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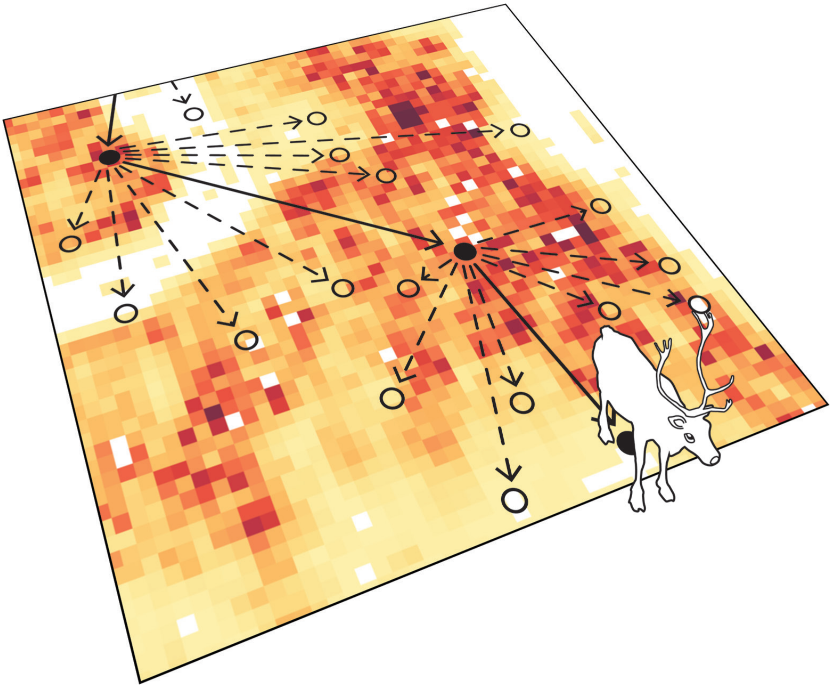
From pixels to pastures

Methods for multi-scale assessment of ground lichen as a reindeer grazing resource

ERIK CRONVALL



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Methods for multi-scale assessment of ground lichen as a reindeer grazing resource

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Cover: A reindeer moves over a lichen cover map with used and available steps shown. Illustration by Erik Cronvall.

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Abstract

Ground lichens are a critical winter food source for reindeer, yet lichen resources have declined substantially over recent decades in Sweden. Pressure from competing land uses and climate change further affects their accessibility, determining whether reindeer can reach and utilise the lichen that remains. Reliable and transparent methods to map and measure lichen and assess accessibility of lichen are therefore much needed to support the management and planning of reindeer winter grazing areas. This thesis develops and evaluates such methods across three spatial scales, and demonstrates how reindeer movement data can be used to analyse the accessibility of lichen pastures.

At the broad scale, a method was developed that uses reindeer GPS locations to validate a satellite-based lichen cover map of the Swedish reindeer winter grazing area. At the local scale, a drone-based method was developed to estimate lichen cover and biomass within specific areas. At the plot scale, field methods for estimating lichen cover were evaluated and compared, and a deep learning image segmentation model was developed to classify lichen in ground-level photographs, providing a more objective and consistent alternative to visual assessment. To link lichen estimates to reindeer, a simple approach to estimate reindeer grazing days from lichen biomass is also presented.

The thesis also demonstrates methods for analysing how access to lichen pastures is affected by industrial development and other disturbances, accounting for cumulative impacts from infrastructure such as wind power plants, mining, and roads.

Together, these methods form a complementary toolkit that can be applied independently or in combination to map and quantify lichen resources across multiple scales in a transparent and reproducible way.

Keywords: Ground lichen, *Rangifer tarandus,* Reindeer husbandry, Reindeer lichen, Lichen mapping, Lichen biomass, Reindeer grazing days, Habitat selection, Semantic segmentation, Cumulative impacts

Från pixlar till betesmarker

Sammanfattning

Marklav är en livsviktig födoresurs för renar under vintern, men marklaven i Sverige har minskat kraftigt under de senaste decennierna. Konkurrens från annan markanvändning och klimatförändringar påverkar också lavens tillgänglighet, och avgör om renarna faktiskt kan nyttja den lav som finns kvar. Tillförlitliga och objektiva metoder för att kartera, kvantifiera och analysera tillgängligheten av lav är därför viktiga som underlag för planering och förvaltning av lavrika marker. Denna avhandling utvecklar och utvärderar sådana metoder i tre rumsliga skalor och visar också hur GPS data från renar kan användas för att analysera hur tillgängliga de lavrika betesmarkerna är för renen.

På storskalig nivå utvecklades en metod som nyttjar den starka kopplingen mellan lav och ren genom att använda GPS-positioner från renar för att validera en satellitbaserad lavkarta över renens svenska vinterbetesområde. På lokal nivå utvecklades en metod för att uppskatta lavtäckning och lavbiomassa inom mindre områden där information insamlad med drönare användes för utlägg av provytor. På provytenivå utvärderades och jämfördes fältmetoder för att uppskatta lavtäckning, och en modell för bildbaserad semantisk segmentering utvecklades för att klassificera lav i markfotografier. Det är ett mer objektivt alternativ med mindre variation mellan personer och bedömningstillfälle än visuella uppskattningar. För att koppla skattad lavmängd till renantal presenteras även ett enkelt sätt att beräkna antalet rensbetesdagar utifrån lavbiomassa.

Avhandlingen presenterar också metoder för att analysera hur lavens tillgänglighet påverkas av annan markanvändning och störningar, med hänsyn taget till kumulativa effekter av olika typer av infrastruktur som vindkraftsparker, gruvor och vägar.

Sammantaget utgör dessa metoder en samling verktyg som kan användas enskilt eller i kombination för att kartera och kvantifiera lavresurser på flera nivåer på ett objektivt och reproducerbart sätt.

Nyckelord: Marklav, *Rangifer tarandus*, Ren, Renskötsel, Renlav, Lavkartering, Lavbiomassa, Rensbetesdagar, Habitatval, Semantisk segmentering, Kumulativa effekter

Dedication

Till Bodil

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Cronvall, E., Adler, S., Brandão Niebuhr, B., Sandström, P., Skarin, A. (2026). Cross-species mapping validation: leveraging reindeer-borne tracking and consumer-resource relationship to validate a satellite-based lichen map. (submitted and under revision)

II. Cronvall, E., Adler, S., Sandström, P., Skarin, A. (2025). Quantifying winter forage resources for reindeer: Developing a method to estimate ground lichen cover and biomass at a local scale. Trees, Forests and People, Volume 19, https://doi.org/10.1016/j.tfp.2024.100768

III. Cronvall, E., Adler, S., Brandão Niebuhr, B., Sandström, P., Skarin, A. (2026). Improving the consistency of vegetation cover estimation — deep learning-based segmentation of reindeer lichen from field photographs. (manuscript)

IV. Brandão Niebuhr, B., Cronvall, E., Duris, L., Alam, M., Panzacchi, M., van Moorter, B., Sandström, P., Skarin, A. (2026). Reindeer habitat selection and movement changes with cumulative impacts from mining and wind power development. (submitted)

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The contribution of Erik Cronvall to the papers included in this thesis was as follows:

I. Designed the study together with SA, BBN, PS and AS. Performed data preparation and all analysis for the ecological validation using reindeer GPS position. Wrote the manuscript with support from the co-authors. SA produced the lichen map.

II. Designed the study together with SA, PS, and AS. Collected all drone and field data and conducted the literature review. Performed the analysis. Wrote the manuscript with support from the co-authors.

III. Designed the study together with SA. Produced the training data and performed all model training and analysis. Wrote the manuscript with support from the co-authors.

IV. Contributed to data curation, investigation, analysis, and the manuscript.

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Abbreviations

AIC	Akaike Information Criterion
CCC	Concordance correlation coefficient
CV	Cross-validation
GAM	Generalised additive model
HSA	Habitat selection analysis
IoU	Intersection over Union
iSSF	Integrated step selection function
MiT	Mix Transformer
NDSI	Normalised difference snow index
NDVI	Normalised difference vegetation index
NFI	National Forest Inventory
NMD	National Land Cover Database (Nationella Marktäckedata)
pp	Percentage points
RHA	Reindeer husbandry area
RHC	Reindeer herding community
RMSE	Root mean square error
RSE	Relative standard error
RSS	Relative selection strength
SE	Standard error
VIF	Variance inflation factor
ZOI	Zone of influence

AI declaration

Generative AI tools were used at several stages during the preparation of this thesis and the papers included in it. Large language models, primarily Claude (Anthropic) and ChatGPT (OpenAI), were used as coding assistants for the development and debugging of R and Python scripts, including data processing pipelines, statistical analyses, and visualisation code. These tools were also used for writing assistance, including checking grammar and spelling, suggesting rephrasing of sentences, and improving the flow and clarity of text. All content was critically reviewed, revised, and approved by the author.

During development of the mobile application in Android Studio, the built-in Gemini-based AI assistant was used for debugging and generation of Kotlin code.

Components of Figure 14 were created using the text-to-image AI tool Midjourney.

1. Introduction

Lichens are among the most resilient organisms on Earth. Through a symbiosis between fungi and photosynthetic algae or cyanobacteria, they can survive extreme cold, drought, and low nutrient availability (Nash 2008; Armstrong 2017). This tolerance allows lichens to form a major component of ground vegetation across boreal and tundra ecosystems, often occupying the least productive sites while contributing substantially to biomass production, nutrient cycling, and biodiversity (Oksanen & Ahti 1982; Asplund & Wardle 2017). These landscapes support reindeer and caribou (*Rangifer tarandus*) that are unique among ruminants in eating and efficiently digesting substantial amounts of lichen (Storeheier et al. 2002). Mat-forming terrestrial lichens, mainly *Cladonia spp*. and *Cetraria spp*., constitute a key winter forage resource for reindeer (Danell et al. 1994; Kumpula 2001; Heggberget et al. 2002). They are therefore also essential to many Indigenous cultures across northern Eurasia and North America, for whom reindeer husbandry or caribou hunting forms a central part of both livelihood and cultural identity (Jernsletten & Klokov 2002; Nuttall et al. 2005; Borish et al. 2021).

In northern Sweden, reindeer husbandry coexists with several other, often competing, land uses. Since the industrialisation of resource extraction in the early to mid-20th century, the boreal landscape has increasingly been shaped by commercial forestry, expanding infrastructure, hydropower and wind power development, mining and other human activities (Horstkotte et al. 2022). During this period, ground lichen cover and the extent of lichen-rich forests have declined dramatically (Sandström et al. 2016; Roos et al. 2025). As a land use form that depends on large and spatially connected landscapes, reindeer husbandry is especially vulnerable to these pressures (Skarin & Åhman 2014). The resulting loss of lichen pastures has increased the demand for reliable methods to map and quantify ground lichens. Such data are sought by a wide range of land users for purposes spanning forest management, land-use planning and environmental impact assessment, and are essential for understanding the distribution of reindeer forage lichens across the landscape and for supporting decision-making related to reindeer grazing, land-use conflicts and the sustainable management of reindeer husbandry areas.

Recent advances in remote sensing and machine learning, particularly deep learning, provide new opportunities to estimate lichen abundance at multiple scales and GPS-based animal movement analysis enables assessment of how reindeer can utilise these resources across large landscapes.

2. Aims

The main aim of this thesis was to develop and improve methods for mapping and quantifying ground lichen across multiple spatial scales, but also to assess what these estimates mean for reindeer by linking lichen measures to grazing capacity, habitat selection, and pasture accessibility. The work integrates modern technologies with a strong focus on practical application, aiming to develop objective, repeatable methods, as well as ready to use maps and tools that are useful for diverse land users and management contexts.

1. Broad-scale mapping: present a lichen cover map for Swedish winter grazing area using Sentinel-2 satellite data and NFI field data and develop a validation approach based on reindeer GPS locations (Paper I).

2. Local-scale biomass estimation: develop a method for lichen biomass quantification using data derived from drone footage, and link lichen volume to biomass using a relationship derived from literature (Paper II).

3. Plot-scale cover estimation: develop an automated, deep learning-based method for lichen cover estimation at plot level and compare it to traditional methods (Papers III and II).

4. Link lichen measures to reindeer grazing and lichen accessibility: assess methods for analysing reindeer habitat selection and how industrial development and other disturbances influence landscape use, accounting for cumulative impacts across space and time; and convert lichen estimates to grazing day capacity (Paper IV, I and II).

3. Lichen, reindeer, and approaches to studying them

Before turning to the papers, this chapter provides context and background knowledge that underpins them. The development of methods for quantifying lichen abundance and analysing animal movement is outlined, along with the considerations needed to link lichen measures to reindeer as a forage resource. Understanding the role of lichen-rich landscapes as winter pastures and the relationship between lichen and reindeer requires knowledge of both lichen ecology and reindeer behaviour. The fact that all reindeer in Sweden are managed within a herding system also shapes how such analyses are conducted; together, these topics form the broader context for the work presented in the four papers.

3.1 Lichen and reindeer

3.1.1 Lichens consumed by reindeer

In addition to their taxonomic classification, lichens can be classified according to both morphological characteristics and substrate associations. Traditionally, the three main morphological groups are crustose, foliose, and fruticose. Crustose lichens form thin crusts tightly adhered to substrates, foliose lichens possess leaf-like lobes with distinct upper and lower surfaces, and fruticose lichens exhibit shrubby or hair-like three-dimensional structures (Nash 2008). Lichens are further categorised by their substrate preferences: epiphytic lichens grow on trees, saxicolous lichens colonise rock surfaces, and terricolous (or epigeic) lichens grow on soil (Stenroos et al. 2021). Lichens utilised by reindeer are generally divided into two groups: ground (terrestrial) and arboreal lichens (Johnson et al. 2000; Kivinen et al. 2010; Kumpula et al. 2014). Arboreal lichens are pendulous, fruticose epiphytes, primarily in the *Bryoria, Alectoria,* and *Usnea* families, while ground lichens are ground-dwelling fruticose species, dominated by the reindeer lichens in the genus *Cladonia* (formerly *Cladina*), particularly *C. rangiferina*, *C. stellaris*, *C. arbuscula* and *C. mitis*, but also include *Cetraria spp*. and *Stereocaulon spp*. (Moen et al. 2007; Kumpula et al. 2014). Modern forestry has greatly reduced arboreal lichen availability, but when present they remain an important winter food resource, particularly when deep, dense, or hard-packed snow, or ice crusts formed by freeze–thaw cycles or rain-on-snow events, render ground pastures inaccessible (Johnson et al. 2001; Horstkotte et al. 2011). Nevertheless, ground lichens typically constitute the primary component of the reindeer winter diet and are the focus of this thesis.

3.1.2 Reindeer husbandry in Sweden

Reindeer are native to arctic and subarctic regions and have constituted a vital resource for humans since prehistoric times. Across Sápmi, the traditional Sámi territory covering much of northern Sweden, Norway, Finland, and northwestern Russia, reindeer husbandry is an integral part of Sámi culture and livelihood (Holand et al. 2022). In Fennoscandia, reindeer were initially hunted before small numbers of domesticated animals were gradually incorporated into a mixed economy of hunting, fishing, and trade (Bjørklund 2013). Large-scale nomadic reindeer husbandry with seasonal migrations between summer and winter pastures then emerged from the 17th century onwards (Lundmark 2007). In Sweden, reindeer husbandry is practised by the Sámi people across 51 reindeer herding communities (RHCs) that together form the reindeer husbandry area (RHA). This area covers approximately 22.6 million hectares, roughly the northern half of Sweden's land base (Sandström 2015). The herding system is organised around three RHC types: mountain, forest, and concession RHCs. Mountain RHCs undertake long-range seasonal migrations between alpine summer pastures and forested winter pastures, representing some of the last large-scale ungulate migrations remaining in the northern hemisphere (Vors & Boyce 2009), while forest and concession RHCs remain in forested landscapes year-round. Within each RHC, land is divided into year-round land and winter pastures. On the latter, reindeer are only permitted between 1 October and 30 April (Skarin et al. 2022).

During the 20th century, reindeer husbandry transitioned from a more intensive, closely managed system towards the extensive approach practised today where large herds graze freely across wide areas and are gathered only at strategic points in the annual cycle (Lundmark 2007; Kivinen et al. 2010). Key herding events are calf marking that usually takes place from late June to early August, bull slaughter that occurs in mid-September just before the rut taking place in late September until mid-October, and the main calf slaughter starting in mid-October, often in connection with autumn migration when herds are also gathered and separated into winter grazing groups. Herders generally influence large-scale migrations and the choice of regional grazing areas, while shorter movements within seasonal pastures and the selection of specific grazing patches are mostly determined by the reindeer themselves (Skarin et al. 2022).

Reindeer population sizes in Sweden are regulated by the state at the level of individual RHCs. Under the current Reindeer Husbandry Act (SFS 1971:437), the County Administrative Boards are tasked with setting the maximum number of reindeer permitted in each district (Sarkki et al. 2022). According to the latest available statistics, the number of reindeer in Sweden was approximately 227,000 in 2023 (Sametinget 2024) referring to post-slaughter winter herd sizes, with numbers considerably higher in summer following spring calving. The number of reindeer has oscillated repeatedly over the last 140 years, with extremes of roughly 150,000 and 300,000 and a long-term average of around 230,000 (Bernes et al. 2013; Sametinget 2024). Although reindeer husbandry has undergone considerable change and incorporated modern technologies such as snowmobiles, all-terrain vehicles, helicopters, trucks, drones, and GPS collars, as well as supplementary feeding with factory-made feed (Andersson & Keskitalo 2017; Uboni et al. 2020; Wagner & Harvard 2024), it remains fundamentally structured around the availability of natural pastures and relies on reindeer satisfying their nutritional requirements through free-ranging foraging.

3.1.3 Reindeer grazing and ground lichen as a forage resource

Reindeer (*Rangifer tarandus*) are generalist feeders adapted to the highly seasonal food availability of arctic and sub-arctic environments. Although winter is a bottleneck and snow- or ice-locked pastures can lead to starvation, it is also important to note that weight loss and negative energy balance are normal, regulated processes in reindeer, and not necessarily signs of starvation or poor nutrition. Reindeer show seasonal cycles in appetite and growth, driven partly by photoperiod and hormones, which reduce food intake in winter and lead to the gradual use of fat reserves (Tyler & Blix 1990; Åhman & White 2018). Most reindeer herds undertake seasonal migrations, following the spring green-up of vegetation and seeking winter ranges with favourable snow conditions for foraging (Åhman & White 2018). Generally, spring and summer forage is the primary determinant of growth and body size, while winter forage availability is the primary driver of population-level mortality and density regulation (Klein 1965). In spring, nutrient-rich forage is critical for reindeer recovering from winter food shortages and is particularly important for pregnant females approaching calving. Early-growing plants that began developing beneath the snow emerge rapidly during snowmelt, with young shoots high in protein, sugars, and minerals, and areas with early snowmelt therefore offer valuable high-quality forage in spring (Warenberg 1982). After snowmelt through summer, vascular plants dominate the diet, with graminoids, deciduous shrubs and forbs providing highly digestible forage rich in protein and minerals making it possible for young animals to grow and for adults to rebuild body reserves. The seasonal variation in food availability and quality has adapted reindeer to have a high capacity for storing energy and protein as fat and muscle tissue (Åhman & White 2018). In late summer and autumn the diet gradually shifts, with mushrooms offering a protein-rich, highly digestible addition to graminoids, woody plants and herbs, before reindeer increasingly incorporate lichens into the diet, which typically becomes the dominant forage component through winter (Nieminen & Heiskari 1989).

Reindeer are uniquely adapted to efficiently digest lichens, which most herbivores cannot do. This requires specialised rumen microbes capable of breaking down lichen polysaccharides and fully degrading the usnic acid found in many lichen species eaten by reindeer (Åhman & White 2018). While the proportion of ground lichens in the diet depends on their availability (Trudell & White 1981; Johnson et al. 2001), diet selection more broadly reflects a complex trade-off between competing fitness demands, including growth, survival, and reproductive output, mediated by both nutritional requirements and predation risk (Kie 1999; Parker et al. 2009). According to optimal foraging theory, animals are generally expected to select diets that maximize net energy intake relative to foraging costs (Stephens & Krebs 1986). In regions where snow-free patches exist and are dominated by vascular plants, reindeer have been shown to prioritise foraging these areas over cratering for lichens beneath the snow (Holtan et al. 2023). However, reindeer generally occupy areas where they must access forage through the snow and are highly adapted to winters with persistent snow cover, with lichens often constituting more than 50% of their diet and can exceed 80% when abundant (Heggberget et al. 2002; Åhman & White 2018).

Compared to many plants consumed by reindeer the nutritional quality of lichen is considerably lower, particularly in terms of protein and mineral content (Nieminen & Heiskari 1989; Storeheier et al. 2003). They, however, contain energy-rich carbohydrates highly digestible to reindeer, making them primarily an energy source that is critical for the energetically demanding work of accessing forage through the snow (Fancy & White 1985; Ophof et al. 2013).

