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Soil moisture conditions control nutrient accumulation, carbon storage and tree growth in boreal forest landscapes

JOHANNES LARSON



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Johannes Larson

Faculty of Forest Sciences

Department of Forest Ecology and Management

Umeå



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Swedish University of Agricultural Sciences, Department of Forest Ecology and Management,
Umeå, Sweden

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Abstract

Forest and soil properties change across landscapes due to the complex interactions between various environmental factors. In many landscapes, topography exerts a major influence on the variation in soil moisture conditions, which in turn largely affects soil properties and processes. This thesis synthesises the results from four studies (papers I-IV), with the underlying aim to increase the understanding of how environmental factors, in particular, soil moisture, control the variation of nutrient accumulation, carbon storage, and tree growth within boreal landscapes. The four studies were all based on an extensive survey of a 68 km² boreal forest landscape in northern Sweden. In Paper I, soil moisture conditions were predicted using multiple terrain indices. The results emphasised within-study validation and how digital elevation model resolution together with user-defined thresholds influence prediction accuracy. Paper II focused on how multiple environmental drivers influence the variation in soil carbon-to-nitrogen (C/N) ratios, with a noteworthy result that the ratio decreases as soil moisture conditions increase. Paper III presented how, soil moisture conditions significantly controls the distribution and partitioning of carbon stocks, with large increases in total carbon stock observed as soil moisture conditions increases, which was observed at both plot and landscape scale. The results in paper IV showed that, estimates of forest site quality decrease in response to increased soil moisture conditions. In conclusion, the research discussed in this thesis emphasises the importance of studying forest ecosystems on a landscape scale, an approach that can provide key insights into the factors that influence variation of different attributes of boreal forest ecosystems.

Keywords: boreal forest, carbon stock, C/N ratio, site quality, soil properties, soil moisture, landscape, ALS

Markfuktighet kontrollerar ackumuleringen av näringsämnen, kolförråd och tillväxt i boreala skogslandskap

Sammanfattning

Variationen i ett skogslandskap är resultatet av en stor mängd komplexa interaktioner mellan olika miljöfaktorer. I de flesta landskap spelar topografin en avgörande roll för variationen i markfuktighet, vilket i sin tur har stor påverkan på markens egenskaper och processer. Avhandlingen binder samman resultat från fyra studier (Studie I-IV), med syftet att öka förståelsen för hur olika miljöfaktorer, särskilt markfuktighet, styr ackumuleringen av näringsämnen, kolförråd och skogens tillväxt i ett borealt landskap. Alla studier baserades på en omfattande inventering inom ett 68 km² skogslandskap i Västerbotten. Studie I fokuserade på att skatta variationen i markfuktighet med hjälp av olika terrängindici baserade på digitala höjdmodeller. Resultaten visade att höjdmodellernas upplösning spelar en avgörande roll för modellens noggrannhet, samt vikten av att validera modeller inom studieområden. I Studie II, låg fokus på kol-kväve (C/N) kvoter i marken där låga kvoter indikerar högre näringstillgång. Variationen i C/N kvoten relaterades till dominerande trädslag, jordart och markfuktighet. En ökad markfuktighet ledde till en signifikant minskning av kvoten. Studie III fokuserade på markfuktighetens roll för skogens kolförråd samt dess påverkan på fördelningen ovan och under jord. Det totala kolförrådet ökade markant med markfuktigheten, framförallt orsakat av en ökning i det organiska jordlagret. I Studie IV skattades den potentiella träd tillväxten över hela studieområdet, där en minskad potentiell tillväxt påvisades med ökande markfuktighet. Avhandlingen bidrar med ett unikt landskapsperspektiv som ger viktiga insikter om skogsekosystems variation och dess kontrollerande processer.

Nyckelord: kolförråd, kol-kväve (C/N) kvot, skogslandskap, tillväxt, markfuktighet, fjärranalys, skogsmark



Photo: Andreas Palmén



Photo: Andreas Palmén

Dedication

In memory of my father Mikael Larson (1963-2022)



Photo: Johannes Larson

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List of publications

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

- I. Larson, J.*, Lidberg, W., Ågren, A. M., Laudon, H. (2022). Predicting soil moisture across a heterogeneous boreal catchment using terrain indices. *Hydrology and Earth System Sciences*, vol (26), 4837-4851. <https://doi.org/10.5194/hess-26-4837-2022>
- II. Larson, J.*, Kuglerová, L., Högberg, P., Laudon, H. Deciphering how local environmental conditions influence soil Carbon-to-Nitrogen ratios within a boreal forested catchment (manuscript)
- III. Larson, J.*, Wallerman, J., Peichl, M., Laudon, H. (2023) Soil moisture controls the partitioning of carbon stocks across a managed boreal forest landscape. *Scientific Reports*, vol(13), 14909. <https://doi.org/10.1038/s41598-023-42091-4>
- IV. Larson, J.*, Vigen, C. A., Wallerman, J., Ågren, A. M., Appiah Mensah, A., Laudon, H. Do soil moisture conditions control tree growth within a boreal landscape? (manuscript)

Papers I and III are reproduced with the permission of the publishers.

*Corresponding author

The contributions of Johannes Larson to the papers included in this thesis are as follows:

- I. JL is the main author. Johannes developed the research idea together with AA, HL and WL. JL compiled the data and performed the statistical analysis. JL wrote the manuscript in collaboration with the co-authors.
- II. JL is the main author. JL developed the research idea in collaboration with HL. JL was in charge of, and conducted, the field survey, as well as performed the data compilation and statistical analysis. JL wrote the manuscript in collaboration with the co-authors.
- III. JL is the main author. JL developed the research idea together with HL. JL was in charge of, and conducted, the majority of the field survey, as well as performed the data compilation and statistical analysis. JL wrote the manuscript in collaboration with the co-authors.
- IV. JL is the main author. JL developed the research idea together with HL. JL was responsible for a major part of the data collection. JL conducted the statistical analysis in collaboration with CAV and AAM. JL wrote the manuscript in collaboration with the co-authors.

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Abbreviations

ALS	Airborne Laser Scanning
DEM	Digital Elevation Model
DI	Downslope Index
DTW	Depth To Water
EAS	Elevation Above Stream
LiDAR	Light Detection And Ranging
M10	Mineral soil samples at sample depth 0-10 cm
M20	Mineral soil samples at sample depth 10-20 cm
M65	Mineral soil samples at sample depth 55-65 cm
NFI	The Swedish National Forest Inventory
O	Organic layer samples
OPLS	Orthogonal Projection to Latent Structures
SFSI	Swedish Forest Soil Inventory
SLU	SLU soil moisture map
SOC	Soil Organic Carbon
TWI	Topographic Wetness Index

1. Introduction

The boreal forest provides a wide range of ecosystem services. One of the critical services being the ability to sequester and store vast amounts of carbon (C), which plays a major role in climate change mitigation, in addition to providing renewable resources (Ameray et al. 2021). It has been calculated that boreal forests store approximately one-third of the entire terrestrial C stock (Pan et al. 2011), with the majority stored in the soil as soil organic carbon (SOC) (Bradshaw & Warkentin 2015). Given that northern latitudes are expected to undergo major shifts in weather patterns in the coming decades due to climate change, it is important to understand how key environmental factors cause variation in the forest systems. Deciphering the connections between ecosystem services and the forest landscape variation is therefore essential. Forest landscapes should not be viewed as uniform entities; but rather considered to be heterogeneous landscapes characterised by distinct variations in functions and roles. However, spatial information about forest and soil properties is often the primary limiting factor for spatially distributed models and land management. It should be noted that past and present forest management across much of the boreal landscape adds further complexity to the interpretation of which factors drive variation in boreal forest ecosystem attributes (Gauthier et al. 2023). Recent decades have seen significant advances in landscape analysis which are mostly linked to improvements in the remote sensing of soil and forest attributes (Coops et al. 2021; Shary 2023). However, large knowledge gaps still exist, and will need to be addressed if we are to reliably understand how different environmental factors influence the variation in forests across boreal landscapes.

