	
Cladchl	*Cladonia chlorophaea*	(Flörke ex Sommerf.) Spreng.	
Cladcoc	*Cladonia coccifera*	(L.) Willd.	

Cladcor	*Cladonia cornuta*	(L.) Hoffm.	
Cladecm	*Cladonia ecmocyna*	Leight.	
Cladgra	*Cladonia gracilis*	(L.) Willd.	
Cladmit	*Cladonia mitis*	Sandst.	
Cladpyx	*Cladonia pyxidata*	(L.) Hoffm.	
Cladran	*Cladonia rangiferina*	(L.) Weber ex F.H.Wigg.	
Cladspp	*Cladonia* spp.	P.Browne	
Cladste	*Cladonia stellaris*	(Opiz) Pouzar & Vězda	
Cladsty	*Cladonia stygia*	(Fr.) Ruoss	
Cladsul	*Cladonia sulphurina*	(Michx.) Fr.	
Cladunc	*Cladonia uncialis*	L.	
Cornsue	*Cornus suecica*	L.	*Chamaepericlymenum suecicum* (L.) Asch. & Graebn.
Descalp	*Deschampsia alpina*	(L.) Roem. & Schult.	*D. cespitosa* subsp. *alpina* (L.) Tzvelv
Descfle	*Deschampsia flexuosa*	L.	
Diaplap	*Diapensia lapponica*	L.	
Dicrsco	*Dicranum scoparium*	Hedw.	
Dicrspp	*Dicranum* spp.	Hedw.	
Diphalp	*Diphasiastrum alpinum*	(L.) Holub	
Draboxy	*Draba oxycarpa*	Boiss.	
Drabsp	*Draba* sp.	Dill. ex. L.	
Dryaoct	*Dryas octopetala*	L.	
Dupofis	*Dupontia fisheri*	R.Br.	
Empenig	*Empetrum nigrum*	L.	
Equiarv	*Equisetum arvense* subsp. *Alpestre*	(Wahlenb.) Schönsw. & Elven	
Eriosch	*Eriophorum scheuchzeri* subsp. *arcticum*	M.S.Novos.	
Eriovag	*Eriophorum vaginatum*	H	
Festovi	*Festuca ovina*	L.	
Festrub	*Festuca rubra*	L.	
Festspp	*Festuca* spp.	Tourn. ex. L.	
Festviv	*Festuca viviparoidea*	Krajina ex Pavlick	
Alecnig	*Gowardia nigricans*	(Ach.) Halonen, Myllys, Velmala & Hyvärinen	*Alectoria nigricans* (Ach.) Nyl.
Gymnsp	*Gymnomitrion* sp.	Corda	
Hieralp	*Hieracium* sect. *Alpina*	(Griseb.) Gremli	
Hupearc	*Huperzia arctica*	(Tolm.) Sipliv.	
Hylospl	*Hylocomium splendens*	W.P.Schimper	
Hypnvau	*Hypnum vaucheri*	Lesquereux	*Buckia vaucheri* (Lesq.) D.Rios, M.T.Gallego & J.Guerra
Icmaeri	*Icmadophila ericetorum*	(L.) Zahlbr.	
Juncbig	*Juncus biglumis*	L.	
Junctri	*Juncus trifidus*	L.	
Kalmpro	*Kalmia procumbens*	(L.) Gift, Kron & P.F.Stevens	