Deep, dense, or crusted snow greatly increases the effort reindeer need to reach food by making both travel and cratering more energetically costly, and at some point the costs become too high to make the effort worthwhile (Fancy & White 1985; Åhman & White 2018). Reindeer are able to detect and distinguish lichen patches by smell through soft snow exceeding 90 cm, and typically crater in snow depths of up to 80 cm, beyond which accessing lichen becomes increasingly difficult, although craters deeper than 120 cm have been reported (Johnson 1980; Eriksson et al. 1981; Helle 1984). Cratering strategy can also change depending on snow conditions: Helle (1984) found that digging time increased with snow depth in soft snow but decreased sharply in hard snow, indicating a shift from opening new craters to exploiting existing ones. Lichen utilisation from feeding holes increased from about 20% in soft shallow snow to around 85% under the most demanding conditions.

Despite their importance as a winter forage resource, reindeer cannot survive winter on lichens alone and must supplement them with plants for protein and minerals. Some of the most important semi-evergreen or wintergreen plants are forest wiregrass (*Deschampsia flexuosa*), cottongrass (*Eriophorum spp.*), horsetails (*Equisetum spp.*) and sedges (*Carex spp.*). Dwarf shrubs such as bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*) and crowberry (*Empetrum hermaphroditum*), and dwarf birch (*Betula nana*) are also regularly consumed for their mineral content (Warenberg 1982; Nieminen & Heiskari 1989; Danell et al. 1994).

3.1.4 Reindeer ground lichen requirement during winter

Estimating how many reindeer a winter pasture can sustain requires not only measures of ground lichen availability but also data on how much lichen an individual reindeer consumes during winter. Total dry matter intake for free-ranging adult female reindeer on natural winter pasture in northern Norway has been estimated at 37–66 g DM day^{-1} kg^{-1} $BM^{0.75}$ in March, when voluntary food intake is at its seasonal minimum (Storeheier et al. 2003). Integrated across the full September–May period, Staaland & Hove (2000) estimated a higher overall total dry matter intake of around 1800 g day^{-1} (74 g/ day^{-1} kg^{-1} BM$^{0.75}$). Intake is expressed per unit metabolic body mass (BM$^{0.75}$) rather than per kg body weight, because energy requirements scale non-linearly with body size, a larger animal needs less food per kg of body weight than a smaller one, and dividing by BM$^{0.75}$ corrects for this. These total intake figures are lower than the lichen-specific estimate of Kumpula (2001), who estimated 2.6 kg lichen DM day^{-1} during the most intensive cratering period in Finnish woodland lichen pasture, during which body condition was maintained or improved. The Swedish-Norwegian Reindeer Pasture Commission of 1964 employed a standardised system called Feed Units (foderenheter; f.e.), with a winter norm of 1.4 f.e. representing the daily nutritional requirement of a reindeer (Svensk-norska renbeteskommissionen av 1964 1967). Given the Commission's estimate that naturally occurring fodder (including lichen) provides approximately 0.6–0.7 f.e. kg^{-1} DM, a reindeer requires approximately 2.0–2.3 kg DM day^{-1} to meet this requirement. Based on earlier Norwegian estimates of 2.0–2.5 kg DM day^{-1} and drawing on Storeheier et al. (2002), Gaare et al. (2006) suggest that 1.5–2.0 kg DM day^{-1} should be sufficient provided the diet consists of a mixture of lichen and protein-containing vascular plants. To translate total dry matter intake into an estimate of lichen consumption specifically, knowledge of the proportion of lichen in the diet is also needed. This proportion varies considerably depending on lichen availability, but as mentioned above, lichens often constitute more than 50% of the winter diet (Heggberget et al. 2002).

3.1.5 Lichen habitat and succession

Reindeer lichens are most abundant in dry, nutrient-poor environments where their slow growth and low resource requirements allow them to compete successfully with vascular plants and bryophytes (Ahti & Oksanen 1990). In boreal Fennoscandia, these species can dominate the bottom layer of pine forests on dry, oligotrophic, sandy soils and on rocky ground where low nutrient availability restricts the development of competing field-layer vegetation (Esseen et al. 1997; Kivinen et al. 2010). The competitive advantage of reindeer lichens is closely tied to disturbance history. Immediately following a fire or severe disturbance, the bare mineral or humus soil is first colonised by fast-growing, effectively dispersed crustose lichens and pioneer bryophytes (Ahti & Oksanen 1990; Väre et al. 1995). As succession progresses, larger lichens begin to enter the community, and cup- and needle-like *Cladonia* species become abundant (Ahti & Oksanen 1990; Esseen et al. 1997). In a natural post-fire setting, reindeer lichens are slow to regenerate, and recovery time varies considerably with ecological region, stand type, and latitude. Greuel et al. (2021) estimated the time to reach 50% of maximum predicted biomass to range from 28 to 73 years in Canadian boreal forests, with peak dominance typically not achieved until 40–120 years after fire (Ahti & Oksanen 1990; Berg et al. 2008). However, Roturier et al. (2017) demonstrated that lichen fragments transplanted two years after burning can survive on the burnt substrate and establish a new lichen mat within a decade. In the natural succession after a fire, *Cladonia mitis* is usually the first species to become dominant, often 30–50 years after a fire. It is followed by *Cladonia rangiferina* and *Cladonia arbuscula*, which dominate during the middle stage, about 30–100 years after fire. *Cladonia stellaris* appears last, grows the slowest, and typically becomes dominant 80–120 years after fire, eventually forming dense mats that shade out earlier species (Ahti & Oksanen 1990; Webb 1998). The accumulation of organic matter and increased moisture retention in the long-term absence of fire allows feather mosses and dwarf shrubs such as *Vaccinium* and *Empetrum* to displace them (Ahti & Oksanen 1990; Kivinen et al. 2010; Berg et al. 2008). In a 19-year vegetation removal experiment across a boreal forest chronosequence in northern Sweden, Fanin et al. (2025) found that both ericaceous dwarf shrubs and feather mosses suppressed lichen biomass, though the effect of shrubs was considerably stronger. Removing either group increased lichen biomass, and the combined removal of both had the most pronounced effect.

Forest structure is a critical factor; dense canopies suppress reindeer lichens through shading. In a transplant experiment across northern Scandinavia, Jonsson Čabrajič et al. (2010) found that both *C. stellaris* and *C. islandica* reached light saturation at roughly 40% site openness in canopy cover, corresponding to a basal area of approximately 15 m^2 ha^{-1}. Canopy cover exceeding approximately 60% thus provides suboptimal light conditions, favouring the expansion of mosses (Jonsson Čabrajič et al. 2010; Kivinen et al. 2010; Horstkotte & Moen 2019). Consequently, the richest lichen pastures are associated with open, mature pine stands or young forests where competition is kept low by site conditions, rather than productive, closed-canopy forests (Kivinen et al. 2010; Horstkotte & Moen 2019; Uboni et al. 2019). Reindeer grazing itself can further influence this dynamic, as heavy grazing may accelerate the transition toward bryophyte dominance by opening the lichen mat (Väre et al. 1995).

3.1.6 Lichen reproduction and dispersion

Lichens are symbiotic organisms usually composed of a fungal partner (mycobiont) and one or more photosynthetic partner, either green algae or cyanobacteria (photobiont). The mycobiont provides the structural framework of the thallus and protects the photobiont from high light intensities, temperature extremes, and desiccation, while the photobiont in turn supplies the mycobiont with carbohydrates through photosynthesis (Nash 2008). Lichen reproduction is categorised into sexual and asexual forms. Sexual reproduction is almost exclusively a function of the mycobiont, which produces ascospores in fruiting bodies called apothecia. These spores disperse alone and must encounter a compatible photosynthetic partner in the environment to re-establish the symbiosis. Asexual reproduction is often more efficient as it disperses the entire symbiotic system simultaneously, and many lichens produce specialised propagules such as soredia, microscopic clusters of fungal hyphae enclosing algal cells that can establish new thalli independently (Honegger 2008; Honegger & Scherrer 2008). Reindeer lichens are not known to have soredia, and although apothecia have been documented and shown to release viable, germinating ascospores (Athukorala et al. 2015), fragmentation of the thallus is regarded as the primary means of reproduction and dispersal (Webb 1998; Duncan 2015).

Lichen fragments can spread by wind, water, and animals (Heinken 1999; Seaward 2008). Most fragments travel only short distances, during a 15-day study most wind-dispersed fragments remained within 20 cm of the source, with a maximum of under 70 cm in open vegetation, while animal disturbance moved fragments up to approximately 10 metres (Heinken 1999). Movement and establishment of fragments are also strongly influenced by substrate: in a one-year field experiment, only 7% of fragments remained within a 3-cm radius on bare mineral soil in a clear-cut, whereas on moss and twig substrates 70–76% remained within a 3-cm radius . Over longer timescales, repeated inventories around restoration sites found that it took between 5 and 10 years for lichen fragments to colonise areas 10 m from the edge of a transplanted plot, and within eleven growing seasons reindeer lichen had dispersed by at least 20 m from the restoration plots on all sites, with some fragments reaching up to 60 m (Roturier et al. 2024). Fragmentation occurs mainly through trampling and grazing by animals, but also by frost heave during freeze-thaw cycles and physical disruption by encroaching ericaceous shrubs and is promoted by the high brittleness of dry thalli (Yarranton 1975; Heinken 1999). Invertebrates such as snails may also play a role, as viable thalli have been shown to regenerate from fecal pellets after gut passage (Boch et al. 2011).

3.1.7 Factors affecting lichen growth

Lichen growth is highly dependent on the simultaneous availability of moisture and light, as photobiotic activity, and thus growth, is restricted to periods when the thallus is hydrated (Gaio-Oliveira et al. 2006). As poikilohydric organisms, lichens lack active control over their water status, which equilibrates passively with the surrounding environment. Although reindeer lichen growth has been shown to be correlated with mean daily rainfall (Kärenlampi 1971), it is not total precipitation per se that matters, but the duration of photosynthetically active hydration. Peak growth therefore occurs during those periods within the snow-free season when moisture and light coincide, whereas wet periods in darkness represent a net carbon cost through continued respiration without photosynthetic gain (Palmqvist 2000; Jonsson Čabrajič et al. 2010). Consequently, lichens in open, well-lit habitats intercept substantially more light during wet and active periods, resulting in faster growth than in shaded conditions (Palmqvist et al. 2008; McMullin & Rapai 2020). Of the three principal environmental drivers, water availability and light are together the dominant controls on lichen productivity, while temperature plays a comparatively minor role, at least in boreal and temperate climates (Palmqvist 2000). Temperature nonetheless acts both indirectly, by influencing how quickly the thallus dries out, and directly, by affecting photosynthetic and respiratory rates (Benedict 1990). Although lichens can maintain active photosynthesis below 0°C, rates are substantially reduced compared to higher temperature optima, with variation among species and environments (Lechowicz 1982; Harrisson et al. 1989). For *Cladonia rangiferina* in boreal forest, net photosynthesis peaks at moderate thallus hydration and temperatures between 15 and 25°C, requiring only about 30% of full sunlight to reach maximum photosynthetic rates (approximately 600 µmol photons m^{-2} s^{-1}) (Tegler & Kershaw 1980).

3.1.8 Lichen growth rates

Lichens are typically long-lived and slow-growing (Asplund & Wardle 2017). Growth rates of reindeer lichens are most often expressed as linear growth. Following the method of Andreev (1954), it is measured by counting the branching points along the podetia, where each section between two branching points represents one year's growth, and dividing the total height of the living podetium by that number. McMullin & Rapai (2020) synthesised 17 studies from six countries and found mean linear growth rates of 4.7 mm yr^{-1} for *Cladonia arbuscula/mitis*, 5.1 mm yr^{-1} for *C. rangiferina/stygia*, and 4.8 mm yr^{-1} for *C. stellaris*. In boreal pine forest in Finland, which is comparable to conditions in Swedish reindeer winter pastures, the growth rate for *Cladonia rangiferina* ranged from 3.9 to 4.3 mm $year^{-1}$ and for *Cladonia mitis* from 3.0 to 3.5 mm $year^{-1}$ (Helle et al. 1983). While practical and widely used, this measure only captures upward growth and does not account for sideway expansion, or the balance between new growth and the buildup of dead material at the base. For questions of long-term pasture productivity and recovery, biomass-based growth might therefore be more informative.

Biomass growth is commonly expressed as the relative growth rate (RGR; g g^{-1} yr^{-1}), which represents the proportional increase in biomass per unit time, an RGR of 0.08 yr^{-1} thus corresponds directly to an 8% annual biomass increase relative to standing stock. Across the literature, RGR of reindeer lichens varies widely depending on study system, from approximately 2% yr^{-1} under severe post-overgrazing conditions (Ektova & Morozova 2015) to over 26% in undisturbed reconstructed mats (Crittenden et al. 1994). In grazed boreal pine forest stands, annual biomass growth rates are generally low, typically in the range of 2–3% in dense intact mats (Gaio-Oliveira et al. 2006) and around 2% across heavily grazed Finnish ranges (den Herder et al. 2003). Peak productivity approaches 6–7% in ungrazed stands at intermediate lichen biomass levels (Kumpula et al. 2000). Higher rates have been reported during recovery from overexploitation in tundra settings, with mean RGR of 8.3% in open plots on Finnmarksvidda (Tømmervik et al. 2012), though the open conditions at the tundra and an unusually wet study period limit direct transferability to Swedish boreal forest.

The effect of grazing on RGR depends on grazing intensity. Moderate grazing keeps the mat young and prevents self-shading, increasing RGR per unit biomass, while heavy grazing removes the photobiont-rich upper thallus parts leaving only unproductive lower tissue, strongly reducing RGR (den Herder et al. 2003). Gaio-Oliveira et al. (2006) confirmed this experimentally, showing that thinned mats retaining upper thallus parts had substantially higher RGR than intact dense controls or treatments leaving only lower parts. However, even if RGR per unit biomass is temporarily elevated in a grazed mat, total pasture output depends on both growth rate and standing stock. Kumpula et al. (2000) illustrate this clearly: a heavily grazed stand at 300 kg DM ha^{-1} growing at 7% produces only 21 kg DM ha^{-1} yr^{-1}, compared to 175 kg DM ha^{-1} yr^{-1} at the productivity optimum of 2700 kg DM ha^{-1}, meaning that reductions in standing stock through overgrazing dramatically reduce absolute pasture productivity regardless of the proportional growth rate.

3.1.9 Lichen accessibility

For reindeer, the presence of lichen does not guarantee a usable resource, accessibility depends on whether forage can actually be reached and utilised (Horstkotte et al. 2022). Accessibility is constrained by seasonal snow and ice conditions, and further reduced by direct and indirect impacts from competing land use through physical barriers, behavioural disturbance from human activity and predators that disrupts grazing peace and may force abandonment of otherwise rich pastures (Skarin & Åhman 2014; Tyler et al. 2021). Together, these factors narrow the functionally available pasture, often far beyond what the physical footprint of infrastructure or land cover maps alone would suggest (Niebuhr et al. 2022).

Snow and ice constitute the most pervasive seasonal barrier. The characteristics of the snow cover are primarily governed by climatic drivers, while topographic as well as vegetation structure and forest canopy, act as modifying forces (Horstkotte & Roturier 2013). Extreme winter events are particularly consequential: rain-on-snow and freeze–thaw cycles create ice-locked pastures with impenetrable layers within the snowpack or basal ice directly on the ground (Hansen et al. 2011), and such events are projected to increase in frequency with a warming climate (Putkonen & Roe 2003; Hansen et al. 2011; Eira et al. 2018). Rugged terrain creates greater variation in snow and ice conditions through its effects on wind exposure and meltwater runoff (Skogland 1978; Hansen et al. 2011). Forest structure also plays an important role, as canopy characteristics influence snow interception, depth, and hardness on the forest floor (Horstkotte & Roturier 2013; Kater & Baxter 2022). Old-growth pine forests with large, wide-crowned trees shelter the ground and produce shallower, more variable snow, while clear-cuts and young dense stands accumulate deeper snow and are more exposed to wind-hardening and icing (Inga 2009; Horstkotte & Roturier 2013; Kater & Baxter 2022). In order to respond to weather variations and maintain access to forage through the winter diversity in the landscape is needed (Roturier & Roué 2009; Horstkotte & Roturier 2013). Because snow conditions strongly influence winter habitat selection, their spatial and temporal variability must be accounted for in assessments of pasture quality and habitat selection. Detailed snowpack models are now able to predict challenging conditions such as deep snow, hard layers, and ice crusts (Vikhamar-Schuler et al. 2013; Turunen et al. 2016; Perkins et al. 2024). Modelling snow conditions is a key to projecting how climate change may alter lichen accessibility over time, particularly as warming is expected to be strongest in the north and during winter (IPCC 2023; Strandberg et al. 2026).

Apart from removing valuable lichen resources, forestry may also create physical barriers through dense young regenerating stands with high stem density that limit the ability to manoeuvre and dig for lichens. (Kater & Baxter 2022). This effect is particularly pronounced in plantations of the exotic lodgepole pine (*Pinus contorta*), whose dense canopies and low branches can create stands that impede reindeer use of the area (Horstkotte et al. 2023). Logging residues, branches and tree crowns left after harvest, can render roughly one-third of a logged area physically inaccessible for at least five years (Berg et al. 2008). Roads may act as semi-permeable barriers that reduce movement between pastures (Beyer et al. 2016). While these barriers occupy a limited spatial footprint, for some of them the influence extends further through avoidance behaviour.

Avoidance is a behavioural response triggered by visual, auditory, or scent-based cues from humans or human-made structures, whether perceived directly or through learned associations with infrastructure (Tyler et al. 2021). The resulting losses in habitat use are spatially extensive yet easily overlooked. The effect is typically described as a zone of influence (ZOI), defined as the distance from infrastructure at which the effect on habitat selection diminishes to background levels (Boulanger et al. 2021). The extent of the ZOI varies considerably between herds, seasons, and years, reflecting the interplay between habitat quality, forage availability, and the perceived level of disturbance (Vistnes & Nellemann 2008; Boulanger et al. 2021; Lessard et al. 2026). Avoidance and effects on reindeer behaviour have been documented across a wide range of infrastructure and activity types, including mines (Plante et al. 2018; Boulanger et al. 2021), wind power plants (Skarin et al. 2018), hydropower developments (Nellemann et al. 2003; Dorber et al. 2023), roads (Beyer et al. 2016; Plante et al. 2018), power lines (Vistnes & Nellemann 2001), cabins and tourist resorts, and skiing and snowmobile trails (Vistnes & Nellemann 2001; Panzacchi et al. 2013; Boulanger et al. 2021; Lessard et al. 2026). Predation and the perceived risk of predation represent a further source of functional habitat loss. Reindeer may avoid areas with high predator density even when forage conditions are favourable, effectively shrinking the usable pasture area (Sivertsen et al. 2016; Rivrud et al. 2018; Viejou et al. 2018).

The effects of individual disturbance sources are rarely experienced in isolation. Reindeer herds must simultaneously contend with forestry-driven changes in vegetation and snow conditions, expanding infrastructure networks, and climatic variability, and the combined impact of these stressors may exceed what would be predicted from any single factor alone. While the need to account for such cumulative effects on Rangifer is widely acknowledged (Vistnes & Nellemann 2008; Johnson et al. 2015), most empirical studies still assess each infrastructure type in isolation, typically by measuring the distance to the nearest feature (Niebuhr et al. 2023; Lessard et al. 2026). Niebuhr et al. (2023) proposed a cumulative ZOI framework that estimates the combined effect of multiple anthropogenic features distributed across a landscape, offering a more realistic basis for quantifying functional habitat loss.

3.2 Evolution of methods for lichen assessment and animal movement analysis

3.2.1 Methods for mapping and quantifying lichens

Assessing reindeer pastures has a long history in Sweden, following the general development of vegetation studies, originally relying on direct field mapping and vegetation inventories (Küchler 1967; Mueller-Dombois & Ellenberg 1974). As early as 1909 and 1913, the Reindeer Pasture Commissions established a foundational methodology for reindeer pasture grading systems based on the distribution and composition of distinct plant communities (Skunke 1958). The work of the 1964 Swedish–Norwegian Reindeer Pasture Commission built upon this foundation. While earlier investigations relied heavily on subjective grading by experts, the 1964 commission further developed this methodology by transitioning to more objective, measurable data (Svensk-norska renbeteskommissionen av 1964 1967). The commission identified 20 vegetation types and calculated the annual gross production for each, measured in feed units (f.e.) per km², both for the winter season—divided into lichen and non-lichen—and for the snow-free season. By linking the energy output of these plant communities to the daily nutritional needs of reindeer, the commission was able to calculate the biologically optimal number of reindeer the land could support. They also calculated practically optimal reindeer numbers, a reduced figure that accounted for real-world limiting factors such as difficult terrain, climate, and the effects of other land uses. The commission's approach to divide an area into vegetation classes and use data on how much each class produce still has application, for example to calculate pasture loss following industrial development (Tømmervik et al. 2022).