1.1 Environmental factors

Forests vary across distances due to changes in environmental factors, which vary in importance. For instance, climate – primarily measured in terms of temperature and precipitation – is a key factor that drives variation in forest characteristics at the regional and global scales. On the other hand, soil properties have a central role influencing the variation in forest ecosystems across all scales from global to within a single stand. Soil formation are commonly described using the five soil forming factors, namely, climate, biota, time, parent material and topography (Jenny 1941). Anthropogenic influence, such as forestry and agriculture also exerts an impact on soil formation; as such, this factor is either included within biota or as a sixth soil forming factor. On small spatial scales, many of these factors can be considered constant, which allows researchers to focus on a limited subset of environmental factors.

1.2 Topographic control of forest hydrology

At the landscape scale (defined as up to tens of km² in this thesis), local topography commonly plays a central role in determining the hydrological flow paths across the landscape; hence, topography is a primary controlling factor for the spatial variability in soil moisture conditions as well as biogeochemical processes (Högberg 2001; Ågren et al. 2014). This is particularly true within boreal landscapes because of glacial history. In till soils, which dominate the boreal region, hydrological conductivity generally increases exponentially towards the soil surface (Lind & Lundin 1990). Because of this, neighbouring areas can greatly vary in groundwater table depth and soil moisture conditions. This variation can range from local conditions where tree growth is limited by the lack of soil moisture, to areas where forest growth is constrained by too much water leading to anoxic conditions (Simard et al. 2009; Sikström & Hökkä 2016). Because of the strong connection between topographic variation and forest hydrology, topographical information has become essential for mapping stream networks and predicting soil moisture conditions as well as soil properties (Beven & Kirkby 1979; Murphy et al. 2008; Ågren et al. 2014). In addition to the accumulation of water, hydrological pathways also control the transport of nutrients and mineral solutes (Jutebring Sterte et al. 2021), and hence likely to affect the variation in forest growth.

1.3 Nutrient accumulation

In boreal landscapes, nitrogen (N) levels commonly limit forest growth potential (Tamm 1991), and thereby influence various fundamental ecosystem processes as well as species composition. Evidence of these dynamics is that remarkable differences in nutrient availability, vegetation composition and forest growth can be observed when moving from recharge to discharge areas (Giesler et al. 1998). Within a range of 100 meters, it is possible for the soil carbon-to-nitrogen (C/N) ratios to shift from a high value of 35-40 in recharge areas, to as low as 15-20 in groundwater discharge areas (Giesler et al. 2002). Although groundwater discharge areas constitute only a small portion of the landscape, they nevertheless receive nutrients from the considerably larger groundwater recharge areas through topographically driven hydrological pathways. The differences in forest growth between these areas involves complex interactions among additional ecosystem factors such as microbial turnover rates, retention of N in mycorrhiza and the nitrogen fixation (Högberg et al. 2017). However, it is important to state that the distribution of these areas is predominantly controlled by topographically-driven hydrological pathways, which largely influence soil moisture conditions (Kuglerová et al. 2016).

1.4 Carbon storage

It is well established that the accumulation of SOC is significantly influenced by soil moisture conditions (Olsson et al. 2009; Dalsgaard et al. 2016; Wiesmeier et al. 2019). Soil moisture conditions affect both the carbon inputs via the regulation of plant production, as well as decomposition rates. The accumulation of above-ground carbon stocks is significantly affected by growth conditions at the site, as well as disturbances, such as forest fires and forest management (Gauthier et al. 2015; Ameray et al. 2021). Both above- and below-ground carbon stocks have attracted extensive research across various scales due to its key link to the global carbon cycle (Bradshaw & Warkentin 2015; De Vos et al. 2015; Wiesmeier et al. 2019). National forest soil inventories is a valuable resource for studying environmental drivers of carbon stocks (Callesen et al. 2003; Hounkpatin et al. 2021). However, studies on smaller landscape scales are rare, limiting our understanding of variation of C stocks, along with how this information can be used to develop sustainable forest management practices.

1.5 Site quality

The direct comparison of forest growth across landscapes is complex because of the variation in stand characteristics such as tree age, stem density and species composition. This is particularly true in landscapes affected by forest management. Site quality describes a specific site's forest growth potential, determined by the physical and biological factors which characterizes a particular location (Assmann 1970; Bontemps & Bouriaud 2014). In comparison to measures such as stem volume growth, site quality can be considered constant. Site productivity is a quantitative measure of site quality that refers to the proportion of growth potential realised by the given stand (Skovsgaard & Vanclay 2008). Reliable estimates of site quality and site productivity are important for the sustainable management of forest resources and has therefore received a lot of research attention to develop improved model approaches (Tomé et al. 2006; Bontemps & Bouriaud 2014; Appiah Mensah et al. 2023). One significant drawback of the most commonly used methods for assessing site productivity lies in their reliance on fixed sample plots, requiring information about age and species, which imposes constraints on the possibility of extrapolating findings across broader scales (Hägglund & Lundmark 1977; Skovsgaard & Vanclay 2008). Therefore, the use of approaches to estimate site quality which are independent of both age and species has the potential to provide unbiased assessments of forest growth potential across broader scales (Tomé et al. 2006). Soil properties are usually considered a main determinant of site quality and site productivity (Hägglund & Lundmark 1977; Skovsgaard & Vanclay 2008). Therefore, improved understanding on how soil moisture affects the variation in site quality may provide valuable information for further growth models.

1.6 Remote sensing

Recent decades have been characterised by significant advances in remote sensing, which have also greatly improved the quality of landscape analysis. Airborne Laser Scanning (ALS) has emerged as a valuable tool for extracting landscape properties, such as topography, as well as resolving the three-dimensional properties of forest vegetation structure.

Because topography plays a central role in determining hydrological flow paths, topographical models have long been used to extract hydrological features across landscapes. ALS has greatly increased the accuracy and resolution of digital elevation models (DEM), which in turn has led to significant advances in the terrain indices used to model hydrological pathways and soil moisture conditions. However, the predictive performance of different terrain indices is highly dependent on the selection of an optimal DEM resolution and user-defined thresholds (Sørensen & Seibert 2007; Lin et al. 2010; Ågren et al. 2014). This type of hydrological maps has also proven effective when used to predict the spatial patterns in soil properties (Zinko et al. 2005; Seibert et al. 2007; Li et al. 2017). The combination of machine learning techniques, multiple terrain indices, and additional geographical information has enabled researchers to model soil moisture conditions across Sweden (Ågren et al. 2021). This is important as accurate predictions of soil moisture conditions holds significant potential for improving our understanding of how forest and soil properties are regulated across landscapes.

ALS has become a key method for collecting precise three-dimensional information about forest structure, which can be used to estimate various key forest characteristics with a great degree of accuracy and detail (Næsset 2002; Tompalski et al. 2021). This technique has been widely used due to the ability to provide continuous and detailed forest information across large areas at low costs.