Leprdac	*Lepra dactylina*	(Ach.) Hafellner	*Pertusaria dactylina* (Ach.) Nyl.
Lichalp	*Lichenomphalia alpina*	(Britzelm.) Redhead, Lutzoni, Moncalvo & Vilgalys	
Lophsp	*Lophozia* sp.	(Dumort.) Dumort.	
Luzucon	*Luzula confusa*	Lindeb.	
Luzumult	*Luzula multiflora*	(Retz.) Lej.	
Luzuspp	*Luzula* spp.	DC.	
Lysieur	*Lysimachia europaea*	(L.) U.Manns & Anderb.	
Melasylv	*Melampyrum sylvaticum*	L.	
Micrniv	*Micranthes nivalis*	(L.) Small	
Nardstr	*Nardus stricta*	L.	
Nepharc	*Nephroma arcticum*	(L.) Torss.	
Nepexp	*Nephroma expallidum*	(Nyl.) Nyl.	
Nephcuc	*Nephromopsis cucullata*	(Bellardi) Divakar, A.Crespo & Lumbsch	*Flavocetraria cucullata* (Bellardi) Kärnefelt & A.Thell
Nephniv	*Nephromopsis nivalis*	(L.) Divakar, A.Crespo & Lumbsch	*Flavocetraria nivalis* (L.) Kärnefelt & A.Thell
Ochrfri	*Ochrolechia frigida*	(Sw.) Lynge	
Oxyrdig	*Oxyria digyna*	(L.) Hill	
Pedidas	*Pedicularis dasyantha*	(Trautv.) Hadac	
Peltaph	*Peltigera aphthosa*	(L.) Willd.	
Peltsp	*Peltigera* sp.	Willd.	
Phylcae	*Phyllodoce caerulea*	(L.) Bab.	
Pleusch	*Pleurozium schreberi*	Mitten	
Poaarc	*Poa arctica*	R.Br.	
Pholcru	*Pohlia cruda*	Lindberg	
Pohlsp	*Pohlia* sp.	Hedw.	
Polycom	*Polytrichum commune*	Hedw.	
Polyjun	*Polytrichum juniperinum*	Hedw.	
Polypil	*Polytrichum piliferum*	Hedw.	
Polysp	*Polytrichum* sp.	Hedw.	
Polystr	*Polytrichum strictum*	Menzies ex Bridel	
Ptilcil	*Ptilidium ciliare*	(L.) Hampe	
Racolan	*Racomitrium lanuginosum*	Brid.	
Racosp	*Racomitrium* sp.	Brid.	
Ranusub	*Ranunculus subborealis*	Tzvelev	
Rhodtom	*Rhododendron tomentosum*	(Stokes) Harmaja	
Rhytsqu	*Rhytidiadelphus squarrosus*	(Hedw.) Warnst.	
Rhytrug	*Rhytidium rugosum*	Kindberg	
Rubucha	*Rubus chamaemorus*	L.	
Saburub	*Sabulina rubella*	(Wahlenb.) Dillenb. & Kadereit	*Minuartia rubella* (Wahlenb.) Hiern
Sabusp	*Sabulina* sp.	Rchb.	
Saginiv	*Sagina nivalis*	(Lindblom) Fr.	
Saliher	*Salix herbacea*	L.	
Salipol	*Salix polaris*	Wahlenb.	
Saniunc	*Sanionia uncinata*	(Hedw.) Loeske	

Saxicer	*Saxifraga cernua*	L.
Saxices	*Saxifraga cespitosa*	L.
Saxiopp	*Saxifraga oppositifolia*	L.
Saxisp	*Saxifraga sp.*	L.
Scorsp	*Scorpidium* sp.	(Schimp.) Limpr.
Sileaca	*Silene acaulis*	(L.) Jacq.
Sphaglo	*Sphaerophorus globosus*	(Hudson) Vainio
Sphawar	*Sphagnum warnstorfii*	Russow
Sterspp	*Stereocaulon* spp.	Hoffm.
Thalalp	*Thalictrum alpinum*	L.
Thamver	*Thamnolia vermicularis*	(Sw.) Schaer.
Tomenit	*Tomentypnum nitens*	(Hedw.) Loeske
Trisspi	*Trisetum spicatum*	(L.) K.Richt.
Vaccmyr	*Vaccinium myrtillus*	L.
Vacculi	*Vaccinium uliginosum*	L.
Vaccvit	*Vaccinium vitis-idaea*	L.
Vicicra	*Vicia cracca*	L.
Violbif	*Viola biflora*	L.

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PAPER II

PAPER III