A notable feature of the 1964 commission's work was the use of helicopters and airplanes to conduct line-transect surveys in which observers directly recorded the frequency of different vegetation types from the air. The continued development of such aircraft platforms, along with satellites and advances in sensor and camera technologies throughout the 20th century, led to the establishment of remote sensing as a standard approach for vegetation mapping and land-cover analysis (Campbell & Wynne 2011; Lillesand et al. 2015). For lichen mapping, satellite imagery has been used to classify discrete pasture type classes (Colpaert et al. 2003; Théau et al. 2005), lichen cover classes (Gilichinsky et al. 2011), continuous lichen cover

(Nelson et al. 2013; Hillman & Nielsen 2020; Kennedy et al. 2020; He et al. 2024), lichen volume (Falldorf et al. 2014), as well as lichen biomass (Erlandsson et al. 2022).

While the approaches described above are primarily used at broader scales, a range of field-based methods has also been applied for more detailed estimation of lichen cover and biomass, as well as for providing ground truth data for remote sensing mapping. Field inventories of ground lichen typically collect data on cover alone or on both cover and height, measured in subjectively, randomly, and/or systematically distributed sample plots (Thomas et al. 1996; Rosso et al. 2014; Greuel et al. 2021; Errington et al. 2022) using either visual estimates or point-intercept methods (Moen et al. 2007; Rosso et al. 2014). Where biomass estimates are required, an allometric equation is commonly used to relate either lichen cover alone (Thomas et al. 1996; Dunford et al. 2006; McMullin et al. 2011) or lichen volume (cover × height) (Arseneault et al. 1997; Kumpula et al. 2000; Moen et al. 2007; Olofsson et al. 2011; Odland et al. 2014; Rosso et al. 2014; Greuel et al. 2021; Errington et al. 2022) to biomass.

More recent developments in remote sensing technologies have further advanced vegetation mapping and monitoring. Unoccupied aerial vehicles (UAVs), commonly operated as small drones, have emerged as flexible and cost-effective platforms for acquiring high-resolution spatial data, bridging the gap between traditional field-based vegetation surveys and satellite remote sensing (Anderson & Gaston 2013; Tmušić et al. 2020). In parallel, new machine learning approaches—particularly deep learning methods—are increasingly applied to automate vegetation classification, mapping, and feature extraction from diverse data sources (Maxwell et al. 2018; Ma et al. 2019). Several studies have explored the use of UAVs for lichen mapping, using classical machine learning methods such as random forest (Macander et al. 2020; Fraser et al. 2022), while others have combined UAV imagery with deep learning approaches including neural networks and image segmentation (He et al. 2021; Jozdani et al. 2021; Richardson et al. 2021; G. Richardson et al. 2023). At the field level, image segmentation using U-Net has also been applied to estimate the cover of reindeer lichens from ground photographs (Lovitt et al. 2022).

3.2.2 Methods for analysing animal movement and habitat selection

Early approaches to quantifying animal habitat use focused on the utilization distribution (UD), a probability surface describing the relative frequency of space use estimated using kernel density methods (Worton 1989). Resource selection functions (RSFs) formalised the link between space use and environmental covariates by comparing used to available locations using logistic regression (Boyce et al. 2002; Manly et al. 2002; Johnson et al. 2006), and are well established as a tool for identifying key habitat features and quantifying functional habitat loss following landscape change. However, RSFs typically treat locations as independent observations and do not explicitly account for the movement process connecting them.

Step selection functions (SSFs) addressed this by framing habitat selection in terms of movement steps between consecutive relocations, anchoring availability to the animal's actual movement capacity (Fortin et al. 2005; Thurfjell et al. 2014). Integrated step selection functions (iSSFs) extended this by simultaneously estimating habitat selection and movement parameters, step length and turning angle distributions, within a single conditional logistic regression model (Avgar et al. 2016; Signer et al. 2019; Fieberg et al. 2021). Because iSSFs explicitly estimate movement parameters, they can detect changes in movement behaviour itself, such as reduced step lengths or altered turning angles near roads, fences, or industrial infrastructure (Prokopenko et al. 2017), making them particularly powerful for assessing disturbance and barrier effects.

Utilization distribution estimation has developed in parallel. Brownian bridge movement models (BBMMs; Horne et al. 2007) improved on kernel density methods by conditioning the UD on the path between consecutive locations. The dynamic Brownian bridge movement model (dBBMM; Kranstauber et al. 2012) further allowed the diffusion parameter to vary along the trajectory, enabling detection of behavioural shifts between resident and transient movement modes. Both approaches produce UD surfaces that can be compared before and after landscape changes to quantify displacement from key habitats (Benhamou & Cornélis 2010; Sawyer & Kauffman 2011).

In addition, continuous-time movement models represent the trajectory as a continuous stochastic process, with Ornstein–Uhlenbeck-based models capturing both home range attraction and movement autocorrelation (Fleming et al. 2014; Calabrese et al. 2016). These enable more rigorous UD estimation from autocorrelated telemetry data through autocorrelated kernel density estimation (AKDE; Fleming et al. 2015), correcting the bias that arises when serially dependent locations are treated as independent.

Deep learning has also been proposed as a flexible alternative for modelling animal movement. Forrest et al. (2026) introduced deepSSF, a deep learning extension of the iSSF framework that learns movement and selection processes directly from data without requiring the modeller to decide in advance how each covariate should shape the response.

Both iSSF and deepSSF models can also be used to simulate animal trajectories, enabling prediction of utilization distributions, evaluation of model fit, and assessment of landscape connectivity (Signer et al. 2024; Forrest et al. 2026).

Together, these developments reflect a broader shift from describing where animals are found to modelling how they move and respond to their environment, enabling more realistic inference about animal–landscape interactions.

4. Material and methods

The data used in the four papers of this thesis originate from several reindeer herding communities and study sites across the Sámi reindeer husbandry area in Sweden. Each study area used in each paper is indicated in Figure 1.

Figure 1. Overview of the study areas used across the papers in this thesis. The map shows the Sámi reindeer husbandry area (RHA) in Sweden (darker area). The dotted areas with white borders indicate the eight reindeer herding communities (RHCs) from which GPS data were used to validate the lichen map in Paper I (north to south: Gällivare, Udtja, and Malå, which are forest RHCs where reindeer remain in the boreal forest year-round, and Vilhelmina norra, Vilhelmina södra, Njaarke, Tåssåsen, and Mittådalen, which are mountain RHCs where reindeer typically migrate seasonally between winter grazing areas in the boreal forest and summer pastures in the mountains to the west). Malå RHC, marked with a thicker white border, was also the study area for Paper IV. The area within the dashed magenta border shows the area covered by the lichen map in Paper I. Yellow dots mark the cities nearest the study sites where ground-level photographs for lichen image segmentation were acquired for Paper III (north to south: Fredrika, Umeå, and Sveg). The study sites near Umeå were first used for local-scale method development in Paper II.

This material and methods chapter and the following results chapter present the methods and results structured around the four aims of the thesis, meaning that each section may draw on contributions from multiple papers.

4.1 Broad-scale – a lichen cover map for the reindeer winter grazing area in Sweden validated using reindeer GPS positions (Paper I)

In Paper I we described the development of the first ground lichen cover map of the Swedish winter grazing area. A central contribution of the paper was the validation approach, which tackled the challenge of how predictions made across such extensive areas can be assessed.

Lichen cover was modelled using a generalised additive model (GAM) (Hastie & Tibshirani 1990), with six Sentinel-2 spectral bands and derived indices (NDVI and NDSI), together with LiDAR-derived tree height and canopy cover and soil type as predictors. Lichen cover data from the Swedish National Forest Inventory (NFI) were used as ground truth. We evaluated model performance using root mean square error (RMSE) and root mean square error of Prediction (RMSEP) from 10-fold random cross-validation (Hastie et al. 2009).

In addition to this traditional validation, we used the strong consumer–resource relationship between reindeer and ground lichen to validate the map using reindeer GPS locations. This cross-species validation approach assessed whether, and how consistently, reindeer occurrence and habitat selection patterns aligned with mapped lichen distributions. We expected that areas with high lichen cover would be used more by reindeer than other available areas, and that predicted lichen cover would significantly explain habitat selection and improve model performance compared to other publicly available environmental variables. This was tested using hurdle models and integrated step-selection functions (iSSF).

Integrated step-selection functions estimate habitat selection by comparing environmental characteristics at observed locations (GPS positions) with those at available but unused locations, while accounting for movement constraints such as step length and turning angle distributions (Avgar et al. 2016). We used 2-hour interval GPS data from eight reindeer herding communities, focusing on January to March, when reindeer dependence on lichen is greatest. For each observed location, 20 available points were randomly generated based on observed step lengths and turning angles. We first used this dataset to assess whether the lichen map showed higher lichen cover at locations used by reindeer compared to available locations. Because the mapped lichen cover contained many zeros and a right-skewed distribution of positive values, we applied a hurdle model. We modelled predicted lichen presence/absence using logistic regression, testing whether used locations were more likely to contain lichen than available locations. To test whether used locations had higher predicted lichen cover when lichen was present, we modelled predicted lichen cover using a generalised linear model with a gamma distribution and log link.

To evaluate selection for predicted lichen and the contribution of environmental variables to habitat selection, we fitted four competing iSSF models for each RHC–year combination using the amt package in R: (1) a base model including slope, aspect, wetness, and movement terms; (2) the base model plus land cover from the Swedish National Land Cover Database; (3) the base model plus predicted lichen cover; and (4) a full model including all variables. Model performance was evaluated using in-sample fit (AIC, ΔAIC) and out-of-sample predictive performance based on 5-fold cross-validation (log-likelihood, ΔCV). Full model coefficients were aggregated across RHC–year combinations using inverse-variance weighting ($w = 1/SE^2$) to obtain RHC-level estimates.

4.2 Local-scale – quantifying lichen cover and biomass (Paper II)

In Paper II we developed a method for estimating lichen cover and biomass at a local scale. We used drone-derived auxiliary information correlated with lichen abundance, in this case NDVI and canopy height with the local pivotal method 1 (LPM 1) (Grafström et al. 2012) to select a sample that was well spread both geographically and with respect to the auxiliary variables.

The study sites were pine heath forests on sandy soils, or pine forests on rocky ground, all within the winter grazing area of Ran reindeer herding community, north of Umeå, Sweden. At each site, we collected multispectral drone images from which we derived orthomosaics and a point cloud. From the orthomosaics, we calculated the normalised difference vegetation index using the near-infrared and red bands (NDVI = (NIR − red) / (NIR + red)), and from the point cloud we derived a canopy height model. Both rasters were resampled to 0.5 m resolution so that each pixel corresponded to a potential 0.5 × 0.5 m sample plot. A sample of 40 plots was then selected at each site. At each plot we collected lichen cover and height from which lichen volume was calculated as cover × height. We then estimated total lichen cover, volume and biomass for each study site by applying the unbiased Horvitz–Thompson estimator (Horvitz & Thompson 1952) and estimated variance using a local mean variance estimator suggested for samples selected with the local pivotal method (Grafström & Schelin 2014).

To estimate lichen biomass from volume we used an allometric equation, avoiding the destructive and time-consuming alternative of collecting and weighing all lichen from the sample plots. To derive this equation, we conducted a literature review in which we gathered data from previous studies that had established similar relationships. We then used these data to derive a new relationship by fitting a linear regression through the origin, with lichen biomass (kg dry weight m^{-2}) as the response variable and lichen volume (dm^3 m^{-2}) as the predictor variable.

4.3 Plot-scale – evaluating methods for lichen cover estimation (Paper II and Paper III)

In Paper II we compared three methods used for lichen cover assessment at field-plot scale. At each sample plot, we placed a 0.5 m × 0.5 m frame divided into 36 squares. We measured the height of the lichen to the nearest 0.5 cm by lowering a metal rod (3 mm diameter) to the base of the lichen at each of the 25 intersections created by the 36 squares, recording the measurement at the highest point where the lichen contacted the rod. The average of these measurements was then calculated to represent the lichen height for each plot. We determined percent lichen cover using three different methods, (i) percent of squares with presence of lichen (presence-absence), (ii) percent hits, out of 25, by the rod (point-intercept), and (iii) visual estimate of percent lichen (visual estimate).

In Paper III we built on the experience from Paper II and developed a deep learning semantic segmentation model to classify each pixel in 2048 × 2048 pixel RGB photographs of the 0.5 × 0.5 m sample plots as either ground lichen or non-lichen, giving a direct estimate of cover within the image. Compared to existing field methods, we expected this approach to be more consistent than visual estimation and faster and more convenient than point-intercept sampling. We developed two models in sequence. We first trained a main model on a small set of carefully hand-annotated high-resolution images to achieve the best possible segmentation accuracy. We then used this trained model to generate predicted lichen masks for a much larger set of about 1,250 field photographs collected across a wide range of lichen growth environments. We downsampled the resulting image–mask pairs to a lower resolution (512 × 512 pixels) and used them as training data for a lightweight companion model intended for on-device inference on mobile hardware. This model-assisted annotation workflow made it practical to train the app model on a substantially larger and more diverse dataset than would have been feasible through manual annotation alone.

For both models, we compared several encoder architectures spanning convolutional neural networks (CNNs) and vision transformers, paired with U-Net or UNet++ decoders, under five-fold cross-validation, and retrained the best configuration on all available data. We evaluated predictions against held-out annotations and compared them against visual field cover estimates from three study areas in northern Sweden (Umeå, Sveg, Fredrika). To test the consistency of the cover estimates, we compared predictions from images of the same sample plots taken with different cameras and with and without test-time augmentation, where each image was predicted multiple times using geometric transformations (rotations and flips), with the final cover estimate averaged across predictions. The lightweight model was deployed in a proof-of-concept Android application.

4.4 Linking lichen estimates to reindeer grazing and lichen accessibility (Paper IV, Paper I and Paper II)

4.4.1 Analysing cumulative impacts on reindeer habitat selection (Paper IV and Paper I)

In Paper IV we quantified the cumulative impacts of industrial infrastructure on reindeer behaviour using GPS tracking data spanning multiple years before, during, and after wind power plant construction during the snow-free season. This study demonstrates an analytical framework equally applicable to winter conditions, where ground lichen would be a key environmental driver. The calving site analysis is not covered here as it is not relevant to winter conditions.

The study was conducted in Malå Sámi RHC, Sweden, where reindeer remain in the boreal forest year-round. The analyses were designed following methods presented in Niebuhr et al. (2023), adapted to the situation in a reindeer herding community, to capture three key dimensions of cumulative impacts: effect size, zone of influence (ZOI), and accumulation across multiple features and infrastructure types (Figure 2).

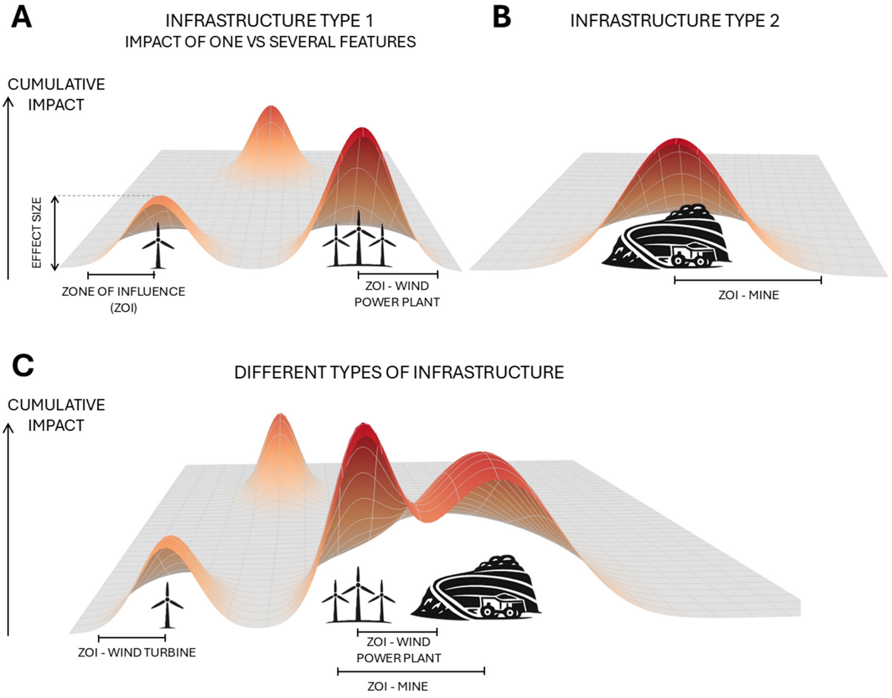


Figure 2. Illustration of the multiple dimensions of impacts measured in Paper IV. (A) A single wind turbine has an effect size and a ZOI radius; when several turbines form a wind power plant, their cumulative impact is larger. (B) The impact of a mine has an effect size and ZOI radius, different from those of wind turbines. (C) When wind turbines and mines are close together, their ZOIs overlap and the total cumulative impact is locally higher. The principle applies to any infrastructure or disturbance type.

Reindeer habitat selection and movement were analysed at two spatial scales. At the landscape scale, habitat selection analyses (HSA) compared used GPS locations to randomly sampled available locations within seasonal ranges. At the patch scale, integrated step-selection analyses (iSSA) jointly modelled habitat selection and movement while accounting for step length and turning angle. To quantify infrastructure impacts, zone of influence variables were calculated as exponentially decaying functions of distance from infrastructure, evaluated across multiple radii (100 m to 10 km). For wind power plants, both distance to the nearest turbine and turbine density within a radius were evaluated to distinguish single-feature from cumulative effects. A before–after design was used to separate baseline, construction, and operation phases. Model selection was based on AIC, allowing simultaneous inference of impact strength, spatial extent, and cumulative effects.

To visualise landscape-scale results, we generated spatial predictions of habitat suitability before, during, and after wind power construction, showing proportional changes relative to the pre-construction period. Habitat suitability was predicted spatially by applying the coefficients from the best-ranked HSA model to raster layers of all environmental and infrastructure predictors across the study area. To isolate the effect of wind power development, predictions were generated separately for each development phase by varying the wind turbine variables while keeping all other predictors constant. The construction and operation maps were then expressed as proportional change relative to the pre-construction baseline, allowing the spatial extent and magnitude of wind power impacts to be visualised across the landscape independently of background variation in habitat quality.

iSSA was also applied in Paper I, where it was used both to validate the lichen cover map and to assess whether it added explanatory value for understanding reindeer habitat selection in winter beyond other publicly available environmental variables such as land cover type, elevation, and wetness.

4.4.2 Lichen biomass to reindeer grazing days

A further step in linking lichen resources to reindeer is taken in Paper II, where we link lichen biomass estimates to reindeer by calculating the number of sustainable reindeer grazing days per hectare at each study site. Assuming that only the annual lichen growth can be consumed for grazing to remain sustainable, we used a growth rate of 4 mm year^{-1} and subtracted 4 mm from the mean lichen height in each sample plot to estimate the previous year's biomass, with the difference representing the annual biomass increase. For daily lichen consumption, we used an average intake of 1.5 kg day^{-1} plus 0.75 kg of wastage from cratering, resulting in a total daily consumption of 2.25 kg per reindeer. The number of grazing days was then estimated by dividing the annual biomass increase by the daily consumption.

5. Main results

5.1 Broad-scale – a lichen cover map for the reindeer winter grazing area in Sweden validated using reindeer GPS positions (Paper I)

The GAM for lichen cover explained 57.4% of the total deviance, with tree height, NDVI, and Sentinel-2 bands 11 and 2 identified as the most influential predictors. Ten-fold cross-validation yielded an RMSE of 0.0179 ± 0.0005 and an RMSEP of 0.0219 ± 0.0053. Lichen cover in the training data was highly skewed, with most plots having zero or less than 5% cover, and few exceeding 20%. This skewness was evident in the observed versus predicted relationship (Figure 3a), which showed substantial scatter around the trend line. Residual analysis further indicated a tendency to underestimate lichen cover at higher predicted values, reflected by negative residuals (Figure 3b). While 57.4% explained deviance alone might raise questions about the map's usefulness, the cross-species validation provided complementary evidence by using reindeer movement as a behavioural indicator of resource distribution, reflecting functional relevance rather than statistical agreement alone.

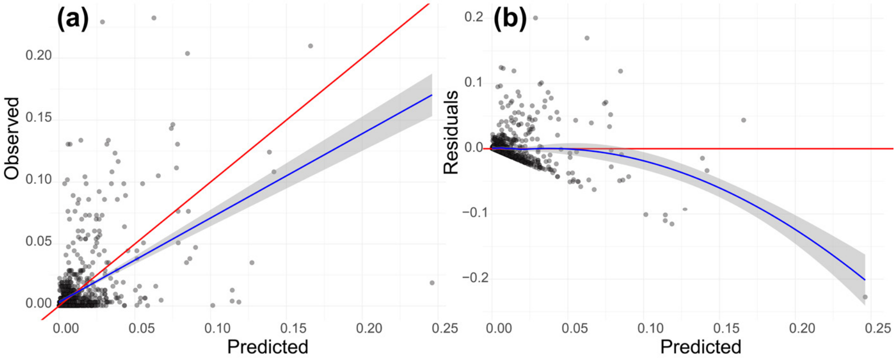


Figure 3. Validation results from 10-fold cross-validation of the GAM model used to produce the lichen map. (a) Observed vs. predicted lichen cover. The red line shows the 1:1 relationship and the blue line the fitted trend. (b) Residuals (observed − predicted lichen cover) vs. predicted values; negative residuals indicate underestimation. Each point represents one validation sample.