One such method is the area-based approach, which is one of the most common modelling techniques for mapping forest attributes, such as standing volume, tree height, or above- and below-ground C stocks, across large areas (Næsset & Gobakken 2008; Kristensen et al. 2015; White et al. 2016). The area-based approach can be divided into two steps (Næsset 2002). The first step involves establishing relationships between field observations of forest attributes and ALS metrics to create an initial model. In the second step, the model is applied to the entire ALS dataset at a spatial resolution that

corresponds to the area of the survey plots. This returns accurate, high-resolution wall-to-wall estimates of the studied forest variable.

Furthermore, recent research has shown that ALS data from multiple surveys can be used to estimate forest growth and site quality across landscapes by applying various modelling techniques (Socha et al. 2017; Noordermeer et al. 2018; Tompalski et al. 2021). However, the relationship between landscape estimates of site quality and soil moisture conditions has not been widely studied, although it should be noted that several studies have shown promising results after improving model accuracy (Mohamedou et al. 2017; Appiah Mensah et al. 2023).

1.7 Knowledge gaps

There is a growing need to improve the understanding of the heterogeneity of the boreal landscape, and how environmental factors control the variation in key ecosystem processes. The techniques presented above provide an opportunity to study variation in environmental drivers and processes at high resolutions. By studying forest ecosystems at the landscape scale, it is possible to focus on a limited subset of environmental factors. To date, extensive survey data at smaller landscape scales are rare within boreal forest ecosystems. This thesis attempts to fill several of these gaps by studying variation across a 68 km² boreal forest landscape with a focus on nutrient accumulation, carbon stocks, and site quality.

2. Research objectives

The overall aim of the research underlying this thesis was to further the understanding of how soil moisture conditions within boreal forest landscapes drive nutrient accumulation, carbon storage, and site quality. The thesis includes four Papers (Paper I-IV). Paper I focused on how topography controls the spatial variation in soil moisture conditions. Paper II presented assessments of the variability in soil C/N ratios and the relationship to various environmental factors, including soil moisture. The research topic of Paper III was how soil moisture conditions control the distribution and partitioning of carbon stocks, and Paper IV discussed the variation in site quality across a boreal landscape along with specific relationships to soil moisture conditions. The specific objectives of this thesis were to:

- Evaluate how DEM resolution, thresholds values, and landscape type affect the potential of using terrain indices to predict soil moisture conditions (Paper I)
- Examine variability in Carbon-to-Nitrogen (C/N) ratios, and explain how this variation is influenced by specific environmental factors (Paper II)
- Further understanding about how soil moisture conditions control the spatial variation and partitioning of carbon stocks across a managed boreal forest landscape (Paper III).
- Study the variation in site quality on the landscape scale and describe the relationships to soil moisture conditions (Paper IV).

The individual papers included in this thesis stated several hypothesis that are directly related to soil moisture conditions:

- Soil moisture conditions within a boreal landscape can be predicted using terrain indices (Paper I).
- C/N ratios decrease towards discharge areas (Paper II).
- Soil moisture conditions controls C stocks at the landscape scale, where increased soil moisture conditions are associated with larger SOC stocks, which primarily is a result of an increase in the organic layer C stocks (Paper III).
- Soil moisture conditions controls the variation of site quality, with the best conditions for forest growth located under intermediate soil moisture conditions (Paper IV).

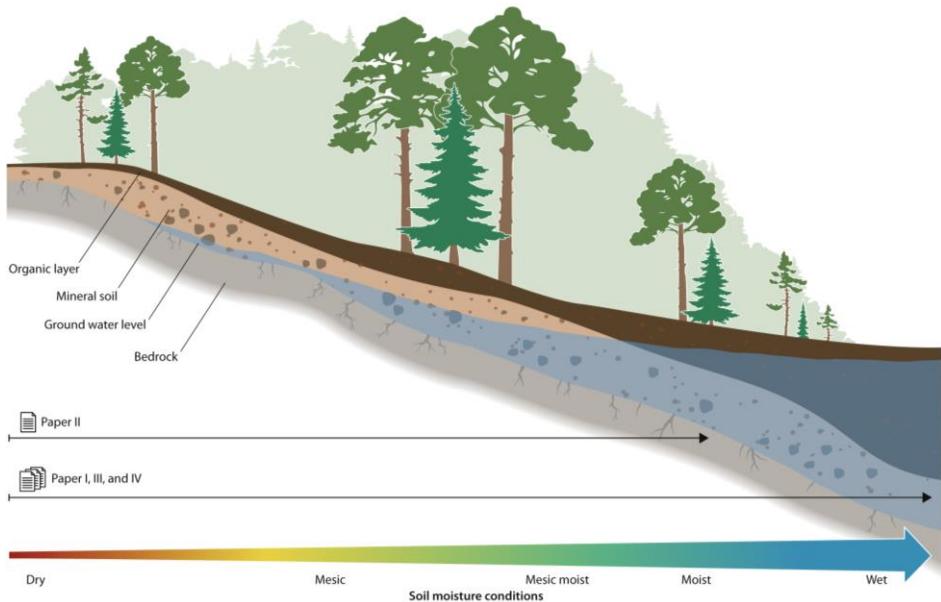


Figure 1. Schematic overview of how the papers included in this thesis are connected to the distribution of soil moisture across a hillslope. Papers I, III and IV focused on the entire landscape whereas Paper III focused on forests located on mineral soils. Illustration: J Lokrantz/Azote.

3. Methods

All of the papers included in this thesis involved analysis of data collected from the same survey grid within the Krycklan catchment (Laudon et al. 2013, 2021). In this section, an overview of the soil and forest survey, remote sensing data, and soil moisture modelling used are provided. This is followed by separate sections where the methods applied in the individual papers are described. Further details can be found in the individual papers.

3.1 Study site

The Krycklan catchment covers 6790 ha and is situated in northern Sweden (Lat. 64°23'N, Long. 19° 78'E) (Fig. 2). The land cover is dominated by forests, accounting for 87% of the total area, but mires (9%) and lakes (1%) are also present (Laudon et al. 2013). The climate is classified as a cold temperate humid type, with snow cover for approximately five months of the year. The catchment has a gentle topography ranging from 127 to 372 m above sea level (m.a.s.l). The highest post-glacial coastline is located at approximately 257 m.a.s.l, which divides the catchment area in two distinct areas. Unsorted sediment soils (51%) of glacial till origin dominate the upper parts of the catchment, while post glacial sorted sediments of primarily fluvial or lacustrine delta origin dominate at lower altitudes. The bedrock is dominated by Svecofennian metasediments/metagreywacke (94%). The forests consist primarily of Scots pine (*Pinus Sylvestris* L.) (63%) and Norway spruce (*Picea abies* (L.) H. Karst) (26%), along with certain deciduous species (mostly *Betula spp.*). The forests are managed by conventional rotation forestry, and are thus predominantly even-aged and mostly artificially regenerated, with thinning and clear-felling representing the standard silvicultural practices.