Hurdle models comparing used and available locations showed that reindeer positively selected for areas with higher predicted lichen cover. Used locations were more likely to have lichen present according to the map, and when lichen was predicted to be present, used locations had higher predicted cover than available locations (Figure 4).

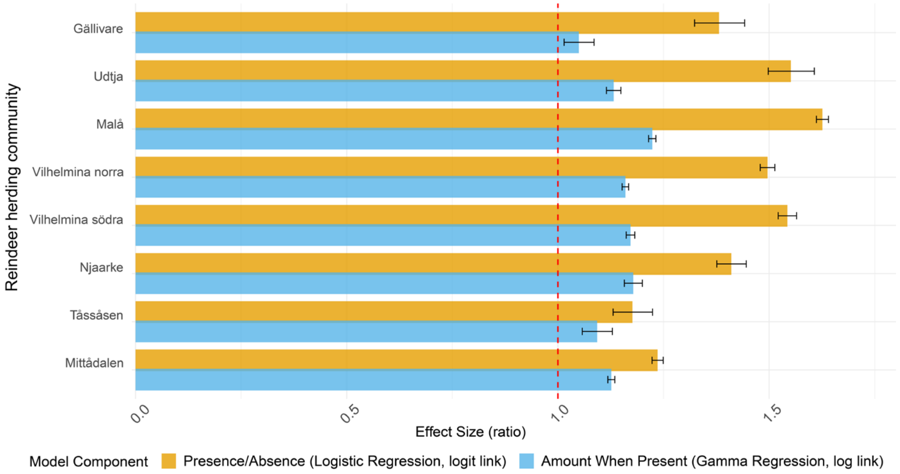


Figure 4. Hurdle models analysing lichen cover in used versus available reindeer locations for each reindeer herding community. Orange bars show odds ratios from logistic regression models of predicted lichen presence at GPS locations used by reindeer compared with available locations. Blue bars show multiplicative effects from a gamma regression (lichen amount when present), testing whether used locations have higher predicted lichen cover when lichen is present. Values > 1 indicate positive selection.

Comparing the four iSSF model structures for each RHC across all available years revealed that adding either predicted lichen cover or land cover classification (NMD) substantially improved model fit over the base model, and the full model combining both outperformed the other model structures across all RHCs (Figure 5). Cross-validation results showed the same pattern: both predicted lichen cover and land cover classification improved model fit, and the full model achieved the highest out-of-sample predictive performance in all RHCs.

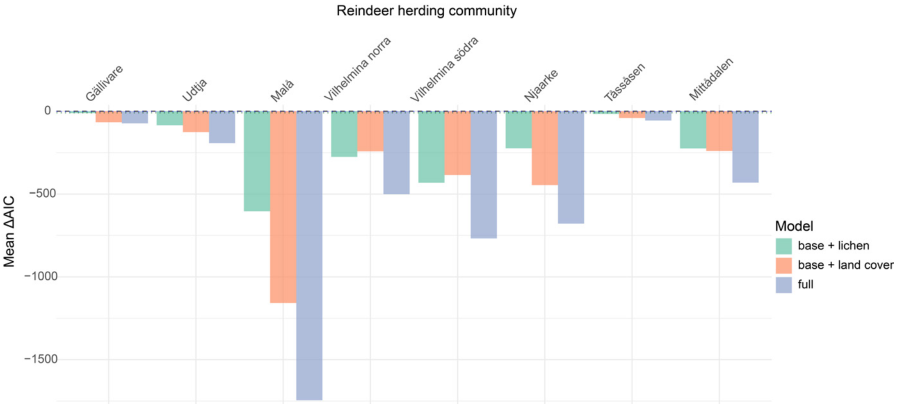


Figure 5. Model fit of four iSSF model structures relative to the base model, expressed as mean ΔAIC across reindeer herding communities, showing the contribution of lichen cover, land cover, and their combination to explaining reindeer habitat selection. More negative values of ΔAIC indicate better model fit relative to the base model that included slope, aspect, wetness, and movement variables. All three enhanced models (base model plus lichen, base model plus land cover, and full model) yielded negative mean ΔAIC values for all RHCs, indicating improved performance compared to the base model.

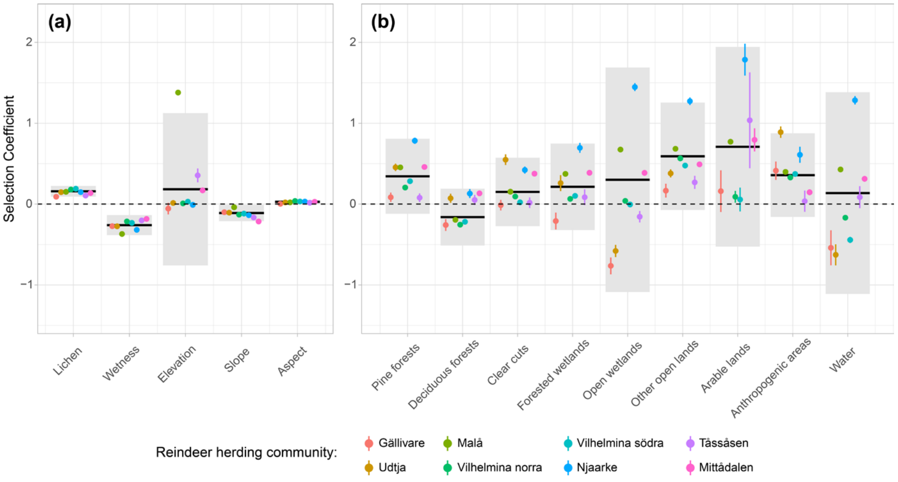


Figure 6. Habitat selection coefficients for each of the variables used to assess reindeer habitat selection at the reindeer herding community (RHC) level. (a) Continuous (standardised) variables and (b) land cover classes. The black horizontal lines represent the weighted mean coefficient across all RHCs. Coloured error bars represent ±1 SE around each RHC's weighted mean, indicating precision of the estimation. Grey bands represent ±1.96 × SD of the RHC-level estimates around the population mean, indicating spatial variation among RHCs.

The full model coefficients showed that reindeer consistently selected areas with higher predicted lichen cover across all RHCs. This pattern was stable, with lower variation among RHCs than for other variables. Although selection for some variables, particularly elevation, was occasionally stronger, selection for lichen was more consistent across reindeer herding communities (Figure 6a). This consistency was also observed across years. Reindeer showed positive selection for all land cover classes except deciduous forests, relative to the reference class (other coniferous forests), although both the strength and spatial consistency of selection varied considerably among RHCs (Figure 6b).

Although our cross-species validation approach — using reindeer to validate the lichen map — does not provide a simple validation score, the consistent selection for lichen across all herding communities and years, combined with the improvement in iSSF model fit when incorporating the lichen map, showed that the map captures meaningful variation in both lichen presence and cover.

The mapping and validation workflow developed in this study is illustrated in three steps in Figure 7.

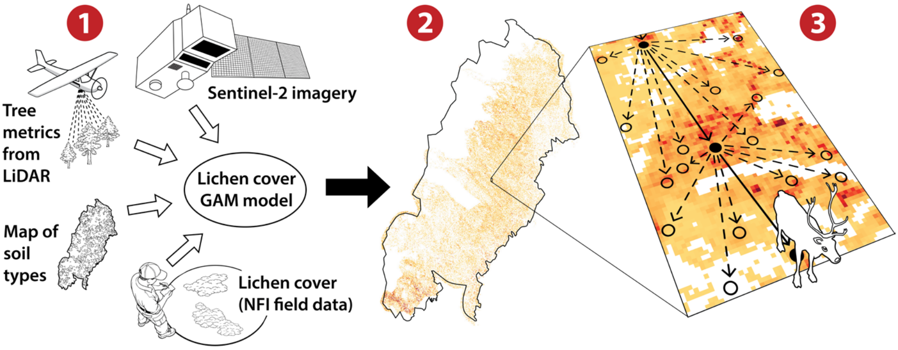


Figure 7. Overview of the production and validation of the ground lichen cover map of the reindeer winter grazing area of Sweden. (1) Training of a generalised additive model (GAM) including traditional model evaluation. (2) The lichen cover map with continuous lichen cover predicted by the GAM model. (3) Cross-species validation using reindeer GPS positions and integrated step selection functions to assess the map.

5.2 Local-scale – quantifying lichen cover and biomass (Paper II)

In our literature review aiming to establish a relationship between lichen volume and biomass we found five adequate studies in which data were accessible. The linear regression through the origin for all data combined resulted in a slope of 0.0148 (Figure 8). Our comparison helped clarify the extent to which the relationships between lichen volume and biomass differed across studies, but pinpointing specific causes was not possible with the available information. Differences likely stem from a combination of methodological variation, observer effects in lichen cover assessment, and differences in species composition and environment. However, our derived slope was similar to that of Moen et al. (2007) and Kumpula et al. (2006), whose data came from comparable conditions, which supported its use in our study, although Kumpula et al. (2006) could not be included in the direct comparison as the underlying data were unavailable.

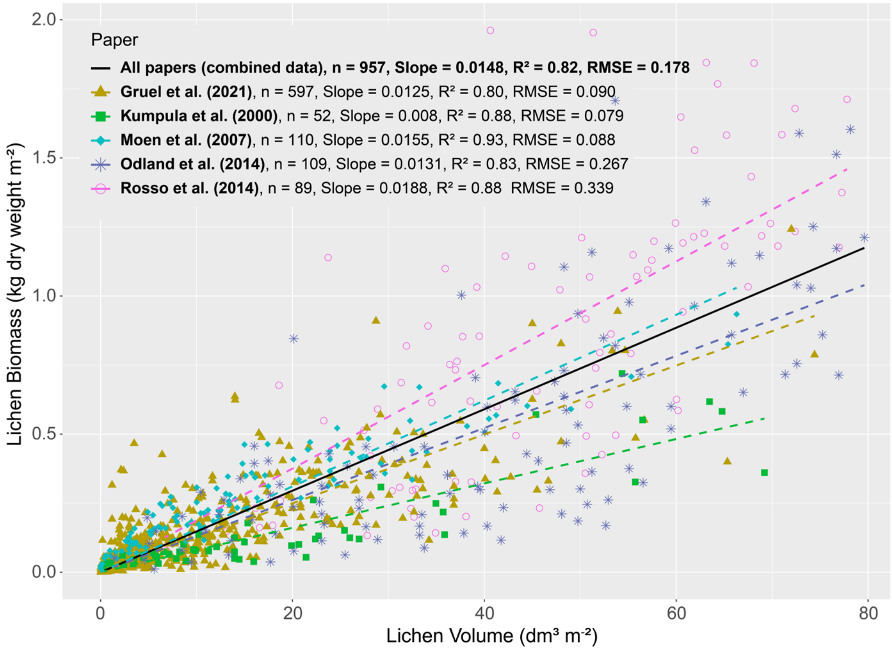
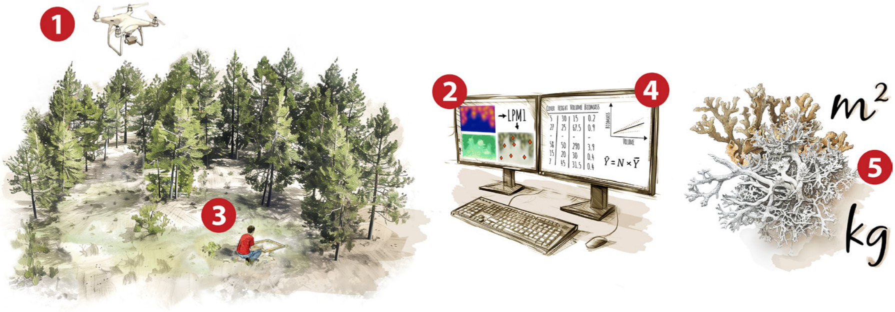


Figure 8. Association between lichen volume (dm^3 m^{-2}) and biomass (kg dry weight m^{-2}). Linear regression through the origin for each paper from our literature review (dashed lines) and for data from all papers combined (solid black line), with the number of points (n), slope, R-squared value (R^2) and root-mean-square error (RMSE).

The estimates of lichen cover and biomass were highly dependent on the method used to assess lichen cover in the sample plots, which is discussed in Section 5.3. Across study sites, point-intercepts resulted in cover estimates of 2270–2840 m² ha⁻¹ and biomass estimates of 649–1232 kg ha⁻¹, while visually estimated cover resulted in considerably lower values: 1190–1715 m² ha⁻¹ for cover and 334–784 kg ha⁻¹ for biomass. The RSE for our biomass estimates was around 15–20%, making a sample size of 40 a reasonable balance between fieldwork effort and estimation precision.

Used with an appropriate method to determine lichen cover in the sample plots, our method (Figure 9) provides a robust and objective approach for estimating ground lichen cover and biomass at the local scale. Both NDVI and canopy height were negatively correlated with lichen. When used as auxiliary variables in the local pivot method with a local mean variance estimator, this can reduce the variance of the Horvitz–Thompson estimates, allowing a desired level of precision to be achieved with fewer sample plots and at lower cost.



Cover	Height	Volume	Biomass
5	30	15	0.2
27	25	67.5	0.9
-	-	-	-
58	50	290	3.9
15	20	30	0.4
7	45	31.5	0.4

Figure 9. Overview of the method developed for estimating ground lichen cover and biomass at the local scale. (1) Drone data collection — Multispectral images collected by a drone were used to acquire detailed and site-specific information about the study site (NDVI and tree height). (2) Sampling using NDVI and tree height as auxiliary data with the local pivotal method 1 (Grafström et al., 2012) to obtain a sample that was well spread both geographically and with respect to the auxiliary variables. (3) Field data collection — lichen cover and height were recorded. (4) Biomass for each sample plot was estimated using the relationship between volume and biomass derived from our literature review. (5) Lichen cover and biomass for the entire site were estimated using the Horvitz–Thompson estimator.

5.3 Plot-scale – evaluating methods for lichen cover estimation (Paper II and Paper III)

The comparison of the methods for assessing lichen cover in Paper II showed that point-intercept yielded higher cover estimates than visual estimation but lower cover than presence-absence (Figure 10). Point-intercept and visual estimates were linearly correlated ($R^2 = 0.77$, slope = 0.70) with errors evenly spread around the regression line. The correlation between visual estimates and presence-absence was weaker ($R^2 = 0.48$, slope = 0.39), and plots with high cover according to presence-absence could have almost any value under visual estimation (Figure 10c). The same pattern held when comparing point-intercept to presence-absence ($R^2 = 0.69$, slope = 0.59; Figure 10b), despite the stronger correlation between these two methods.

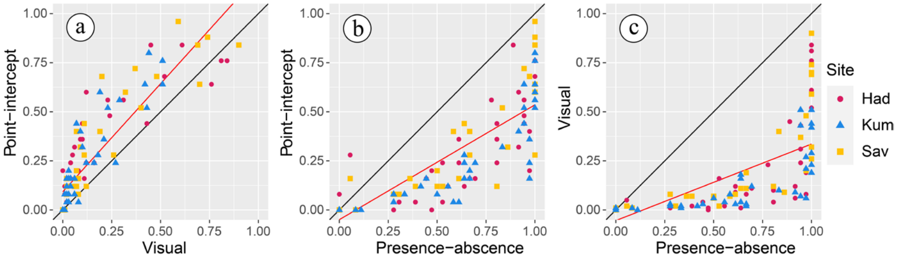


Figure 10. Comparisons between the three methods for estimating lichen cover. a) Point-intercept vs. Visual, b) Point-intercept vs. Presence-absence, and c) Visual vs. Presence-absence. The scale on both axes represents lichen cover, with 1 corresponding to 100% cover. Red lines depict the trend lines resulting from linear regressions, while black lines represent the 1:1 line, indicating a perfect match between the methods. Each data point corresponds to one of the 120 sample plots from the three study sites (Had, Kum, and Sav) in northeastern Sweden, sampled between August and September 2021.

The presence-absence method clearly overestimated cover and is not suitable for this kind of assessment. The other two methods both have advantages: the point-intercept method offers greater objectivity and generally reduces variation between observers compared to visual estimation (Morrison 2016), while visual estimation is faster and with training can provide accurate results.

In Paper III we showed that semantic segmentation of lichen can provide an objective and accurate alternative for measuring cover. Even with a limited amount of training data, we were able to develop a useful segmentation model. Our two-stage workflow, first training a high-resolution model and then using it to generate training data for the lightweight app model, was an effective strategy for scaling up the training set without extensive manual annotation.

For the main model, the MiT-B4 + U-Net combination performed best (mean CV IoU 0.716), with the transformer encoder outperforming the CNN alternatives by a modest margin. Cover prediction error was low (MAE ~1 pp, RMSE 2.42 pp), with only a slight tendency to overestimate. A visual inspection of predicted masks showed successful segmentation across common cases. The lightweight app model (MiT-B1 + U-Net) had lower pixel-level accuracy, as expected from its reduced size, but produced stable cover estimates without extreme outliers, likely benefiting from its larger and more varied training set. A manual inspection indicated that both models performed well across most common cases, producing useful lichen masks overall (Figure 11).

Figure 11. Examples of lichen masks predicted by the final main model. The top row shows the original 2048 × 2048 pixel images and the bottom row the corresponding masks in magenta overlaid on the images. Predicted lichen cover, left to right: 57%, 20%, 66%, 20%.

Test-time augmentation (Figure 12a) and sensor type (camera vs. smartphone) (Figure 12b) both had negligible practical effects on predicted cover, indicating that the model produces reproducible estimates across acquisition conditions. Visual field estimates were systematically higher than model predictions (Figure 12c), with the bias increasing at higher cover levels and varying between observers, consistent with well-documented inconsistencies in visual cover estimation.

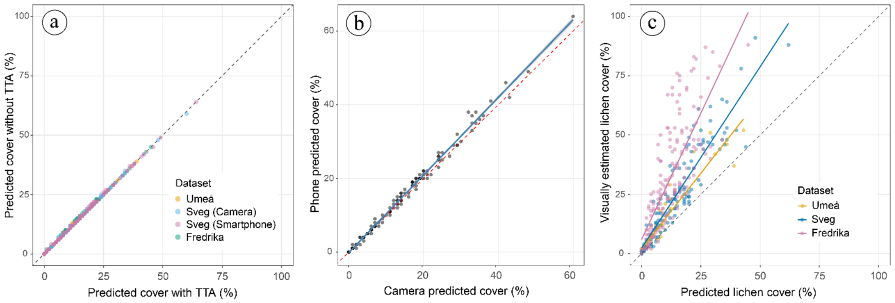


Figure 12. Comparison of predicted lichen cover from the final main model: (a) with and without test-time augmentation, (b) between images of the same sample plots captured with different camera sensors, and (c) against visual field estimates. a) Predicted lichen cover with test-time augmentation (TTA) versus without TTA for all datasets and sensor combinations. The dashed line indicates the 1:1 line. Points fall almost exactly on the identity line, confirming that TTA has a negligible effect on predicted cover values. b) Predicted lichen cover from camera versus smartphone images in the Sveg study area (n = 127). The dashed line indicates the 1:1 line; the solid blue line shows the fitted linear regression. The smartphone images predicted slightly higher cover than the camera images (mean bias = 0.63 pp, concordance correlation coefficient (CCC) = 0.993). c) Predicted lichen cover versus visually estimated lichen cover across the three study areas in northern Sweden. The dashed line indicates the 1:1 line; coloured lines show fitted linear regressions per dataset. Regression slopes substantially greater than one indicate that observers overestimated cover proportionally more at higher cover levels, with the strongest overestimation in the Fredrika (slope = 2.13).

A major source of variation in cover estimates between image acquisition occasions would, for many vegetation types, be seasonal changes in the appearance of the targeted species and the degree to which they are obscured by other vegetation. The targeted lichens are in many ways well-suited in this regard. They are relatively easy to distinguish from other vegetation and background by colour and shape, and the targeted reindeer lichens in the genus *Cladonia* show little variation in appearance across seasons and under varying moisture conditions, making the models robust to differences in image acquisition timing and weather. Furthermore, as described in Section 3.1.5, lichen can only compete effectively with other vegetation on nutrient-poor soils, and where shrubs are abundant, they often outcompete lichen for light; a dense, expansive shrub canopy is therefore rarely associated with high lichen cover. This means that the majority of lichen is typically visible at the surface and not obscured by overtopping vegetation, so cover estimates derived from images tend to capture most of the lichen present within a plot. A further advantage is that many of the co-occurring plant species in these communities, such as lingonberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*), and heather (*Calluna vulgaris*), maintain a relatively stable cover extent throughout the growing season, meaning that the timing of image acquisition introduces comparatively little variation in estimated cover compared to vegetation types with more seasonal variation.

The Android app demonstrated that on-device inference is feasible and could already serve as a calibration aid, though further development and field evaluation are needed before full operational use. Overall, our results suggest that image-based semantic segmentation offers a more objective and consistent alternative to visual estimation for reindeer pasture assessment although it does not measure exactly the same quantity as visual or point-intercept approaches. The clear tendency for visual estimation to overestimate lichen cover also suggests that the volume-to-biomass relationships based on visually estimated cover used for our biomass estimations (Figure 8) cannot be used directly with model-derived cover estimates and may need to be re-established using the more consistent cover measurements provided by image-based segmentation.

5.4 Linking lichen estimates to reindeer grazing and lichen accessibility (Paper IV, Paper I and Paper II)

5.4.1 Analysing cumulative impacts on reindeer habitat selection (Paper IV and Paper I)

Paper IV showed that reindeer behaviour was clearly influenced by the cumulative impacts of mining, wind power plants, and other infrastructure across all analysed snow-free seasons and spatial scales (Table 1). At the landscape scale, both wind power plants and the mine produced large zones of influence (5–10 km), resulting in extensive avoidance and reduced habitat suitability (Figure 13). The mine showed consistent avoidance across all seasons, while wind power plant effects varied with season and development phase.

Table 1. Summary of the impacts of mining and wind power on reindeer habitat selection and movement across seasons, scales, and processes. Rows show seasons and infrastructure type; columns show processes and scales. For each, we show whether the impact was negative (-; avoidance/barrier) or positive (+; selection), the estimated zone of influence (ZOI), and whether wind turbine impacts accumulated across multiple turbines (cumulative) or were best explained by the nearest turbine (nearest). Barrier indicates a significant reduction in the probability of reindeer crossing the wind power plants; movement patterns indicate changes in movement rate and tortuosity near wind turbines.

Season	**Infra-structure**	**Development phase**	**Landscape-scale habitat selection**	**Patch-scale step selection**	**Barrier**	**Movement patterns**
SPRING/CALVING	Wind power plants	Construction	**Nearest** **ZOI 5 km (-)**	**Cumulative** **ZOI 5 km (-)**	**Yes (-)**	**Cumulative** **ZOI 5 km (-)**
		Operation	**Nearest** **ZOI 5 km (-)**	**Cumulative** **ZOI 5 km (-)**	**No**	No effect
	Mine	-	**ZOI 10 km (-)**	No effect	-	-
SUMMER	Wind power plants	Construction	**Cumulative** **ZOI 10 km (+)**	**Nearest** **ZOI 5 km (+)**	**No**	No effect
		Operation	**Cumulative** **ZOI 10 km (+)**	**Nearest** **ZOI 5 km (+)**	**Yes (-)**	No effect
	Mine	-	**ZOI 10 km (-)**	**ZOI 5 km (-)**	-	-
AUTUMN	Wind power plants	Construction	**Nearest** **ZOI 10 km (-)**	No effect	**No**	No effect
		Operation	**Nearest** **ZOI 10 km (-)**	No effect	**No**	No effect
	Mine	-	**ZOI 10 km (-)**	No effect	-	-

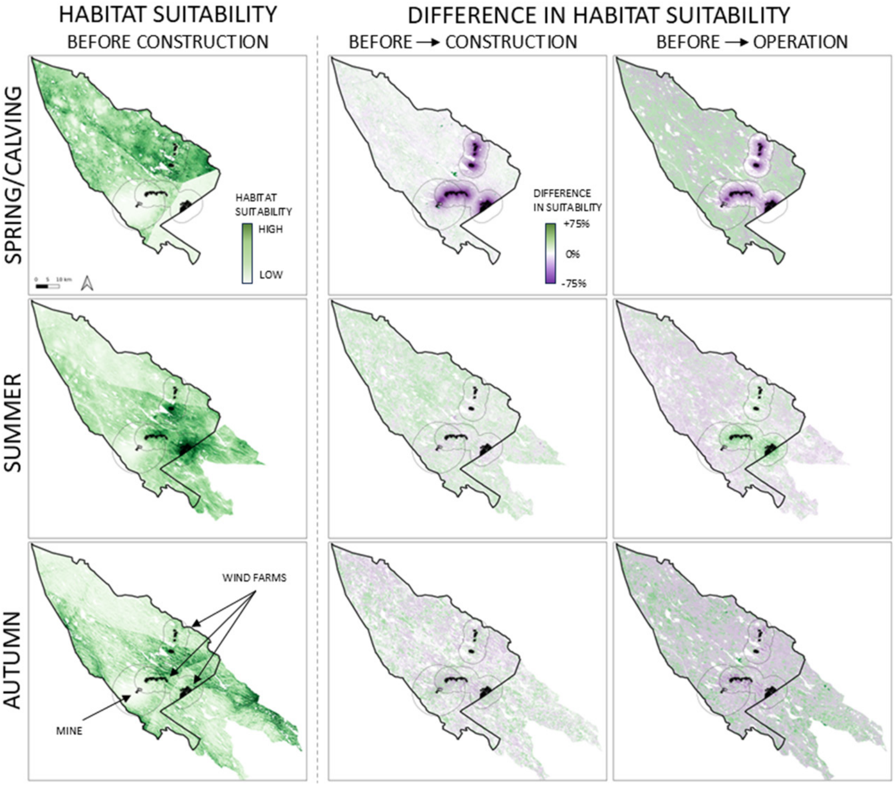


Figure 13. Predicted habitat suitability of reindeer at the landscape scale within each season. The first column shows the pre-construction period (2008–2009). The other two columns show the proportional change during construction (2010–2011) and operation (2015–2018). A 10 km buffer around the mine and a 5 km buffer around the wind power plants are shown for reference. The mine was present throughout and avoided in all seasons.

The strongest impacts occurred during calving, when reindeer avoided wind power plants at both landscape and patch scales and showed altered movement near turbines — moving faster and more directionally during construction, indicating disturbance of grazing behaviour. Cumulative effects of multiple turbines were detected at patch scale during calving and at landscape scale during summer. In contrast, during summer, reindeer showed selection for areas near wind turbines, likely reflecting trade-offs with insect harassment rather than an absence of negative impact. Roads were consistently avoided and acted as movement barriers in all seasons.

The framework presented in Paper IV provides a practical approach to quantify both the spatial extent and accumulation of impacts from multiple disturbances. The large zones of influence (5–10 km) indicate that the effective area influenced by development can be several times larger than the physical footprint, especially when multiple infrastructure types occur in proximity. The context-dependence of cumulative effects, varying by season, spatial scale, and behavioural process, highlights the importance of multi-dimensional assessments that go beyond single-project evaluations.

The approach is directly transferable to winter, where ground lichen availability would be a central environmental driver. This was demonstrated in Paper I, where iSSA showed that the lichen map added valuable information for modelling winter habitat selection, alongside land cover and elevation. The iSSA framework used in Papers I and IV can support comprehensive assessments of how infrastructure development affects reindeer access to and utilisation of lichen-rich pastures.

5.4.2 Calculating reindeer grazing days

Using our approach in Paper II to translate estimated lichen biomass into grazing capacity, the study sites supported between 54 and 67 theoretically sustainable reindeer grazing days ha^{-1} yr^{-1}, calculated from estimated annual biomass increment and a daily consumption of 2.25 kg per reindeer. Although biomass varied roughly twofold between sites, the estimated grazing days were relatively similar, which illustrates that cover rather than biomass determines grazing days in our calculations. The resulting grazing day estimates should be interpreted as a theoretical maximum rather than a realistic expectation. Reindeer forage opportunistically, concentrating in areas where lichen is easily accessible through the snow and cratering is feasible, and do not utilise annual lichen growth evenly across the landscape (Johnson et al. 2001; Heggberget et al. 2002). Our estimates assume that reindeer will access and graze lichen across the entire area over time, an assumption that rarely holds in practice, where lichen distribution, landscape accessibility, snow and ice conditions, human disturbance, infrastructure, and predation all constrain how much of the resource can actually be exploited. As discussed in Section 3.1.8, actual annual lichen growth also varies with lichen height and grazing history, and incorporating a biomass-based growth rate expressed as yearly growth in percent and derived from lichen volume rather than cover alone could potentially improve the accuracy of these estimates. Nonetheless, this approach provides a straightforward way to estimate grazing capacity and can offer valuable input for land-use planning and impact assessments related to reindeer herding.

6. General discussion and conclusions

Access to ground lichen is crucial for reindeer during winter, and reversing the well-documented decline in lichen resources (Sandström et al. 2016; Roos et al. 2025) is therefore a pressing concern for reindeer husbandry. Addressing this requires action across many levels, from policy makers to land users, and is complicated by the fact that reindeer husbandry shares the landscape with a wide range of other interests. Forestry, mining, hydropower and wind power development, transport infrastructure, and tourism all compete for the same areas (Skarin & Åhman 2014; Horstkotte et al. 2022), which also have the potential to deliver important biodiversity values and carbon storage central to climate and conservation policy (Strengbom et al. 2018; Lunde et al. 2025). These often competing interests play out within a legal and institutional framework that has long been a source of contention, particularly regarding Sámi rights to land use and the implementation of free, prior and informed consent in resource development (Larsen et al. 2017; Allard 2018). Many of these dimensions, including legal questions, political conflicts, governance, and cross-sectoral trade-offs, fall outside the scope of this thesis, but they shape the context in which its outputs will be used. In this complex landscape, reliable, objective, and transparent data that can be trusted by all parties is an important foundation for constructive dialogue and informed decisions. Such data on lichen abundance, its distribution across the landscape, and its availability to reindeer are one piece of that puzzle, providing a foundation for informed planning, management, and policy decisions. This thesis aimed to contribute such knowledge by drawing on modern methods and technologies to develop and improve approaches for mapping and quantifying ground lichen at multiple spatial scales (Figure 14). In addition, it aimed to demonstrate how these estimates can be linked to reindeer through habitat selection analyses, and how such analyses can inform assessments of pasture accessibility.

To contribute to **broad-scale** satellite-based mapping, we developed a cross-species validation method that addresses the difficulty of validating maps at this scale (Paper I). Commonly used accuracy metrics can give an overly

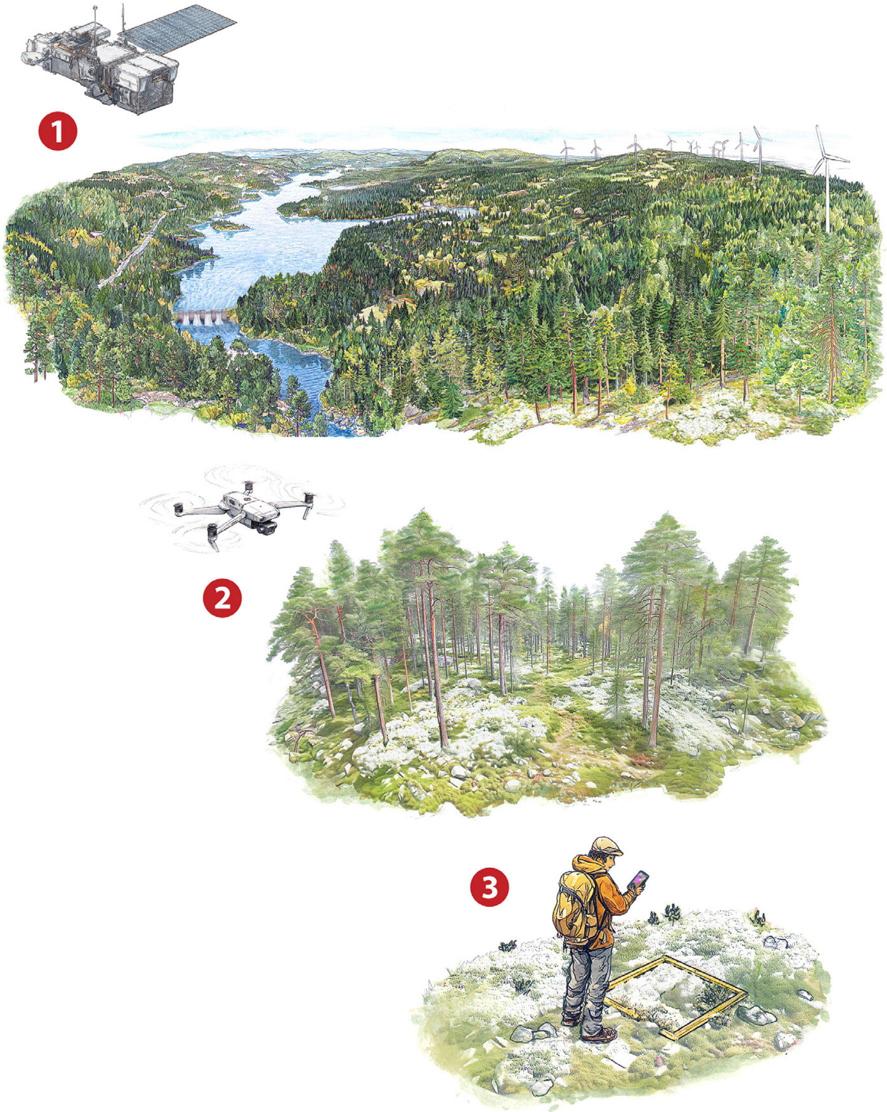


Figure 14. Multiscale framework for assessing lichen distribution and abundance. The illustration presents three complementary methodological scales: **(1)** at the **broad-scale**, satellite-based mapping, validated using reindeer GPS positions, provides a landscape-level overview of lichen distribution; **(2)** at the **local-scale**, drone-derived data are used for the sampling of field plots, from which lichen data are collected and used to estimate lichen cover and biomass; and **(3)** at the **plot-scale**, image segmentation models were developed for automated estimation of lichen cover.

optimistic picture of model performance, particularly when mapping extensive unsampled landscapes (Wenger & Olden 2012; Ploton et al. 2020; Meyer & Pebesma 2022). Building on advances in animal movement analysis, we applied integrated step selection functions (Avgar et al. 2016; Signer et al. 2019) using existing, spatially extensive reindeer GPS data to evaluate the map through its ability to explain habitat selection. This novel approach builds on the strong consumer–resource relationship between reindeer and lichen. While it does not provide a simple quantitative measure directly comparable to traditional accuracy metrics, it allows the map to be evaluated across large areas without the costly process of collecting additional field data and thus offers a useful complement to such metrics. In this case, it showed that the map helps explain reindeer habitat selection and provides valuable input for further analyses of this kind, such as those demonstrated in Paper IV when applied to winter conditions. Maps produced at this scale also provide a spatial overview of lichen distribution across the landscape, forming a basis for planning and management, important to preserve the remaining lichen hotspots in the landscape. However, this type of map is often too imprecise for site-specific use, and even when overall accuracy is reported, pixel-level uncertainty is rarely communicated (Jansen et al. 2022).

The **local-scale** drone-based method, on the other hand, can provide more detailed estimates of both lichen cover and biomass in specific areas (Paper II). Direct drone-based mapping of ground lichen has been used (Jozdani et al. 2021; Richardson et al. 2021). However, in boreal forest settings the approach is limited by trees and other vegetation that obscure the lichen and reduce the accuracy of cover predictions (Hernandez-Santin et al. 2019). Other lichen species important to reindeer, such as *Cetraria islandica*, are also likely more difficult to separate from surrounding vegetation than the bright *Cladonia* species targeted in those studies. Rather than mapping lichen directly from drone imagery, we based our estimates on field data collected within a sampling design where drone-derived NDVI and canopy height were used as auxiliary information to select a representative sample (Grafström & Schelin 2014). A more practical alternative worth exploring would be to derive auxiliary data from existing sources such as LiDAR, aerial photographs, or satellite imagery, removing the need for a dedicated drone survey and allowing the method to be completed in a single field visit. Depending on what is available, NDVI and canopy height could be complemented or replaced by other variables correlated with lichen presence, for example vegetation indices derived from RGB imagery or, given the importance of light for lichen growth (Section 3.1.7), modelled estimates of understory light availability. In Paper II, the lichen biomass estimates achieved a relative standard error of around 15–20%, making the method well suited for monitoring, for example to track how different forest management practices affect lichen or to evaluate the outcomes of restoration efforts. It can also support environmental impact assessments, either by comparing lichen resources across candidate sites or by quantifying losses attributable to industrial development.

Data at the **plot-scale** underpin the other methods, serving as training data for the broad-scale modelling and as the basis for biomass estimation at the local scale. The quality of these maps and estimates therefore depends on reliable cover data from the sample plots, yet our method comparison in Paper II showed that different methods commonly used for assessing lichen cover yield substantially different results. Paper III revealed large differences between observers using visual estimation, a well-documented limitation when using visual estimations for cover assessment (Morrison 2016). The point-intercept method is less subjective and allows height measurements to be taken simultaneously as lichen hits are recorded, but it is more time-consuming and less practical. To address these limitations, we used deep learning which has substantially advanced the performance of image segmentation across a wide range of applications (Maxwell et al. 2018; Ma et al. 2019), offering an alternative that combines the objectivity of point-intercept with the practicality of visual estimation. Image segmentation has recently been applied to lichen in ground-level photographs (Lovitt et al. 2022). Unlike that study, our models are made publicly available, with a model also deployed in a mobile app to demonstrate how image-based cover estimation can be integrated into field workflows. Our main model (MiT-B4 + U-Net) achieved a mean cross-validation IoU of 0.716, with a cover prediction error of approximately 1 percentage point (RMSE 2.42 pp), offering a practical and efficient means of estimating lichen cover from ground-level photographs collected in the field. Applying the model to photographs collected across larger areas also opens the possibility of tracking changes in lichen cover over time, for example in restoration or dispersal studies of the kind described in Sections 3.1.5 and 3.1.6. Richardson et al. (2021) demonstrated that segmentation models trained on ground photographs can be used to classify lichen in drone orthomosaics. Unlike the 0.5 × 0.5 m sample plots used in Paper II, which are much smaller than a single satellite pixel and cover only a few drone pixels, segmentation applied to high-resolution ground or drone imagery can produce continuous lichen masks across larger areas, better matching the spatial extent of satellite pixels and providing more representative ground truth for training broad-scale models. Such masks provide ground truth that may better suit the pattern-recognition strengths of deep learning and better match the spatial extent of satellite pixels, potentially improving lichen mapping performance at both broad and local scales.

Despite their importance and direct usability, the maps and estimates provided by the above methods do not by themselves reflect whether the lichen is accessible or usable. As described in Section 3.1.9, accessibility depends on several factors such as snow conditions, anthropogenic disturbance, and predation pressure, all of which vary between winters and across the winter grazing season. In Papers I and IV, we demonstrate how integrated step selection functions and habitat selection analyses can be used to understand and quantify how such factors affect reindeer habitat selection and to identify the conditions under which lichen resources can actually be utilised.

In Paper IV, we showed that mining and wind power plants generated large zones of influence (up to 10 km), substantially reducing functional habitat availability, with cumulative effects of multiple wind turbines evident in some seasons and scales. Although this study focused on snow-free seasons and did not include lichen as a variable, it highlights the importance of accounting for cumulative effects across the landscape and how these effects may vary both over the course of infrastructure development and within the season when assessing how industrial development affects reindeer access to lichen pastures. In addition, when evaluating cumulative impacts on reindeer, it should be recognised that disturbances in summer may also have consequences for winter survival. Reindeer are adapted to use stored energy reserves over winter and lose body mass as a result, which makes the relatively short snow-free season critical for rebuilding and supplementing those reserves (Åhman & White 2018). Even when grazing resources are abundant in summer, disturbances that hinder effective foraging can leave reindeer less prepared for the winter ahead (Simmonds et al. 2025).

As demonstrated by the habitat selection analysis in Paper IV, fitted habitat selection models including both habitat and disturbance data can be used to predict habitat suitability maps. This represents a step from quantifying resources to representing where they are functionally available to reindeer. Fitted iSSF models can additionally be used to simulate animal trajectories, enabling prediction of short- and long-term utilisation distributions and assessment of landscape connectivity (Signer et al. 2024). A large-scale example of similar maps for reindeer is provided by the Norwegian Institute for Nature Research (NINA), which has produced nationwide habitat quality and permeability maps for wild reindeer in Norway, combined with corridor and functional habitat maps for individual wild reindeer areas (Panzacchi et al. 2022). Such maps and the habitat selection analysis demonstrated in Paper IV can help assess how proposed infrastructure, industrial development, forestry practices, or other disturbances affect reindeer access to key foraging areas. They can also guide decisions about where to restore migration routes, remove barriers, or establish wildlife crossings, evaluate forest practices aimed at promoting ground lichen, and support broader efforts to restore lichen-rich pastures and improve landscape connectivity.

Taken together, the papers in this thesis address all four aims and deliver useful tools and outputs across all scales that can be applied independently or in combination. The methods are designed to be transparent, reproducible, and accessible — through publicly available lichen maps, open models, and a mobile app — so that they can be adopted by a wide range of users. While each method has limitations and room for further development, together they provide a more objective, complete, and operational framework for ground lichen assessment than has previously been available.