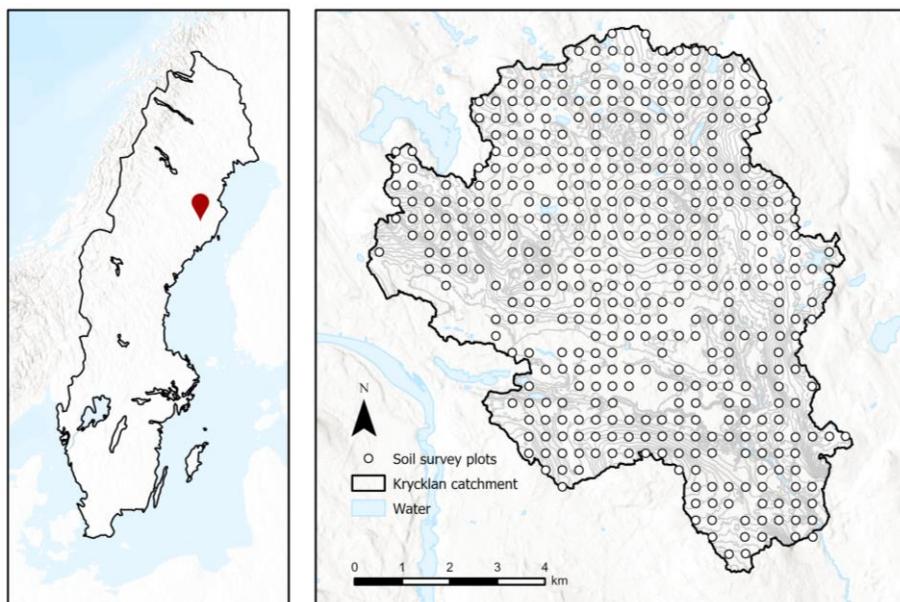


Figure 2. Map of the Krycklan catchment, including the locations of the 441 survey plots included in the soil survey, distributed over a 350 x 350 m square grid.

3.2 The survey grid

The data used in all four studies included in this thesis were based on a survey grid of plots with a 10 m radius (314 m^2) spread across the entire study area; the survey grid was established in the fall of 2014. The goal of the survey was to measure approximately 500 survey plots located in forest with the overall aim of developing methods for remote-sensing mapping of forest biomass. A regular square grid, with 350 m spacing between plots that covered the entire area was created using a randomly chosen origin. The exact positions of plot centres were measured using a high-precision GPS instrument (Trimble GeoXTR GNSS receiver; Trimble, Westminster, CO).

3.3 Soil survey

The Krycklan soil survey was conducted during the snow free seasons of 2019 and 2020, in a way that largely followed the methods of the Swedish Forest Soil Inventory (SFSI) (Fridman et al. 2014), with some modifications. Soil sampling was carried out within a 1 m radius subplot, with additional measurements spread across the entire plot (Fig. 3b). The organic layer was sampled volumetrically using a 10 cm diameter corer with a serrated blade to a maximum depth of 30 cm, excluding the litter layer. The organic layer samples were collected from 1-9 pre-defined sample points within the 1 m radius subplot until a target volume of 1.5 L was obtained. At each organic layer sample point, the organic layer thickness was measured and the humus form classified. Within the subplot, a soil pit was dug to a depth of 65 cm (or to bedrock or boulder) measured from top of the mineral soil.

Mineral soil samples (ca. 500 mL) were collected at three fixed intervals: depth of 0-10 cm (M10); depth of 10-20 cm (M20); and depth of 55-65 cm (M65) measured from the top of the mineral soil. Parent material and soil texture was determined at predefined depths in the upper and lower parts of the soil profile. Each soil profile was classified according to the World Reference Base for Soil Resources (IUSS Working Group WRB 2015). Stoniness was estimated using the rod penetration method at 12 points spread across the entire 10 m survey plot (Viro 1952; Stendahl et al. 2009).

Soil analysis of all samples was performed on the fine fraction (<2 mm) after samples had been dried at 65 C°, sieved and homogenised. A subsample was ground into a fine powder, which was subsequently analysed for C and N concentrations by mass spectrometry (DeltaV IRMS coupled to a Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). The analyses were performed on 5-50 mg of soil material, depending on the organic matter content.

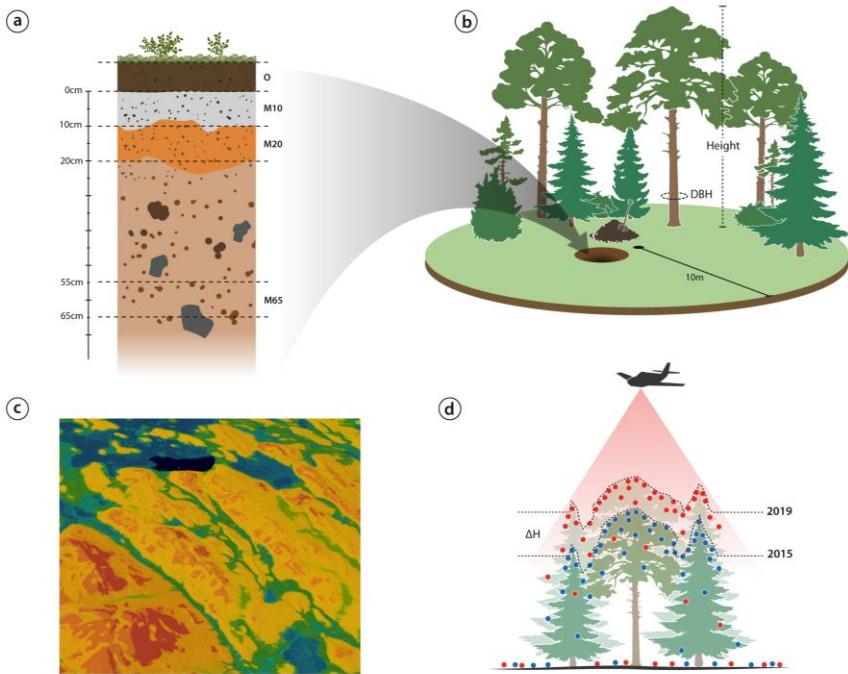


Figure 3. Overview of the main data sources included in the Papers. Soil sampling depths of the soil survey (a), a schematic illustration of the 10 m radius survey plots (b), soil moisture modelling (c), and the bi-temporal ALS data (d). Illustration: J Lokrantz/Azote.

3.4 Forest survey

The forest survey was conducted twice with a five-year interval. The first forest survey was conducted in the fall of 2014 and finalised in the spring of 2015, thereafter repeated in the fall of 2019 and finalized the following spring. Within each survey plot, diameter at breast height (DBH, 1.3m) and species identity was recorded for all trees with a DBH >4 cm (Fig. 3b). A sub-sample of trees was chosen to survey tree height, measured using a laser-guided hypsometer, for the purpose of capturing variation in the tree size of different species. The heights of the remaining trees were estimated using specifically developed local species-specific tree height functions that were fitted to the sub-sampled tree data from the surveys. Forest state variables used in this thesis included above- and below-ground biomass, and basal-area weighted height (Lorey's mean height) which was estimated on individual tree level and summarized for each plot.

3.5 Field classifications of soil moisture conditions

Each survey plot was assigned to one out of five soil moisture classes based on the average depth to the groundwater table which was estimated from its landscape position, soil type and vegetation patterns. The classification was done both in the forest and soil survey. The five soil moisture classes used were dry, mesic, mesic-moist, moist and wet, and are described below; further details can be found in the field instructions of the Swedish National Forest Inventory (NFI) (Swedish NFI 2014).