7. Future work and perspectives

While the papers in this thesis deliver useful tools and outputs, room for improvement remains at each of them, as does potential in exploring how these methods and tools can be better integrated, refined, and adapted to the rapidly evolving technological landscape and to the needs of those who will use them.

Specific improvements include continued development of the app and models for lichen segmentation to include all lichen species consumed by reindeer, and possibly also vegetation commonly co-occurring in lichen-rich habitats. This would allow tracking how cover of lichen and other vegetation change over time and how they respond to each other. Depending on the need, the model-predicted lichen masks could provide a cover estimate directly, or serve as a calibration tool or starting point for improving visual estimates. One remaining challenge is the lack of an objective method for collecting lichen height data when image segmentation is used for cover measurements. Taking height measurements at a few locations within the plot considered representative is a simple solution that likely gives a reasonable estimate in most cases, but a more objective and reproducible method would be preferable. Given sufficient training data, it may be possible to train a classifier to estimate lichen height class directly from photographs with usable accuracy, something worth exploring to make a fully automated image-based approach to biomass estimation possible. Improved segmentation models will in turn provide better input data for estimates and mapping at coarser scales.

Beyond these specific developments, the methodological landscape itself is evolving rapidly. Remote sensing is moving towards higher spatial, spectral, and temporal resolution. New satellite missions and increasingly accessible airborne and drone-based hyperspectral and LiDAR sensors can improve current approaches and open new possibilities for lichen mapping (Tagliabue et al. 2022; Timilsina et al. 2024). Hyperspectral data in particular may help separate lichen from spectrally similar surfaces such as bare ground, dry vegetation, or pale rock (Salehi et al. 2020). Continued growth in computational capacity and deep learning architectures will make it increasingly feasible to apply such methods at large spatial extents, including for animal movement analysis through approaches like deepSSF (Forrest et al. 2026).

Equally important as the technical development is developing the methods together with the land users they are intended to serve. The methods themselves do not change anything on the ground; their value depends on whether and how they are taken up in practice. Much of what our methods reveal about habitat suitability and landscape use may not be new to the reindeer herders themselves, but the data can still play a valuable complementary role by lending objective support to that knowledge and presenting it in a form that is easier to communicate to other land users and authorities. Future work therefore includes tailoring the methods and tools to the specific needs of those who will use them, from reindeer herding communities and land managers to environmental assessors and policymakers, and making methods and data as accessible as possible through open tools, standardised workflows, and integration with existing platforms and decision-support systems such as reindeer husbandry plans and RenGIS (Sandström 2015; Sandström et al. 2023), so that they can translate into real impact in the management, protection, and restoration of reindeer pastures.

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Popular science summary

In the forests of northern Scandinavia, ground lichens constitute the most important food source for reindeer during winter, often making up more than half of the diet. Access to lichen is therefore not only important for the reindeer itself but is a prerequisite for the survival of traditional reindeer husbandry based on naturally occurring forage, which is a central part of Sámi culture and livelihoods. In Sweden, reindeer husbandry is practised by Sámi people who are members of one of 51 reindeer herding communities that together make up the reindeer husbandry area, covering approximately half of Sweden's land area.

Ground lichens have, however, declined substantially in Sweden over the past century. Modern forestry has replaced older lichen-rich forests with younger, denser stands where lichens struggle to survive, and together with roads, wind and hydropower installations, mines, and other infrastructure has contributed to fragmenting the landscape, reducing reindeer's ability to make use of their pastures. Climate change has further complicated the situation by making thaw periods and winter rainfall more frequent, which can seal lichen beneath impenetrable ice layers. Together, these changes have created a great need for reliable and objective information showing how much lichen exists and how it is distributed across the landscape — information that can form the basis for improved planning and management of lichen-rich areas.

This thesis attempts to meet that need by developing and evaluating complementary methods for producing maps and estimates of the amount and distribution of ground lichen at different scales, and by showing how these can be linked to reindeer through analyses of habitat use — how reindeer use the landscape and how this is affected by external factors and disturbances.

At the broad scale, we developed a method for evaluating a lichen map covering the entire reindeer winter grazing area in Sweden. The map was produced using modelling based on satellite imagery and LiDAR data together with field data from the National Forest Inventory. To assess how well the map captures lichen amounts and distribution, we used GPS positions from reindeer during winter, when lichen determines where they move. By analysing reindeer movement patterns, we found that they consistently chose to move towards areas that the lichen map showed had more lichen than other available areas. This shows that the map successfully captures differences in lichen cover and provides important information for understanding and analysing how reindeer use the landscape.

At the local scale, we developed a method for estimating lichen cover and lichen biomass within smaller forest areas. A drone was used to collect data on tree cover and NDVI, a vegetation index that indicates the amount of living vegetation. This information was then used as auxiliary data to select a representative set of field sample plots. At each plot, lichen cover and lichen height were recorded and converted to biomass using a relationship we derived by compiling data from previously published scientific literature. From these plot-level values, we calculated lichen cover and biomass for the entire area, and also demonstrated a method for estimating reindeer grazing days.

At the sample plot scale, we compared three commonly used field methods for estimating lichen cover, and developed a deep learning model to identify and measure lichen cover from ground-level photographs. Compared to visual assessment by a human observer, the model produced more consistent estimates of lichen cover. To make this technology usable in the field, we also developed a smartphone app for direct field measurement of lichen cover.

While these methods quantify where lichen occurs and in what amounts, they do not address whether reindeer can actually reach and make use of it. Using GPS data and statistical models of habitat selection, the thesis also shows how reindeer movement patterns can be used to quantify how industrial infrastructure and other disturbances affect reindeer's ability to reach and use the lichen. These analyses also account for the fact that several smaller sources of disturbance — such as buildings and individual wind turbines — can together create a larger, combined impact than each one would alone, so-called cumulative effects.

Taken together, the methods in this thesis form a collection of tools that can be used individually or in combination depending on the question at hand. The methods are designed to be objective and reproducible, and are made freely available — as open lichen maps, models, and a mobile app — in the hope that they will find practical use in the planning, management, and conservation of reindeer pastures.

Populärvetenskaplig sammanfattning

I norra Skandinaviens skogar är lav den viktigaste födan för ren under vintern och kan utgöra mer än hälften av vad de äter. Tillgång till lav är därför inte bara viktigt för renen, utan är en förutsättning för den traditionella naturbetesbaserade renskötselns fortlevnad, som är en central del av samisk kultur och de samiska näringar som är byggda kring den. I Sverige bedrivs renskötseln av samer som är medlemmar i någon av de 51 samebyar som tillsammans utgör renskötselområdet, vilket täcker ungefär halva Sveriges yta.

Ett stort problem för renskötseln är att marklavarna har minskat kraftigt i Sverige under det senaste seklet. Det moderna skogsbruket har ersatt äldre lavrika skogar med yngre och tätare bestånd där lavar har svårt att överleva, och har tillsammans med vägar, vind- och vattenkraftsanläggningar, gruvor och annan infrastruktur bidragit till att fragmentera landskapet vilket försämrat renens möjlighet att nyttja betesmarkerna. Klimatförändringarna har ytterligare komplicerat situationen genom att det blivit vanligare med töväder och regn under vintern, vilket kan låsa laven under ogenomträngliga islager. Sammantaget har detta skapat ett stort behov av tillförlitlig och objektiv information som visar hur mycket lav det finns och hur den är fördelad över landskapet. Sådan information kan utgöra underlag för att förbättra planering och skötsel av lavrika områden.

Denna avhandling försöker möta det behovet genom att utveckla och utvärdera kompletterande metoder för att ta fram kartor och beräkningar av mängd och utbredning av marklav på olika skalor, samt att visa hur dessa kan kopplas till renar genom analyser av habitatval, hur renarna använder landskapet och hur det påverkas av yttre faktorer och störningar.

För användning på storskalig nivå tog vi fram en metod för att utvärdera en lavkarta över hela vinterbetesområdet för ren i Sverige. Kartan är framtagen med hjälp av modellering med data från satellitbilder och LiDAR tillsammans med fältdata från Riksskogstaxeringen. För att undersöka hur väl kartan lyckas fånga lavmängd och utbredning använde vi GPS-positioner från renar under vintern då laven styr var de befinner sig. Genom att analysera renens rörelser kunde vi se att de konsekvent valde att ta sig till områden som lavkartan visade hade mer lav än andra tillgängliga områden. Detta visar att kartan lyckas fånga skillnader i lavförekomst och bidrar med viktig information för att förstå och analysera hur renen nyttjar landskapet.

På lokal nivå utvecklade vi en metod för att uppskatta lavtäckning och lavbiomassa inom mindre skogsområden. En drönare användes för att samla in data om trädtäckning och NDVI, ett vegetationsindex som indikerar mängden levande vegetation. Denna information användes sedan som hjälpinformation för att ta fram ett representativt urval av fältprovytor. Vid varje provyta registrerades lavtäckning och lavhöjd, som sedan omvandlades till biomassa med hjälp av ett samband vi tog fram genom att samla data från tidigare publicerad vetenskaplig litteratur. Utifrån dessa provytevärden kunde vi beräkna täckning och biomassa av lav för hela området och även exemplifiera en metod för att beräkna rensbetesdygn.

På provytenivå jämförde vi tre etablerade fältmetoder för att uppskatta lavtäckning, och en djupinlärningsmodell utvecklades för att identifiera och mäta lavens täckningsgrad utifrån markfotografier. Den framtagna modellen gav mer konsekventa bedömningar av lavtäckning än när en person visuellt uppskattade täckningen. För att möjliggöra användning av denna teknik i fält tog vi även fram en mobilapp för direkt fältmätning av lavtäckning.

Metoderna vi tagit fram beskriver var laven finns och hur mycket det finns, men inte om renarna faktiskt kan nyttja den. Med hjälp av GPS-data och statistiska modeller för habitatval visar avhandlingen också hur rörelsemönster hos renar kan användas för att kvantifiera hur industriell infrastruktur och andra störningar påverkar renens möjlighet att nå och nyttja laven. Dessa analyser tar även hänsyn till att flera mindre påverkansfaktorer, till exempel byggnader och enskilda vindkraftverk, vilka tillsammans kan skapa en större, sammanlagd påverkan än vad varje enskild del gör, så kallade kumulativa effekter.

Sammantaget utgör metoderna i denna avhandling en samling verktyg som kan användas enskilt eller i kombination beroende på frågeställning. Metoderna är utformade för att vara objektiva och reproducerbara, och de görs fritt tillgängliga, som öppna lavkartor, modeller och en mobilapp, i förhoppningen att de ska komma till praktisk nytta inom planering, förvaltning och skötsel av renbetesmarker.

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II

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Quantifying winter forage resources for reindeer: Developing a method to estimate ground lichen cover and biomass at a local scale

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ABSTRACT

Boreal forests serve as the primary winter range for reindeer (*Rangifer tarandus*) in Sweden, where ground lichens constitute the main food source. Lichen-rich forests have declined drastically, and modern forest practices, along with other land uses, impact both the quantity and availability of lichen. The resulting reduction in lichen has serious consequences for reindeer and Sami reindeer husbandry. Consequently, robust methods for mapping and measuring lichen are highly sought after.

We developed and implemented a multistep method for objectively estimating lichen cover and biomass. We collected data at three study sites in lichen-rich pine forests in northern Sweden during July–August 2021. First, we collected data on NDVI and tree cover using a drone. These data informed a spatially balanced sampling approach to provide a distribution of plots for a representative field sample. Following this, we collected field data on lichen cover and height in these plots. In addition, we compared methods for assessing lichen cover in the field and found that visual estimates resulted in lower values than a point-intercept method. We recommend the point-intercept method for its objectivity and consistency between observers. By combining data from a literature review and fitting a linear regression on lichen volume ($dm^3\ m^{-2}$) and biomass (kg dry weight m^{-2}) through the origin, we determined a slope of 0.0148 for estimating biomass from volume measures. Using this relationship with field data on lichen cover and height, we obtained statistically unbiased estimates of lichen cover and biomass. This approach reduces the time required compared to destructive methods involving lichen collection and weighing.

While our method provides lichen cover and biomass estimates, we also demonstrate how these biomass estimates can be linked to the number of reindeer grazing days an area can sustain each year, enhancing the usefulness of the results. Our estimates will be valuable in planning and management of reindeer husbandry, as well as for quantifying the loss of the ground lichen resource in forestry, energy and mining industries.

1. Introduction

Reindeer and caribou (*Rangifer tarandus* sp. hereafter referred to as reindeer) are recognized as a keystone species in the northern hemisphere and occupy 25% of the global land biome (Vors and Boyce, 2009). In Eurasia, many reindeer populations are domesticated and herded, and are vital to more than 20 indigenous cultures (Uboni et al., 2016). Reindeer have a unique adaptation to eat and digest lichens, and in winter, ground lichens such as *Cladonia* spp. and epiphytic pendulous lichens such as *Bryoria fuscescens* and *B. fremontii* may provide up to 80% of their winter diet (Heggberget et al., 2002). Lichens are thus crucial for reindeer survival in winter, and in many populations, lichen-rich boreal forests constitute the main winter range (Berg et al., 2008; Skarin et al., 2022). In Sweden, the boreal region has experienced significant changes due to human activities, especially from intensive forestry practices that have affected a large portion of the forest area (Östlund et al., 1997; Svensson et al., 2019). This has contributed to a long-term decline in lichen-rich forests (Sandström et al., 2016). Forestry, alongside other land uses like hydropower, wind power, mining, and infrastructure, impacts both the amount and availability of winter food for reindeer, as well as their ability to navigate the landscape (Kivinen et al., 2010; Axelsson-Linkowski et al., 2020; Horstkotte et al., 2022).

All reindeer in Sweden are owned and herded as a part of the Sami reindeer husbandry system and considered a cornerstone of Sami culture

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(Holand et al., 2022). Hence, mapping, and quantifying the declining availability of ground lichens is especially important. Robust methods of mapping and quantifying ground lichens are important not only for reindeer husbandry, but for other users of forested land including forestry, energy, and mining. Knowledge about where, and how much lichen can be found within specific areas is necessary for well-informed forest planning and management decisions, environmental impact assessments, and consultation processes.

Over time, various methods have been developed to map and quantify ground lichen cover and biomass. For methods that rely primarily on field data, allometric equations are commonly used to estimate biomass, minimizing the need for labor-intensive collection and weighing of lichens (Greuel et al., 2021). These equations relate either lichen cover alone (Thomas et al., 1996; Dunford et al., 2006; McMullin et al., 2011) or a combination of cover and height (Arseneault et al., 1997; Kumpula et al., 2000; Moen et al., 2007; Olofsson et al., 2011; Odland et al., 2014; Rosso et al., 2014; Greuel et al., 2021; Errington et al., 2022) to lichen biomass. Using volume (cover × height) provides more accurate results than using cover alone, particularly in regions impacted by reindeer grazing (Moen et al., 2007; Odland et al., 2014; Rosso et al., 2014). To date, no comprehensive comparison across studies has been conducted to assess the general applicability of these volume-to-biomass relationships.

In addition, most field studies rely on visual estimates to assess lichen cover. Although experienced observers can make accurate visual estimates, variability between observers is generally higher than when using frequency-based methods, such as point-intercept methods (Morrison, 2015). To choose the most suitable method, it is also necessary to understand the extent to which results produced by different methods for assessing lichen cover in the field differ from one another.

The methods described above that rely primarily on field data are mainly intended for fine-scale assessments focused on limited areas. At broader scales, from national to landscape levels, methods to map and quantify ground lichens involve building models that incorporate (objective) information from satellite imagery, along with field data for training and validation (Gilichinsky et al., 2011; Nelson et al., 2013; Falldorf et al., 2014; Hillman and Nielsen, 2020; Kennedy et al., 2020; Erlandsson et al., 2022; Horstkotte et al., 2023). The resulting models produce lichen maps with resolutions ranging from a few meters up to 30 m. At local or site-specific levels, when higher resolution is asked for, such model-based methods are not precise enough to be useful, and they often do not provide error estimates (Jansen et al., 2022). In recent years, drones have emerged as a tool to produce lichen cover maps with a resolution of a few centimeters. However, these maps have primarily served as training data for satellite image-based models and have predominantly focused on lichens with pale surfaces (Macander et al., 2020; He et al., 2021; Jozdani et al., 2021; Richardson et al., 2021; Fraser et al., 2022, 2023). Additionally, the accuracy of lichen cover predictions may decrease when the ground is not fully visible in drone imagery. Detailed mapping of ground vegetation using drones is limited by trees and other vegetation that can obscure significant portions of the ground and reducing the accuracy of cover predictions (Hernandez-Santin et al., 2019).

Advancements in remote sensing have not only enhanced lichen mapping but also created opportunities to employ new sampling methods that integrate land cover data into the sampling design (Grafström et al., 2014). Selecting a suitable sampling design is essential for precise estimates of population characteristics (Kermorvant et al., 2019). Spatially balanced survey designs, which allow for the selection of well-spread, representative samples across the population, is increasingly being used in biological and environmental management surveys (Grafström et al., 2014; Brown et al., 2015; Kermorvant et al., 2019).

The goal of our study was to develop and evaluate an objective method to accurately estimate ground lichen cover and biomass at the local scale. The method was designed to produce results that were both objective and easy to interpret, ensuring that all land users can trust the findings in situations when there are conflicting land use interests. To achieve this, we (i) developed a multi-step method that combined high-resolution remote sensing data to select sample plots where field data on lichen cover and height were collected, (ii) analyzed and compared three methods for measuring lichen cover in the field sample plots, and (iii) reviewed existing scientific studies regarding the relationship between lichen volume and biomass to derive biomass estimates from volume measurements. Additionally, we (iv) demonstrated how biomass estimates can be used to calculate the number of reindeer grazing days an area can sustainably support each year.

2. Material and methods

2.1. Study areas

Sami reindeer husbandry can be carried out on the northern 55% of Sweden's land area (Fig. 1a). We established three study sites, each constituting an area of 1–1.5 ha (Table 1), within Ran reindeer herding community's winter grazing area, near the city of Umeå (Fig. 1b). At each site, we collected drone and field data.

We selected sites to cover the two most common types of lichen-rich forests within reindeer husbandry area in Sweden. The Haddingen (Had) site is located on pine heath forest on sandy soils, and Kummelsberget (Kum) and Sävar (Sav) are pine forests on rocky ground. Besides the dominating pine (*Pinus sylvestris*) the sparse tree cover in these two forest types contained some *Picea abies* and *Betula pendula*. Lichen dominated patches were mixed with patches dominated by dwarf shrubs, mainly *Vaccinium vitis-idaea, Calluna vulgaris, Empetrum nigrum* and *Vaccinium myrtillus*, as well as various species of moss. All sites were occasionally grazed by reindeer. We found the lichen species that reindeer consume (*Cladonia arbuscula, C. mitis, C. rangiferina, C. stellaris, C. uncialis, Cetraria islandica*, and *Stereocaulon paschale)* in at least one of the study sites. Hereafter referred to as lichen. At the time of our field data collection, grazing was evident in some parts of the Kum site with low lichen thalli as a result, while the other sites showed no obvious signs of recent grazing.

2.2. Overview of the method

Our method is outlined step-by-step in Fig. 2, with each step further detailed in the following sections.

2.3. Drone data collection

As a first step in our method development, we used a DJI Phantom 4 Multispectral quadcopter to collect high resolution images on August 16, 2021. The multispectral camera array covered blue, green, red, red edge, and near-infrared bands, all at 2 megapixels. Data were collected at 45 m above ground to get images with a ground resolution of about 2.5 cm pixel^{-1}. The drone was equipped with a RTK module connected to the Swedish national network of permanent reference stations, SWEPOS, for real time position correction. We set the drone to fly in parallel lines across the study areas to capture images with a front overlap of 90% and a side overlap of 80%. We collected data on days with overcast skies to minimize shadows in the images.

Drone images were processed using Agisoft Metashape Professional 1.7.1 (Agisoft, 2021). For each site, we exported a dense point cloud along with both RGB and multispectral orthomosaics. We used R 4.1.1 (R Core Team, 2021) for all the data processing and statistics. The point cloud from Metashape was used with the R package lidR (Roussel et al., 2020; Roussel and Auty, 2021) to produce a canopy height model with 0.5 m resolution using the 'pit-free' algorithm developed by Khosravipour et al. (2014). The orthomosaic was loaded into R with the terra package (Hijmans, 2021) and we calculated the normalized difference vegetation index (NDVI) from the near-infrared band, 840 nm ± 26 nm

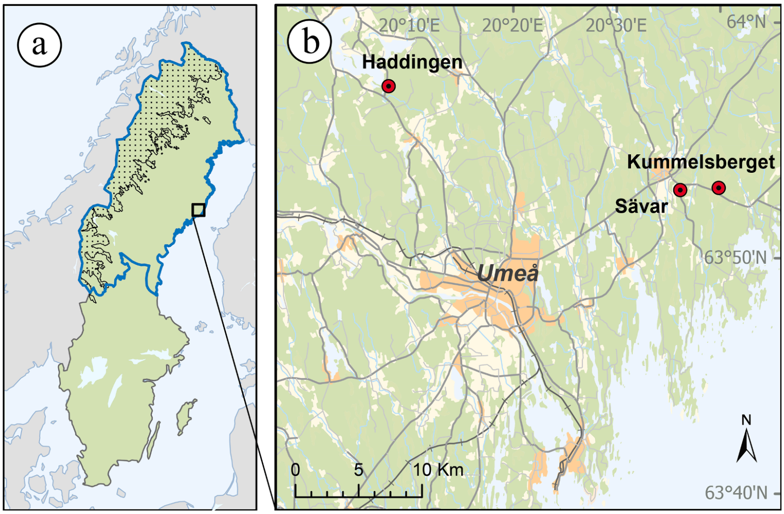

Fig. 1. Location of the study sites in northeastern Sweden where drone and field data were collected in August–September 2021. a) The blue border shows the Reindeer husbandry area in Sweden, where intensive forest practices are carried out on productive forestlands east of the Scandian mountain range (dotted). b) Locations of the three study sites—Haddingen (Had), Kummelsberget (Kum), and Sävar (Sav)—north of Umeå, Sweden.

Table 1
Summary statistics for the three study sites (Had, Kum, and Sav), including site area, tree cover and information on lichens found in the sample plots in northeastern Sweden, sampled in August - September 2021.

	Had	Kum	Sav
Area of study site (m^2)	14,489	14,676	11,109
Tree cover (visually estimated per site) (%)	35	40	20
Number of sample plots with lichen (out of 40)	32	32	28
Lichen cover (mean ± SE) (from point-intercept) (%)	28.4 ± 1.1	22.7 ± 0.9	27 ± 1.2
Lichen height (mean ± SE) (from point-intercept) (mm)	30.9 ± 1.3	23.5 ± 1.5	33.3 ± 1.4
Percent of total lichen cover (from point-intercept)			
Cladonia arbuscula + *C. mitis* + *C. rangiferina*	88.8	84.5	75.1
Cetraria islandica	0.3	1.7	19.9
Cladonia stellaris	10.2	0	4.3
Cladonia uncialis	0.7	12.1	0.7
Stereocaulon sp.	0	1.7	0

(NIR) and the red band, 650 nm ± 16 nm (red) using the formula: NDVI = NIR - red / NIR + red. The resulting image was resampled to a resolution of 0.5 m. The image resolution was chosen to match the 0.5 m × 0.5 m sample plots used for the field data collection, following the methodology described by Moen et al. (2007).

2.4. Sampling - selection of sample plots

Spatially balanced sampling designs are often used to ensure samples are well spread geographically. However, they can also spread samples across multiple additional dimensions defined by auxiliary variables, such as wetness, slope, elevation, and vegetation indices, so that the distribution of these variables in the sample resembles that of the population (Grafström et al., 2012). Samples that are well-spread tend to improve estimates by reducing the variance, provided that the auxiliary variables used have explanatory power for the target variable (Grafström et al., 2014). We used the local pivotal method 1 (LPM 1) (Grafström et al., 2012) from the R package BalancedSampling (Grafström et al., 2024) for our sampling. We used NDVI, canopy height and the x and y coordinates as auxiliary information. NDVI is negatively correlated with increasing lichen cover (Nordberg and Allard, 2002; Erlandsson et al., 2023). The canopy height models were used to collect data from open areas, as well as from areas beneath trees of varying heights, reflecting the diversity in age structure. We included the x and y coordinates of each pixel in the Swedish reference frame 1999 (SWEREF 99) to ensure the sample was geographically distributed across the sites. All the auxiliary variables were standardized to have the same range. We sampled 40 pixels (0.5 m x 0.5 m) from each site, with each pixel representing a sample plot.

2.5. Field data collection – methods for lichen assessment

We collected field data between August 27 and September 9, 2021. We used the ArcGIS Field Maps app with an Emlid Reach RS2 multi-band RTK GNSS receiver, connected to SWEPOS for real-time position correction, to achieve centimeter-level precision locating sample plots. At each plot, we placed a 0.5 m × 0.5 m wooden frame aligned with north-south compass direction. The lichen cover and height within the frame were measured using methods from Moen et al. (2007). The frame was divided into 36 squares (Fig. 3). We measured the height of the lichen thalli to the nearest 0.5 cm by lowering a metal rod (3 mm diameter) to the base of the lichen at each of the 25 intersections created by the 36 squares, recording the measurement at the highest point where the lichen contacted the rod. The average of these measurements was then calculated to represent the lichen height for each plot. We measured percent lichen cover using three different methods, (i) percent of squares with presence of lichen (presence-absence), (ii) percent hits, out of 25, by the rod (point-intercept), and (iii) visual estimate of percent lichen (visual estimate). We measured lichen cover and height for each species separately (except for *Cladonia arbuscula, C. mitis*, and *C. rangiferina*, as it was difficult to distinguish between them when they had been grazed) and for all lichen species together as a group, and used the latter for the biomass estimations. All measurements were done a

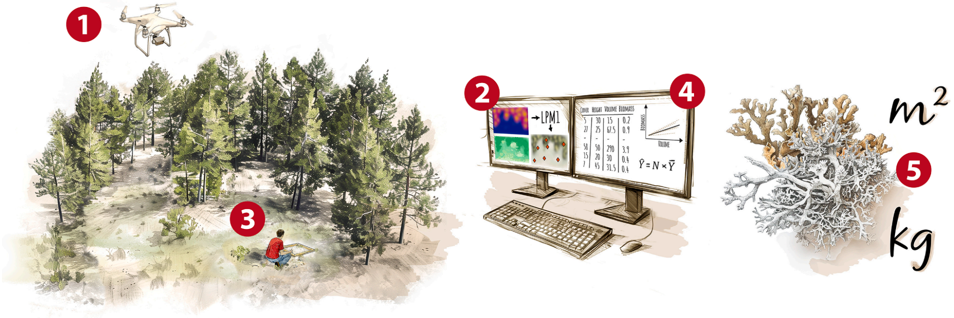

Fig. 2. Overview of the method developed for estimating ground lichen cover and biomass at a local scale. (1) **Drone data collection** - Multispectral images collected by a drone were used to acquire detailed and current information about the entire study site. (2) **Selection of sample plots** - By utilizing NDVI and canopy height data derived from the drone imagery we computed a spatially balanced sampling using the local pivotal method (Grafström et al., 2012), and achieved well-spread, objective, and reproducible sample plots. (3) **Field data collection** - Using these sample plots, we collected field data on lichen cover and height. (4) **Lichen biomass from volume** - We calculated biomass for each sample plot using a relationship between lichen volume (cover × height) and biomass derived from our literature review. (5) **Lichen cover and biomass estimations** - Finally, we computed statistically unbiased estimates of lichen cover and biomass for the entire site.

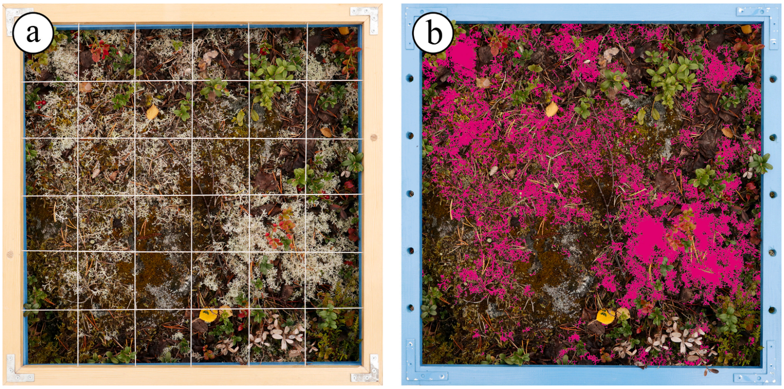

Fig. 3. Illustration of methods used for lichen cover assessment. a) Sample plot with a frame divided in 36 squares making 25 intersections. Lichen cover for this plot using each of the three methods: presence-absence: 97% (35 of 36 squares), point-intercept: 52% (13 of 25 intersections), visual estimate: 38%. b) Manual segmentation of lichen in photo of the same plot as reference: 22% cover.

few days after rainfall, placing the lichen in a state somewhere between moist and dry.

To estimate how time consumption varied across methods, we recorded the time taken to assess the cover for all lichen species combined for each method on 15 sample plots, which were subjectively selected to capture the variation in lichen cover and distribution. Timing began at the start of each assessment and ended once the result was recorded. For the visual estimate and presence-absence methods, this involved recording a single value: percent cover for the visual estimate and the count of lichen-present squares for the presence-absence method. For the point-intercept method, we measured and recorded lichen height at each of the 25 intersections where lichen was hit by the rod.

2.6. *Literature review – lichen biomass from volume*

The process of collecting, cleaning, and weighing lichen samples to determine biomass is very time-consuming (Rosso et al., 2014). Therefore, we conducted a literature review on lichen biomass estimations to compare and potentially utilize data from earlier studies. We searched the major databases, i.e., Google scholar and Web of Science, using the search term ‘lichen biomass’ and widened the search using references in the articles found to identify as many relevant studies as possible. Through our search we found five articles (Appendix A) relating lichen volume to biomass, where data on lichen volume was accessible, either online or presented in graphs in the articles. Data on lichen cover in Rosso et al. (2014), were obtained through both visual estimates and point intercepts. To maintain consistency with the other studies where available data came solely from visual estimates, we used the data on visual estimates. Additionally, from the same study, we selected only data from the species groups found at our sites (*Cladina* and *Cetraria*). We collected data from graphs using the R package metaDigitise (Pick et al., 2019) and recalculated the data from all five articles to matching units (dm^3 m^{-2} for volume and kg m^{-2} for biomass).

To reduce the variation in volume range among the studies, we excluded the most extreme data points with volumes exceeding 80 dm^3

m^{-2} from the full dataset of 910 points, resulting in the removal of seven points. In addition, these values were much higher than the maximum lichen volume of 44 dm^3 m^{-2} observed at our study sites. Finally, we fitted linear regressions through the origin and quadratic regressions, with lichen biomass (kg dry weight m^{-2}) as the response variable and lichen volume (dm^3 m^{-2}) as the predictor variable, for each reviewed study and for all data combined.

2.7. *Lichen cover and biomass estimations*

For each of our 120 sample plots and for each method of assessing lichen cover (presence-absence, point-intercept, and visual estimate), we calculated lichen volume by multiplying lichen cover by mean lichen height. In six plots, lichen was present but no height was recorded as no lichen was hit by the rod using the point-intercept method. Instead, we used the mean height for the species in question across the entire site. To estimate lichen biomass for each sample plot we used lichen volume (cover × height) with the slope from the linear regression on the combined data from all studies in the literature review. We then estimated total lichen cover, volume and biomass for each study site using each cover assessment method by applying the unbiased Horvitz–Thompson estimator (HT) (Horvitz and Thompson, 1952) (eq (1)). Our goal was to estimate a total Y of the lichen variable with value y_i for unit i for a population with N units $Y = \sum_{i=1}^{N} y_i$. The total Y could then be estimated from the sample by HT, which in this case with equal inclusion probabilities, can be expressed as

$$\widehat{Y} = N^{*}\overline{Y} \tag{1}$$

The variance was estimated using a local mean variance estimator suggested for spatially balanced samples selected with the local pivotal method (Grafström and Schelin, 2014):

$$\widehat{V}_{SB}(\widehat{Y}) = \sum_{i \in s} \frac{n_i^{*}}{n_i^{*} - 1} \left(\frac{y_i}{\pi_i} - \frac{1}{n_i^{*}} \sum_{j \in s_i^{*}} \frac{y_j}{\pi_j} \right)^{2} \tag{2}$$

Where s_i^{*} is a coherent subset of s with n_i^{*} units. The coherent subset s_i^{*} includes unit i, and $j \in s_i^{*}$ if $j \in s_i^{*}$ and $d(i, j) = \min j \in s, k \neq i^{d(i,k)}$. We calculated the standard error for the estimator using $\widehat{SE}(\widehat{Y}) = N^{*} \frac{s}{\sqrt{n}}$ and the relative standard error $RSE = \frac{\widehat{SE}}{\widehat{Y}} {*} 100$. Finally, we divided the estimates by the site area in hectares to yield comparable figures for lichen cover (m^2 ha^{-1}) and lichen biomass (kg ha^{-1}).

2.8. *Reindeer grazing days*

To demonstrate how our estimates of biomass can be more directly linked to reindeer grazing, we estimated the number of grazing days per hectare each study site could support each winter. For grazing to remain sustainable over time, we assumed that only the yearly growth can be consumed. In their literature review, McMullin and Rapai (2020) estimated a global average annual linear growth rate for reindeer lichens to be 4.9 mm year^{-1}. The conditions most similar to our sites were dry pine forests in northeastern Finland, where the growth rate for *Cladonia rangiferina* ranged from 3.9 to 4.3 mm year^{-1} and for *Cladonia mitis* from 3.0 to 3.5 mm year^{-1} (Helle et al., 1983). As a compromise and to keep the calculations simple, we used a growth rate of 4 mm year^{-1}. We used data from the point-intercept method and subtracted 4 mm from the mean lichen height in each sample plot and re-estimated lichen biomass to represent the biomass from the previous year. By subtracting this from our original estimate, we obtained the annual biomass increase.

In winter, daily dry matter intake for free-ranging reindeer in Norway has been estimated at 490–1800 g (Storeheier et al., 2003). For our calculations, we used an average intake of 1.5 kg lichen day^{-1}. Besides their actual intake, when reindeer are cratering, they remove additional lichen from the ground. Although these fragments contribute to regrowth within the craters, modeling suggest that 0.5 kg wastage per kg intake should be included to explain the reduction in lichen after winter grazing in Finland (Pekkarinen et al., 2017). Thus, we added 0.75 kg to the average daily intake of 1.5 kg, resulting in a daily consumption estimate of 2.25 kg per reindeer. The number of grazing days was then estimated using the estimated annual increase in lichen biomass divided by the average daily lichen consumption.

To estimate uncertainty in the estimations, we calculated the smallest annual biomass increase as the difference between the lowest biomass estimates from the 95% confidence interval (estimate − SE × 1.96) for both years, and the largest annual biomass increase as the difference between the highest biomass estimates (estimate + SE × 1.96). We then divided these values by the daily intake to determine the minimum and maximum grazing days. The uncertainty was defined as the difference between these extreme values and the grazing days calculated from the average annual biomass increase.

3. Results

3.1. *Drone data*

The drone survey took approximately 20 min to complete at each site, while the processing (mostly automated) and exporting of images (Fig. 4) required about two hours per site on a standard desktop PC equipped with an AMD Ryzen 7 5800 8-core processor, 64 GB of RAM, and an NVIDIA GeForce RTX 3070 graphics card.

Our data on canopy height showed a negative correlation with lichen cover at all sites: Had ($r = -0.45$, $p = 0.0035$), Kum ($r = -0.38$, $p = 0.014$), and Sav ($r = -0.34$, $p = 0.034$). For NDVI, there was also a negative correlation with lichen cover that was significant at the Kum ($r = -0.47, p = 0.0022$) and Sav ($r = -0.5, p = 0.0011$) sites, but not at the Had site ($r = -0.27$, $p = 0.088$).

3.2. *Sampling - selection of sample plots*

The sampling using the local pivotal method resulted in 40 selected pixels (Fig. 4c) for each study site, well spread in the auxiliary information (Fig. 5).

3.3. *Field data*

On average, it took 20 min to complete field data collection at each sample plot. This included accurately locating the exact position, capturing photographs, and recording data for each method and species separately. Lichen species composition, height, and cover varied to some extent between the sites (Table 1). Most of the plots contained lichen, and the most common species across all sites were *Cladonia arbuscula, Cl. mitis* and *Cl. rangiferina*. Among the less common species, *Cetraria islandica, Cladonia unicialis*, and *Cl. stellaris* were each quite common on one of the three study sites, while *Stereocaulon* sp. only appeared in four sample plots at the Kum site. Compared to the Had and Sav sites, lichen height and cover at the Kum site was slightly lower.

3.4. *Methods for lichen assessment*

A comparison of the different methods showed that the point-intercept method yielded higher cover estimates than using visual estimates but lower cover than the presence-absence method (Fig. 3 and 6). Point-intercept and visual estimate were linearly correlated ($R^2 = 0.77$, slope = 0.70) and the plot shows that the error is relatively evenly spread around the regression line. The correlation between visual estimates and presence-absence was weaker ($R^2 = 0.48$, slope = 0.39). A plot with high cover according to presence-absence could have almost any value when visual estimation was used (Fig. 6c). The same was true when comparing point-intercept to presence-absence (Fig. 6b), even if the correlation was stronger between these two methods ($R^2 = 0.69$,

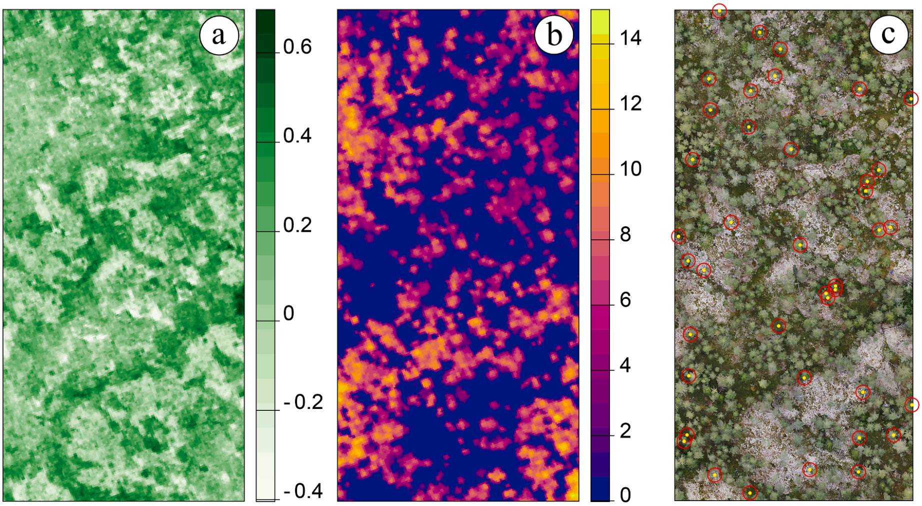

Fig. 4. Example from the site Sav in northeastern Sweden, showing data derived from drone images collected in August 2021 and sample plots selected during the sampling process.a) Normalized difference vegetation index (NDVI), and b) canopy height, both used as auxiliary data in the sampling, and c) RGB orthomosaic with sample plots indicated by a yellow dot surrounded by a red circle.

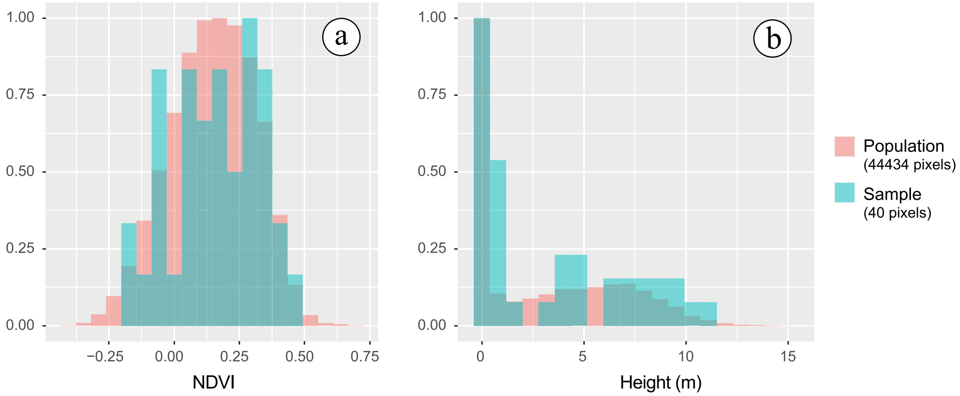

Fig. 5. Example of how the use of the local pivotal method 1 spreads the sample so that the distribution of the auxiliary information in the sample resembles that in the population. Histograms of the distribution of a) the NDVI and b) canopy height variables in the population (red) and sample (blue) for site Sav, when the sample was spread using all auxiliary information: NDVI, canopy height, x and y coordinates in SWEREF 99. The counts on the y-axis are scaled to a maximum of 1.

slope = 0.59) compared to the correlation between visual estimates and presence-absence.

Time consumption depended on the amount of lichen in the sample plots (Appendix B), particularly for the point-intercept method, where time steadily increased with lichen cover—from about one minute for the lowest cover to approximately five minutes as cover approached 100%. The time taken to record cover using the presence-absence and visual estimate methods was quite similar in most cases, typically requiring less than half a minute, with sample plots containing either little or abundant lichen being the quickest to complete. At our study sites where mean lichen cover was 20–30%, the time difference between the point-intercept method and the presence-absence and visual estimate methods was approximately two minutes per sample plot.