- Dry soils have an average depth to the groundwater table of > 2 m. Dry areas tend to be coarse textured and are often found on top of hills, ridges and eskers. The predominant soil types are Leptosols, Arenosols, Regosols and Podzols, and these areas often have a thin organic layer.
- Mesic soils have an average depth to the groundwater table between 1-2 m. Soil types are dominated by Podzols with thin (4-10 cm) mor layer, which is commonly covered by dry land mosses. It is possible to walk dry-footed even directly after rain of shortly after snowmelt.
- Mesic–moist soils have an average depth to groundwater table < 1 m. They are often located in lower parts of the landscape such as toe-slope areas. Whether you can cross in shoes and keep your feet dry depends on the season because the soils tend to stay wet seasonally following snowmelt or heavy rain events. Peat mosses are common, and trees commonly tend to grow on elevated humps. Podzols are common, but often with a thicker organic layer compared to mesic sites. The organic layer is often classified as peaty mor.

- Moist soils are characterised by an average depth to groundwater of <1 m. Surface water is often visible in depressions within the plot. These areas are commonly located in the lower parts of the landscape, e.g. at the lowest parts of slopes and flat areas below larger ranges. It is possible to cross these areas in regular shoes without getting wet by using tussocks and higher-lying ground. Even during dry spells, stepping in depressions result in water forming around the feet. The vegetation includes wetland mosses, trees commonly grow on elevated humps and the predominant soil types are Histosols, Gleysols, and Regosols.
- Wet soils have a ground water table close to the soil surface. Wet areas are often located on open peatlands and coniferous trees seldom develop into stands. Drainage conditions are so weak that these areas cannot be crossed in regular shoes without getting the feet wet. Permanent pools of surface water are common within these areas the typical soil types are Histosols and Gleysols.

3.6 Remote sensing data

Remote sensing in the form of ALS was a crucial source of topographic information (paper I-IV) and estimation of forest variables (Paper III and IV). ALS, which is also commonly referred to as LiDAR (Light Detection And Ranging) is an active remote sensing technology that measures distance based on reflected laser light. ALS generates a georeferenced, three-dimensional point cloud of the landscape by transmitting laser pulses, which, echoes back from the vegetation and ground surface below. High resolution ALS was conducted across the entire study area in late summer of 2015 and 2019 (Fig. 3d). The raw ALS data were pre-processed by classifying point returns as ground, unclassified, or noise. A digital terrain model was then generated and the ALS points were normalised to represent tree canopy height above the ground surface. In all of the included studies, the DEMs generated from point clouds had an average point density of 20 points per m².

For each survey plot, ALS metrics from both acquisitions runs were derived separately using Fusion software (McGaughey 2016). The metrics were calculated on 12.5 x 12.5 m (Paper III) and 10 x 10 m (Paper IV) resolutions describing canopy height and canopy density, including measures such as mean height, maximum height, standard deviation, heights at certain percentiles of height distributions (e.g. 95th) and proportion of points reflected in vegetation.

The area-based approach was used to obtain estimates of forest variables across the entire study area (Næsset 2002). The variable of interest in Paper III was the tree C pool, while for Paper IV it was Lorey's mean height (basal area weighted mean height) at each survey occasion to model site quality. In the first step, predictive models were developed by regressing observed forest attributes from the survey plots on corresponding ALS metrics extracted for each plot. Model assessment was based on regression fit statistics and studies of residual plots. In the second step, the models were applied to the individual grid cells covering the entire catchment to generate wall-to-wall estimates of the studied forest attributes.

3.7 Soil moisture modelling

The modelling of soil moisture conditions was a central element of all studies included in this thesis. Paper I evaluated seven different terrain indices as well as two readily available soil moisture maps (see detailed descriptions in Paper I). The terrain indices differed in approaches but all used various information extracted from the DEM. For example, the Topographic Wetness index (Papers I and II) is defined as $\ln(a/\tan\beta)$, where a is the local upslope contributing area and $\tan\beta$ is the local slope (Beven & Kirkby 1979). Papers I, II and IV utilised a recently developed soil moisture map that covers all of Sweden, and which was created by combining machine learning and geographical information, e.g. multiple terrain indices, climate data, and quaternary deposits (Ågren et al. 2021). The training and validation data set consisted of almost 20,000 soil moisture classifications (section 3.5) from the NFI, spread across the entire country. In the same study, the survey grid included in this thesis was used as an independent validation dataset. The model output was a soil moisture map which shows the predicted probability (0–100%) that a point is classified as wet, the SLU moisture map has a resolution of 2 x 2 m.

3.8 Evaluation of the soil moisture predictions (Paper I)

The overall aim of Paper I was to predict soil moisture conditions across the entire study area using different terrain indices, as well as evaluate how DEM resolution and user-defined thresholds influence the results. The terrain indices were calculated using seven different hydrologically-corrected DEMs (0.5, 1, 2, 4, 8, 16 and 32 m). The Depth To Water (DTW) (Murphy et al. 2008) and Elevation Above Stream (EAS) (Rennó et al. 2008) indices were calculated using stream networks, which can be calculated using different stream initiation thresholds. For each DEM resolution, DTW and EAS were calculated on stream networks based on a stream initiation threshold of 1, 2, 4, 8, 16 and 32 ha. The downslope index (DI) (Hjerdt et al. 2004) includes a predefined vertical distance threshold in Paper I was set to 1 and 2 m. As such, a total of 146 different maps were used to predict soil moisture conditions (Table 1). The value corresponding to each plot centre coordinate was extracted from all of the layers and related to field observed soil moisture. To determine which terrain index offers the most accurate predictions, all layers were assessed using Orthogonal Projection to Latent Structures (OPLS) analysis (Eriksson et al. 2006). The OPLS represents a modification of the partial least squares (PLS) regression, and was carried out using the multivariate program SIMCA 16.0 (Eriksson et al. 2006).

Table 1. All terrain indices and soil moisture maps included in Paper I.

Terrain index	Abbr.	Source	Layers (n)
Topographic Wetness Index	TWI	(Beven & Kirkby 1979)	8
Depth To Water	DTW	(Murphy et al. 2008)	48
Elevation Above Stream	EAS	(Rennó et al. 2008)	48
Downslope Index	DI	(Hjerdt et al. 2004)	16
WILT ¹	WILT	(Meles et al. 2020)	8
Relative topographic position	RTP	(Newman et al. 2018)	8
Plan curvature	PlanC	(Wilson & Gallant 2000)	8
SLU soil moisture map	SLU	(Ågren et al. 2021)	1
SMI	SMI	(Naturvårdsverket 2021)	1

¹Wetness Index based on Landscape and Topography

3.9 Environmental factors that influence soil C/N ratios (Paper II)

In an attempt to explain factors that influence the variation in nutrient accumulation, Paper II focused on the variations in soil C/N ratios. More specifically, Paper II examined individual relationships between environmental factors and several soil properties, i.e., C/N ratio, C%, and N%, across 391 plots and at three sampling depths (O, M10, M20). The research focused on the following environmental factors; topography, parent material, soil texture and dominant tree species. It should be noted that Histosols, i.e., soils with an organic layer thickness of ≥ 40 cm were excluded. The topographic attributes included elevation, aspect, slope, and TWI. The TWI was used since it is among the most commonly used topographical indices in landscape analyses. TWI was calculated using a DEM with a resolution of 16 x 16m, as this resolution was found to be the optimal resolution within the Krycklan catchment (Paper I). Parent material was classified for each survey plot according to sorted and unsorted sediments. Soil texture was determined in the field, and grouped according to four different classes based on parent material. The effects of topography on soil properties were analysed via linear regression and by calculating Spearman's rank correlation values. A one-way ANOVA, followed by Tukey's test, was conducted to examine the significance of C%, N% and C/N ratio differences between dominant tree species and soil texture classes.

3.10 Carbon stocks (Paper III)

The focus of Paper III was how changes in soil moisture conditions influence the variation observed in C stocks. The total C stock was divided into three different pools; i.e., the organic layer C pool, the mineral C pool, and the tree C pool. The organic layer C pool was calculated by multiplying the C% of the sample by its dry weight and divided on the total sampled area. The mineral C pool was estimated down to a depth of 50 cm based on the C% measured at each sampling depth (M10, M20 and M65), bulk density, corrections for stoniness (Stendahl et al. 2009), and linear interpolation between measured layers. Following the SFSI, the bulk density of the mineral soil layers was estimated using a pedotransfer function that depends on C% and sample depth (Nilsson & Lundin 2006). The total SOC pool at each survey plot was obtained by combining the organic and mineral C pools.

For plots with an organic layer thickness >30 cm (maximum sample depth or the organic layer), the organic C stock was calculated to a maximum of 1 m via downward extrapolation.

The tree C pool included both above- and below-ground biomass, which was calculated using tree species-specific allometric functions (Marklund 1988; Petersson & Ståhl 2006). The total tree C pool was calculated by combining above- and below-ground estimates for each plot, this value was then converted to Mg C ha⁻¹, under the assumption of a C concentration of 50%.

The individual C pools and the total C stocks were analysed for different soil moisture conditions observed in field. The relationship between C stocks and SLU soil moisture map was evaluated using linear regression, using polynomial regressions in most cases. The relationships from the SLU soil moisture map were then extrapolated over the entire study area to gain a landscape-level picture. The tree C pool was mapped over the entire study area using the area-based approach.

3.11 Site quality modelling (Paper IV)

In Paper IV, a plot-level site quality estimate was derived using data from the two forest surveys. Site quality was here defined as the asymptote of a growth model exhibiting a sigmoidal shape. The site quality parameter represented the theoretical site-specific maximum mean tree height at the site when time approaches infinity. Site quality was estimated using an age-independent difference formulation of the commonly used Richard's growth model (Richards 1959), originally presented by Tomé et al. (2006).

$$Y_{i+a} = A \left\{ 1 - e^{-ka} \left[1 - \left(\frac{Y_i}{A} \right)^m \right] \right\}^{\frac{1}{m}} \quad (\text{Equation 1})$$

Where Y is Lorey's mean height in metres, and A is the asymptote maximum tree height (m) when time approaches infinity. The parameter k was related to the growth rate whereas m is a shape parameter related to the point of inflection. The number of periods was denoted as a , which in Paper III was five years. The parameter k describes the relative height growth between the two observations of Lorey's mean height and a global parameter b :

$$k = b * \left(\frac{Y_{i+a}}{Y_i} \right) \quad (\text{Equation 2})$$

Equation 2 was substituted into Equation 1 to obtain estimates of the global parameters m and b . The parameters were estimated using the generalised non-linear least squares regression method. A plot-specific site quality (A_o) was then derived by an algebraic reformulation (Equation 3) of Equation 1.

$$A_o = \left(\frac{Y_{i+a}^m - e^{-ka} Y_i^m}{1 - e^{-ka}} \right)^{\frac{1}{m}} \quad (\text{Equation 3})$$

The plot specific site quality was calculated using the field measured Lorey's mean height. The same equation was used to estimate site quality across the entire study area using the ALS estimated Lorey's mean heights from the bi-temporal ALS. Site quality was then related to soil moisture conditions on plot and landscape level. Furthermore, a non-parametric Kruskal-Wallis test (Kruskal & Wallis 1952), followed by a Dunn-Bonferroni post-hoc test (Dunn 1964), was used to test for significant differences between soil moisture classes in order to determine whether the highest site quality values occur at intermediate soil moisture conditions.

4. Results and discussion

The extensive forest and soil survey data analysed in the studies underlying this thesis provide unique insights about the variation in the ecosystem properties of a boreal forest landscape. The Papers included in this thesis focused on studying how strong of an effect soil moisture exerts on the variation in soil properties and forest growth potential within a forest landscape in northern Sweden. In the following sections, I will highlight the most important results and discuss the relevance of these findings.

4.1 Topographic control of soil moisture conditions

In accordance to the overall objectives of this thesis, the assumption that topography drives variation in soil moisture conditions needed to be tested. Paper I described how topography influence the variation in soil moisture conditions by using a wide range of terrain indices at different digital elevation model resolutions and thresholds. Overall, the results confirmed that the tested terrain indices hold potential in predicting soil moisture conditions (Lin et al. 2006; Grabs et al. 2012; Ågren et al. 2014). However, the research also revealed that DEM resolutions has differential effects on the results depending on the terrain index, and that parent material caused challenges in the predictions. The OPLS analysis including all 147 soil moisture predictors revealed how DEM resolution, including user defined-thresholds (relevant for DTW, EAS and DI) contributed to large differences in the soil moisture predictions (Fig. 4).

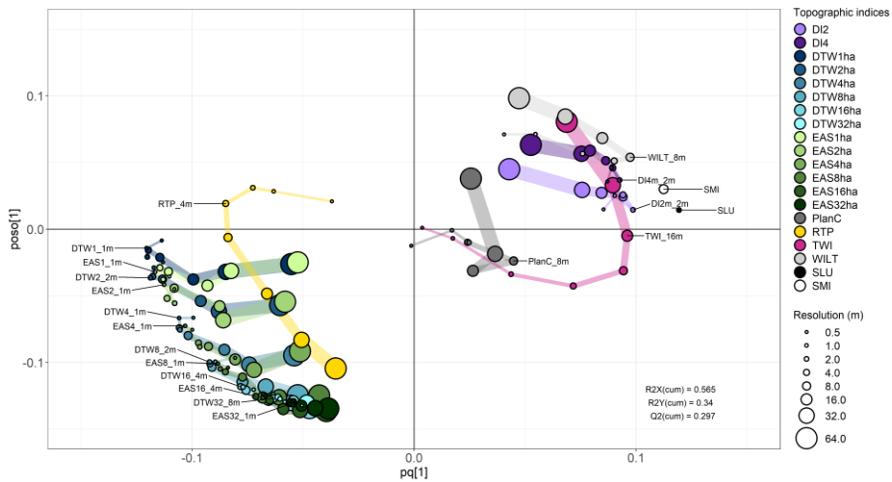


Figure 4. The OPLS loading plot, which illustrates the predicted soil moisture conditions for various terrain indices. Coloured guides connect terrain indices in order of DEM resolutions (circle size depict the resolution size).

The OPLS results showed that the optimum DEM resolution for soil moisture predictions differed between the terrain indices. When ranking the terrain indices, DTW showed the best performed and was closely followed by the SLU soil moisture map. DTW performed best at DEM resolutions of 1 m, while the commonly used TWI showed optimal performance at DEM resolution of 16 m. The results agreed with previous reports that DEM resolution and the thresholds chosen for terrain index calculations have noticeable effects on the predictive ability of different models (Lin et al. 2010; Ågren et al. 2014). The reasons for this is different depending on the terrain index considered. The results in Paper I highlighted the challenges caused by various landscape types, for instance, flat sorted sediment areas. These areas, due to their obvious topographic characteristics of overall flatness, are not strongly influenced by the assumption that topography drives variation in soil moisture, and this must be taken into account during modelling. Paper I provided valuable information about the challenges of modelling soil moisture conditions using topographical information and the importance pre-evaluation within study areas.