3.5. Literature review – lichen biomass from volume

In the regressions of lichen volume and biomass, based on the combined data from the five articles identified in our literature review, the quadratic regression curve and the linear regression line through the origin closely aligned across much of the range (Appendix C). Therefore, we used the simpler linear relationship, where the slopes allowed for easier comparisons between articles. The linear regressions through the origin for each article had slopes varying between 0.008 (Kumpula et al., 2000) and 0.0188 (Rosso et al., 2014) (Fig. 7). By combining data from all articles, we obtained a slope of 0.0148 that we used for our biomass estimations.

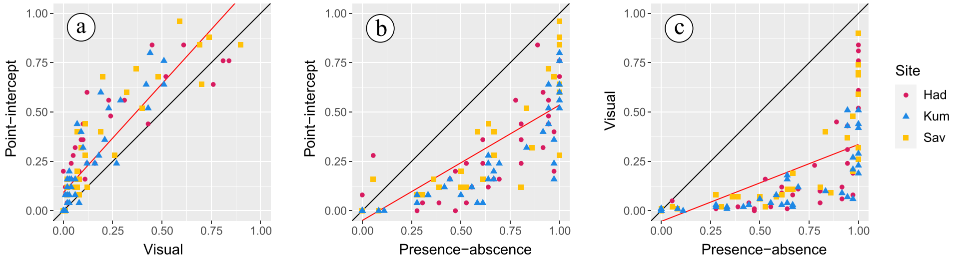

Fig. 6. Comparisons between the three different methods for estimating lichen cover: a) Point-intercept vs. Visual, b) Point-intercept vs. Presence-absence, and c) Visual vs. Presence-absence. The scale on both axes represents lichen cover, with 1 corresponding to 100% cover. Red lines depict the trend lines resulting from linear regressions, while black lines represent the 1:1 line, indicating a perfect match between the methods. Each data point corresponds to one of the 120 sample plots from the three study sites (Had, Kum, and Sav) in northeastern Sweden, sampled between August and September 2021.

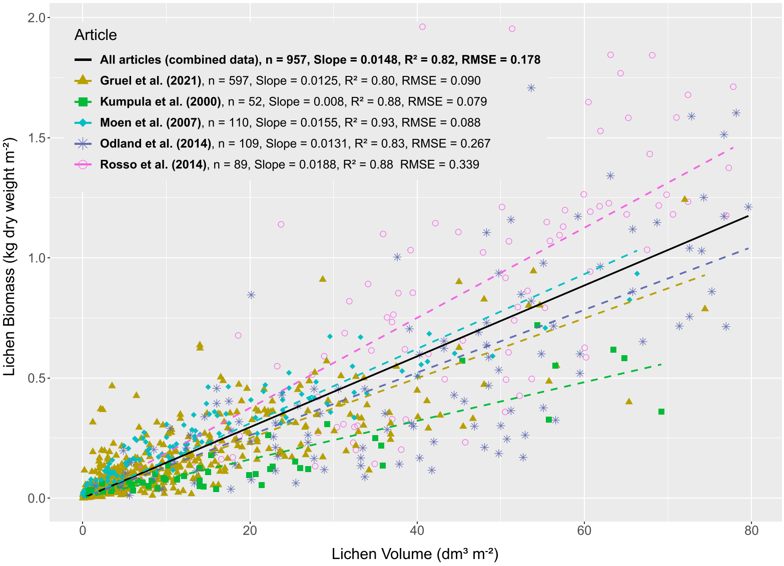

Fig. 7. Association between lichen volume (dm^3 m^{-2}) and biomass (kg dry weight m^{-2}). Linear regression through the origin for each article from our literature review (dashed lines) and for data from all articles combined (solid black line), with the number of points (n), slope, R-squared value (R^2) and root-mean-square error (RMSE).

3.6. Lichen cover and biomass estimations

Our estimates of lichen cover and biomass resulted in considerable differences, depending on the cover measurement method employed (Table 2). Cover estimates ranged from 1190 to 5736 m^2 ha^{-1}, and biomass estimates varied between 334 and 2318 kg ha^{-1}. As expected, the presence-absence method resulted in the highest cover estimates, followed by point-intercept and visual estimate, with consequent effect on biomass estimates. The use of the presence-absence method produced cover estimates, and consequently biomass estimates, that were approximately 2.5 to 5 times higher than those derived from visual estimates. The discrepancies between point-intercept and visual estimates were smaller, with the visual estimates being nearly half as large. In alignment with the estimates, the variance (Var) and standard error (SE) were highest for the presence-absence method, followed by point-intercept and then visual estimates, this pattern was inverted for the relative standard error (RSE). The RSE ranged from 8 to 13% for presence-absence, 13–16% for point-intercept, and 15–22% for visual estimates. The Kum site exhibited the lowest cover and biomass among the study sites. The relative difference in biomass compared to the other sites was clearly larger than the relative difference for cover: estimate cover from point-intercepts was 2270 m^2 ha^{-1} for Kum, versus 2840 and 2700 m^2 ha^{-1} for Had and Sav, respectively; and 649 kg ha^{-1} for Kum, compared to 1232 and 1221 kg ha^{-1} for Had and Sav.

3.7. Reindeer grazing days

The Had and Sav sites, with similar estimated biomass, supported 67 and 64 annual reindeer grazing days per hectare, respectively (Table 3). The Kum site, with biomass just over half that of the other sites,

Table 2

Summary of lichen cover and biomass estimates across the study sites (Had, Kum, Sav) in northeastern Sweden, sampled in August - September 2021, assessed using the presence-absence, point-intercept, and visual estimate methods. Lichen cover (m^2 ha^{-1}) and biomass (kg ha^{-1}) estimated using the unbiased Horvitz–Thompson estimator (eq (1)), along with variance, standard error (SE), and relative standard error (RSE), calculated using eq (2).

	Site	Method	Estimate	Var	SE	RSE (%)
Cover	Had	Presence-absence	5736	302,188	550	10
(m^2 ha^{-1})		Point-intercept	2840	147,767	384	14
		Visual estimate	1665	110,946	333	20
	Kum	Presence-absence	5493	217,179	466	8
		Point-intercept	2270	88,008	297	13
		Visual estimate	1190	33,362	183	15
	Sav	Presence-absence	4660	311,069	558	12
		Point-intercept	2700	169,633	412	15
		Visual estimate	1715	85,297	292	17
Biomass	Had	Presence-absence	2318	68,366	261	11
(kg ha^{-1})		Point-intercept	1232	41,011	203	16
		Visual estimate	717	24,668	157	22
	Kum	Presence-absence	1602	23,774	154	10
		Point-intercept	649	7727	88	14
		Visual estimate	334	3394	58	17
	Sav	Presence-absence	2065	75,429	275	13
		Point-intercept	1221	39,396	198	16
		Visual estimate	784	22,483	150	19

Table 3

Annual sustainable reindeer grazing days per hectare for each of the study sites in northeastern Sweden, calculated based on the estimated biomass, an annual lichen growth rate of 4 mm, and an average daily consumption of 2.25 kg of lichen per reindeer. The table includes the estimated biomass with standard error (SE), annual lichen growth, and reindeer grazing days, with uncertainties derived from the differences between years using the lower and upper bounds of the 95% confidence intervals for the estimates.

Site	Biomass estimate (±SE) (kg/ha)	Biomass estimate previous year (±SE) (kg/ha)	Annual lichen biomass increase (kg)	Reindeer grazing days
Had	1232 ± 203	1080 ± 183	152 ± 38	67 ± 17
Kum	649 ± 88	527 ± 74	121 ± 28	54 ± 12
Sav	1221 ± 198	1077 ± 178	144 ± 41	64 ± 18

supported 54 annual grazing days per hectare, a difference notably smaller than the difference in biomass.

4. Discussion

Effective and reliable methods for quantifying lichen are crucial for the sustainable management of winter forage resources for reindeer. We have demonstrated that our method, which integrates drone-derived site information into the sampling design and incorporates field measurements of ground lichen cover and height, offers a robust and objective approach for estimating ground lichen cover and biomass at the local scale. Furthermore, we identified significant differences in lichen cover between different field methods, leading to difference in biomass estimations. In addition to the lichen assessment method, the slope used to relate lichen volume to biomass is also crucial for the accuracy of these estimates. From our literature review, we derived and applied a slope of 0.0148. The lichen biomass estimates calculated using this slope and the point-intercept method had RSE of approximately 15%. The estimation of the number of reindeer grazing days at our respective field sites, were relatively consistent across sites due to similar lichen cover.

4.1. Sampling - selection of sample plots

The use of spatially balanced sampling can improve the selection of sample plots if units that are close in the auxiliary space have similar values on the variable of interest (Grafström et al., 2012). This means that a smaller sample size could suffice to achieve the desired level of precision, possibly also reducing the overall cost of the sampling process (Kermorvant et al., 2019). We found that both NDVI and canopy height demonstrated negative correlations with lichen cover at our study sites, thus proving to be pertinent auxiliary data for the sampling. Depending on the study area and whether relevant information is already available or easy to collect, additional auxiliary data with explanatory value for lichen presence, beyond NDVI and canopy height, could be integrated. However, incorporating additional auxiliary variables might make the sample less well spread in the other variables.

A primary focus in developing our method was to enhance objectivity and transparency, thereby ensuring that the outcomes will be accepted and trusted among diverse land users. Besides its potential to reduce variance in estimates, spatially balanced sampling also ensures representative samples and provides an objective approach for distributing sample plots, in contrast to subjective placements, which can be more susceptible to questioning.

4.2. Methods for lichen assessment

Our findings highlight the impact that the choice of method for cover assessment can have on the lichen cover and biomass estimates. Compared to the point-intercept method, we found that visual estimates resulted in lower lichen cover values, whereas the use of the presence-absence method led to higher values of lichen cover (Fig. 7). Out of our 120 sample plots, 18 were recorded as having 100% cover using the presence-absence method, while the coverage according to the other methods was lower. The point-intercept method may also generally overestimate cover, but to a lesser extent than the presence-absence method. Dividing the sample plot into smaller squares or employing more points could enhance the accuracy of both these methods, yet this would extend the time needed for data collection. Point-intercept methods are known to be impractical when the cover is low, as a very large number of points are needed to achieve accurate results (Drezner and Drezner, 2021). However, our method is primarily intended for areas with reindeer winter grazing, which typically have abundant lichen. Additionally, single sample plots with very low cover will have a marginal impact on the overall estimates. To improve consistency between observers, precision in the measurements and time consumption, it is advisable to explore alternative methods. A recent study demonstrated the successful application of image segmentation using a U-Net in measuring cover of reindeer lichens (Lovitt et al., 2022). The use of a Convolutional Neural Network has also been explored for differentiating various *Cladonia* species (Galanty et al., 2021). The automated method used by Lovitt et al. (2022) predicted less lichen cover compared to visual estimates, which was also indicated by our manual segmentation example (Fig. 3).

While the point-intercept method offers greater objectivity and generally reduces variation between users compared to visual estimates (Morrison, 2015), it is notably more time-consuming (Appendix B). However, as both cover and height measurements can be taken simultaneously when the rod is lowered to the ground, time is saved compared to other methods. In cases like ours, where the goal was to collect data for all lichen species combined and only one measurement per point is required, the time difference between the visual estimate and the point-intercept method was no more than about two minutes per sample plot, which is relatively small compared to the total time required for fieldwork.

In contrast to the methodology employed for cover assessment, height measurements often receive less attention. In our literature review, we found that the studies using height measurements taken at twenty-five systematically distributed points throughout the plot (Moen et al., 2007; Rosso et al., 2014) had the steepest slopes (Fig. 7), demonstrating sharper changes in biomass for increases in volume compared to other studies that measured height at a few subjectively selected points considered representative (Appendix A). While no definitive conclusions can be drawn from this, it suggests that the methods used for height measurement may yield differing results, deserving further study.

4.3. Literature review – lichen biomass from volume

For our method to be practically useful, a predefined relationship between volume and biomass is essential, offering a more efficient alternative to the highly time-consuming process of collecting and weighing lichen. By fitting a linear regression to all data from our review studies, we obtained a slope of 0.0148. Visual estimates of cover were used in these five studies. Based on our method comparison, it is reasonable to assume that using cover measurements from the point-intercept method, combined with a relationship based on visual estimates, may result in a somewhat inflated biomass estimation, as the point-intercept method yielded higher lichen cover values than visual estimates. However, the results from Moen et al. (2007) and Rosso et al. (2014) suggested smaller differences between these methods compared to our study. The conditions at our study sites were also similar to those in Moen et al. (2007), where visual estimates of cover yielded a slope of 0.0155 in our comparison. Additionally, the linear relationship from Finland reported by Kumpula et al. (2006)—which we did not use due to the unavailability of volume data—was closely aligned with that of Moen et al. (2007). This supports our decision to use the slope of 0.0148 that we derived from the combined dataset. This dataset also offered data points across a wider range of volumes making the resulting relationship more applicable and robust, also beyond our study sites. Still, in environments with significantly different conditions or species compositions, or when using methods like image segmentation that can yield substantially lower estimates of lichen cover, it may be necessary to establish a new volume-to-biomass relationship.

Our comparison helped clarify the extent to which the relationships between lichen volume and biomass differed across studies, but pinpointing specific causes was not possible with the available information. Methodological differences and variations between observers in the assessment of lichen cover and height likely contributed, as well as inconsistencies in the cleaning and removal of dead parts from the collected lichen (Appendix A). Differences in species composition and environments are other factors that likely played a role. Among species, *Cladonia stellaris* and *Cetraria islandica* is noted to have a higher density (weight per volume) compared to *Cladonia rangiferina* and *Cladonia arbuscula* with density differences ranging from 1.2 to 2 times higher (Andrejev, 1971; Fleischman, 1990; Moen et al., 2007; Akujärvi et al., 2014). *Stereocaulon paschale* has been identified as having the highest density among the species present in our study (Andrejev, 1971; Fleischman, 1990; Akujärvi et al., 2014) but was only present in small amounts at one of our sites and absent in the studies reviewed. Additionally, the moisture level of lichen during measurement should be considered. Both Kumpula et al. (2006) and Olofsson et al. (2011) observed that dry lichen of *Cladonia* species is shorter than wet and moist lichen. Kumpula et al. (2006) found that dry lichen was 16.8% shorter than wet lichen. Environmental factors might also affect the growth forms of the lichen and thereby the density. However, Errington et al. (2022) found that equations relating volume to biomass for the *Cladonia* subgenus *Cladina* varied only slightly across topographical or climatic gradients. Similarly, differences among landcover types in Rosso et al. (2014) and among ecoprovinces in Greuel et al. (2021) were small, indicating that volume-to-biomass relationships are relatively unaffected by environmental preconditions.

4.4. Lichen cover and biomass estimations

Our study highlights the importance of considering both cover and height for biomass estimations. We calculated lichen biomass for each sample plot from volume, determined by multiplying cover by height. The fact that both lichen cover and height were lower at the Kum site compared to the other sites explains why the relative difference between sites in estimated biomass was larger than the relative difference in estimated cover, underscoring the importance of using volume rather than cover alone. Given that the RSE for our estimates from data obtained via the point-intercept method was approximately 15%, our selection of 40 samples was in this case a good balance between fieldwork effort and the precision of the estimate. The low RSE resulting from our method also makes it suitable for monitoring over time, enabling early detection of changes in the environment. Our design-based estimations rely solely on the data collected from the sample plots. This makes it straightforward and interpretable compared to the often-used model-based estimations, which sometimes rely on complex models.

4.5. Reindeer grazing days

Our approach to estimate reindeer grazing days offers valuable insights for planning and assessing the impact on reindeer herding in real-world scenarios. Our results of 54 to 67 reindeer grazing days per hectare across the study sites align with the models of Tahvonen et al. (2014), where one hectare, with biomass levels similar to those of our study sites, supported about 60–70 grazing days per year. The relatively small difference in estimated reindeer grazing days for the Kum site compared to the other sites—despite the larger difference in biomass estimates—illustrates that cover rather than biomass determines grazing days in our calculations. Even if the cover, and therefore the theoretical annual grazing days, is similar across areas, less cratering and lower energy consumption are required to access the same amount of lichen in areas with taller lichen and higher biomass. This makes such areas less vulnerable to overgrazing.

4.6. Method application and limitations

Land use by industrial forestry along with the increased demand for natural resources in northern Sweden poses a significant threat to traditional reindeer husbandry based on natural pastures (Harnesk, 2022; Horstkotte et al., 2022). The decline, loss of access to, and destruction of lichen-rich areas increases the need for winter feeding of reindeer (Rautiainen, 2024). When assessing the impact on reindeer husbandry from the often piecemeal development of competing land uses, local-scale information on lichen resources is essential. However, it is important to integrate such information with reindeer herders' traditional knowledge of reindeer landscape use. A narrow focus on isolated lichen patches could inadvertently enable other land users to exploit areas not recognized as lichen-rich, potentially compromising the overall use of the landscape and the availability of grazing lands.

Our method offers a new and efficient way to collect detailed data on lichen biomass and cover. Although it is designed for a local scale, it is applicable to considerably larger areas than those of our study sites. When working with larger areas our method can be effectively combined with other methods utilizing satellite data. This enables the identification of lichen rich areas in the landscape where in-depth assessments of cover and biomass are most needed, optimally applying our method. Providing data on both biomass and cover not only quantifies the amount of lichen present but also indicates how it is distributed. Additionally, the high-resolution orthomosaics derived from drone images make it possible to visually identify the lichen distribution across the study area. Together, this provides a comprehensive understanding of the amount and distribution of lichen to be used in planning and management by both herders and other land users.

The appropriate number of sample plots needed for accurate biomass estimation largely depends on the variability of the study area. Areas with less variability require fewer sample plots, and vice versa. The total area covered by the 40 sample plots in this study ranged from 0.07% to 0.09% of each site. For larger sites, it is advisable to increase the number of sample plots and exclude large, continuous biotopes or vegetation types where lichens are absent. While it took us 20 min to complete each sample plot, in practical applications aimed at estimating the total food resource for reindeer, only one method is used to assess the cover and height for all lichen species combined. This reduces the time required to complete a sample plot by at least half. However, the time needed to locate and navigate between plots may increase with the size of the site and depends on the terrain.

Comprehensive documentation, including access to photos and all data from each sample plot enables anyone to verify the reasonableness of the data used for cover and height in the estimates. All our calculations and estimates were performed using the open-source software R, and the code that we used is freely available. To make the method even more accessible, a vegetation index based on RGB images can be used as auxiliary data in the sampling process instead of NDVI, avoiding the need for a multispectral camera. Additionally, drone image processing can be done using open-source software such as OpenDroneMap (OpenDroneMap Authors, 2020). Methods that directly map lichens from remote sensing images typically focus on pale lichens with distinct spectral signatures. Our method does not require lichens to be identifiable in the images, making it effective for more lichen species important as food for reindeer, such as *Cetraria islandica*. Additionally, when using our method, other resources correlated with the auxiliary variables can be concurrently quantified, further enhancing its overall usability.

5. Conclusions

Using both original and literature data we present a robust and objective method for estimating ground lichen cover and biomass. Our approach introduces a new way to use drones for lichen assessment by integrating drone-derived NDVI and tree height data into the sampling design.

Our study highlights that different lichen cover assessment methods can produce highly divergent results. We recommend the point-intercept method for assessing lichen cover and height due to its objectivity and consistency across observers, despite that it requires more time to finalize and a tendency to yield higher cover values compared to visual estimates. At the same time, we encourage the development and accessibility of alternative approaches. Image segmentation shows promise for delivering accurate and consistent cover estimates efficiently, making it an attractive alternative for collecting lichen cover data necessary in our method, as well as for providing training data for lichen mapping models that incorporate remote sensing images, and for future volume-to-biomass relationships.

The slope of 0.0148, we derived from data in the reviewed literature and used to relate lichen volume to biomass, is applicable beyond the scope of our study. However, further research is needed to clarify the observed differences between studies. Additionally, research is needed to develop objective, accurate, and efficient methods for measuring lichen height, as our findings reinforce previous research demonstrating the importance of considering both lichen cover and height in biomass estimation.

CRediT authorship contribution statement

Erik Cronvall: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sven Adler:** Writing – review & editing, Methodology, Conceptualization. **Per Sandström:** Writing – review & editing, Funding acquisition, Conceptualization. **Anna Skarin:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2024.100768.

Data availability

Data and R scripts are available at https://doi.org/10.5281/zenodo.11440778.

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ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

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Ground lichens are a critical winter forage resource for reindeer and as such a key component of Sámi reindeer husbandry. This thesis develops and evaluates methods for mapping and quantifying ground lichen across multiple spatial scales and demonstrates how reindeer movement data can be used to analyse the accessibility of lichen. These methods provide a framework for evidence-based planning and management of reindeer winter pastures.

Erik Cronvall received his doctoral education at the Department of Forest Resource Management, Swedish University of Agricultural Sciences (SLU). He received his MSc in Environmental Science at Lund University in 2005.

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