4.2 Soil properties in relation to environmental factors

Paper II provided empirical evidence that supports: (1) the significance of topographically-driven hydrological conditions, with C/N ratios decreasing as soil moisture increased; (2) that dominant tree species significantly impacts C/N ratios in the organic layer; and (3) that soil texture is the most important factor for explaining variations in soil chemical properties within mineral soil. The organic layer exhibited a mean C/N ratio of 39, ranging from a minimum of 19 to a maximum of 87. Mineral soil mean C/N ratio decreased from 29 to 25 with sampling depth while maintaining a large range. The studied environmental factors showed varying influences on the C/N ratio that were dependent on the sampling depth. In the organic layer, a significant decrease in C/N ratio was observed in relation to increased soil moisture conditions, which were modelled using TWI ($R^2=0.11$, $p<0.001$). The topographic control on C/N ratio was strongest in unsorted sediments ($R^2=0.15$, $p<0.001$), where topography is the main driver behind the variation in soil moisture conditions. Although a large share of variation remained unexplained, this relationship was in line with the presented hypothesis which was based on reports that there can be large differences in C/N ratios within short distances (Giesler et al. 1998). The relationship between organic layer C/N ratio and TWI was stronger in comparison to previous studies (Zinko et al. 2006; Seibert et al. 2007), most likely related to better DEM resolution, sample size and study area.

The analysis of C/N ratios in different forest types showed significant differences in the samples of the organic layer, where plots dominated by pine had significantly higher C/N ratios compared to plots dominated by other tree species. This is in line with previous findings including both garden experiments (Vesterdal et al. 2008; Hansson et al. 2011; Getino-Álvarez et al. 2023) as well as survey studies (Spohn & Stendahl 2022). On the other hand, no significant differences in C/N ratios were observed in mineral soil samples, which suggests that the influence of tree species on C/N ratio decrease with depth.

In mineral soils, the C/N ratio was mainly affected by soil texture. Significant differences was only observed for mineral soil samples in sorted sediments. There was a gradual decrease in C/N ratios from coarse to fine-textured soils; this result could be explained by the higher charge density of fine textured soils, along with decreased microbial decomposition due to steric hindrance (Lützow et al. 2006). The study demonstrated that multiple

environmental factors influence variations in soil chemical properties within a boreal landscape, yet also revealed sizeable challenges in sufficiently explaining this variation.

4.3 Soil moisture and carbon stock partitioning

The results presented in Paper III showed that soil moisture conditions have a large effect on the spatial distribution and partitioning of carbon stocks. The total SOC pool had a mean 94 Mg C ha^{-1} including peat soils. Total SOC stock ranged from 9 to 959 Mg C ha^{-1} . Both ranges and means within the study area was similar to what was reported in previous, nationwide studies across Sweden (Olsson et al. 2009; Hounkpatin et al. 2021). On average, the total SOC pool accounted for 62% (94 Mg C ha^{-1}) of the total C stock (152 Mg C ha^{-1}). The results showed a large increase in the total SOC pool when moving from dry to wet areas. This change was mainly explained by an increase in the organic layer C pool (Fig. 5). In a majority of the plots (57%), the SOC pool contained over 50% of the total C stock. The proportion of the total C stock stored in the tree C pool decreased as soil moisture increased.

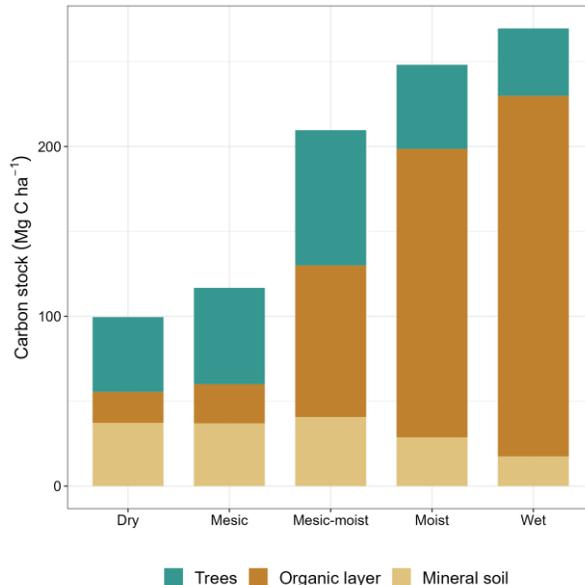


Figure 5. A stacked bar chart showing the individual C pools (tree, organic layer, and mineral soil C pools) across different soil moisture conditions.

A similar trend was observed when the size of different C pools were assessed across the modelled soil moisture conditions. The relationship between modelled soil moisture and the size of the total SOC pool could be described through polynomial regression ($R^2=0.40$) (Fig. 6). The modelled relationship was used to extrapolate SOC stocks across the entire landscape, which could be visually compared to the high resolution estimates of the tree C pool estimated using the area-based method (Fig. 7). The study provided interesting insights about the variation in separate organic and mineral soil C pools, and revealed how the sizes of these pools demonstrate co-variation with the tree C pool. Together the results provided empirical evidence of soil moistures importance for the magnitude and spatial variation for SOC stocks.

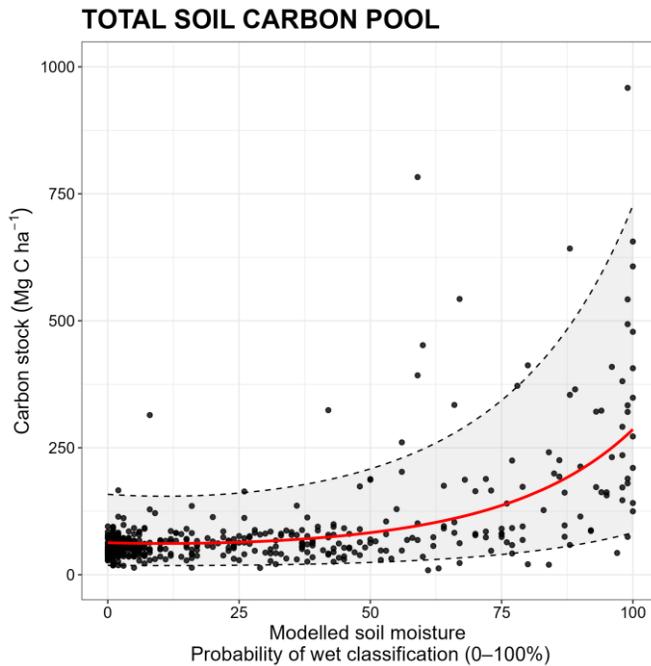


Figure 6. Total SOC pool as a function of modelled soil moisture conditions. The calculated polynomial function is shown as a red line, with the dashed lines representing the boundaries of the 95% prediction intervals. The modelled soil moisture represents the probability of a plot being predicted as wet.

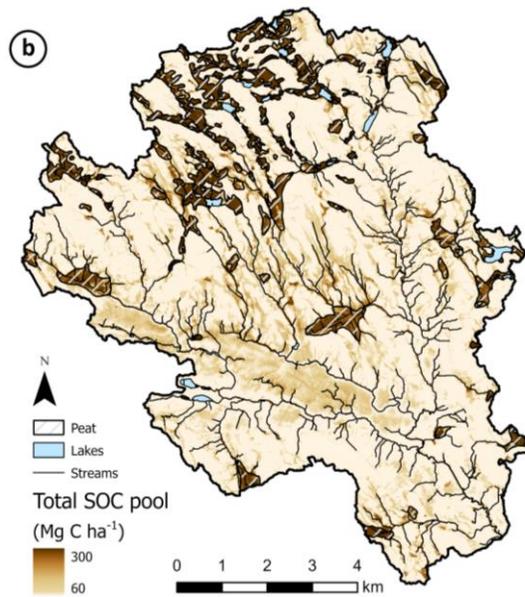
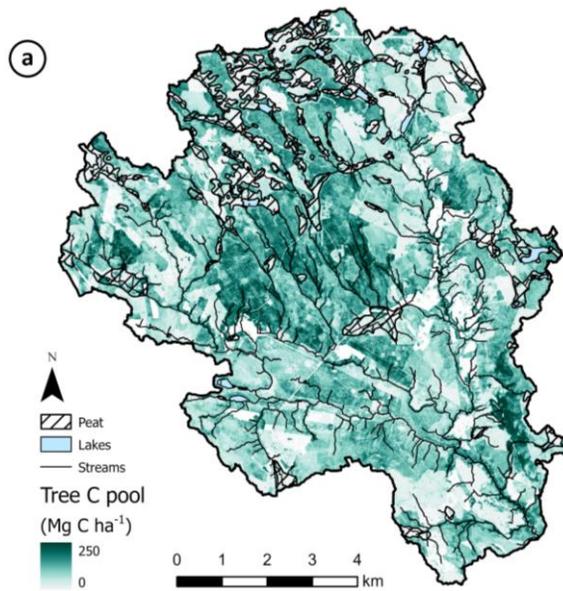


Figure 7. Tree C distribution map derived from ALS data using the area-based method (a), and the total SOC stock distribution derived by regression analysis of modelled soil moisture conditions (b). Areas with low tree C pool (white) are dominated by clear-cuts and open peatland.

4.4 Landscape level variation in site quality and how it is affected by soil moisture conditions

Paper IV presented plot- and landscape-level estimates of site quality. In this study, site quality (A_0) was defined as a site-specific maximum attainable mean tree height when time approaches infinity. Despite considerable variation in site quality estimates, consistent relationships with soil moisture was observed, considering both observed soil moisture conditions at the plot level (Fig. 8) and the modelled soil moisture at the landscape-level (Fig. 9). The lowest site quality was found in the highest soil moisture conditions, which was expected due to saturated soil conditions, that will lead to decline in tree growth potential (Laamrani et al. 2014; Van Sundert et al. 2018). Plots on mesic sites showed a significantly higher site quality in comparison to the wet and moist (Kruskal-Wallis chi-squared = 24.633, df = 4, p-value <0.001) (Fig. 8).

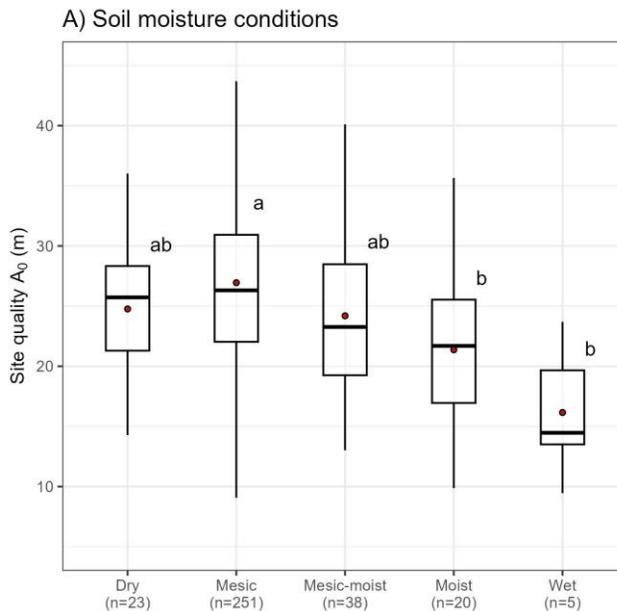


Figure 8. The relationship between plot estimates of site quality and soil moisture conditions.

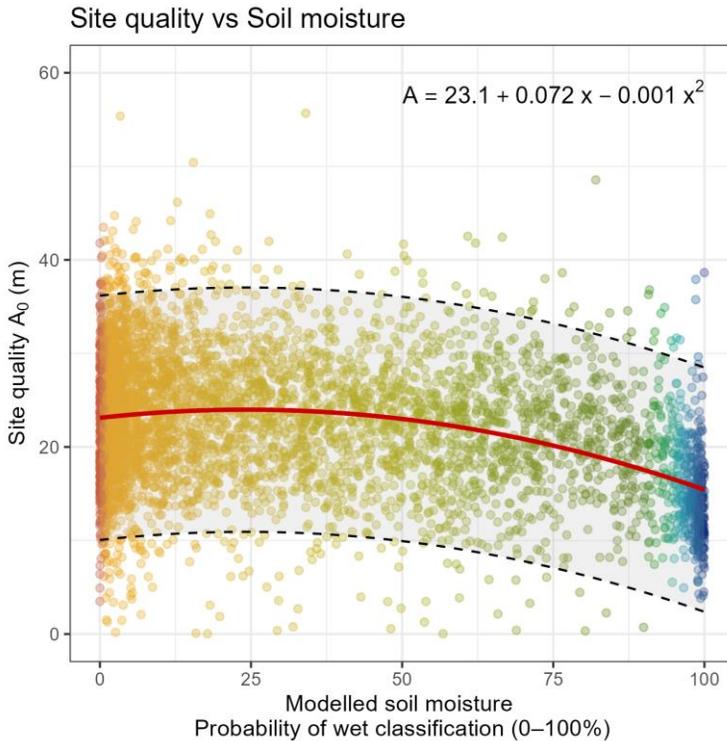


Figure 9. The modelled regression between mapped estimates of site quality (A_0) and soil moisture. The plot displays a random sample of 5000 (10%) raster cells. The regression line is shown in red, with the dashed lines representing the 95% prediction intervals. The modelled soil moisture denotes the probability of a point being predicted as wet. The colours correspond to the colours in the SLU soil moisture map.

The site relationship between modelled soil moisture and wall-to-wall estimates of site quality was described by a second-degree polynomial regression, which captured 11 % of the total variation (Fig. 9). Although there was a weak tendency for lower site quality in the driest areas on the plot-level, this trend was not observed on the landscape-scale. This discrepancy could be explained by the utilised soil moisture map, which was primarily developed to locate high soil moisture conditions and is therefore less successful at differentiating between dry and mesic areas (Ågren et al. 2014). Secondly, the combination of low productive forests within the study area, and a short study period, may cause the ALS estimated difference in

tree height between years to be uncertain or not captured at all. Additionally, it could be postulated that a five-year period may not contain enough information for the successful extraction of site quality estimates. Nonetheless, this study provided valuable insights into how site quality can be estimated using bi-temporal ALS data, an approach which is under rapid development (Socha et al. 2017; Tompalski et al. 2021). The research covered in Paper IV stands out from previous studies based on the extensive amount of survey data that was gathered from a small landscape, which enables the investigation of individual environmental factors. The results highlight the necessity of improving site quality estimates to capture variation within boreal landscapes, and to improve these estimates by considering environmental drivers.

5. Conclusions

This thesis contributes with increased knowledge about the variation of boreal forest ecosystems, focusing on the importance of soil moisture as a key environmental factor. This thesis synthesises strong empirical evidence about the variation of soil properties, C stocks, and site quality across the landscape level (here defined up to tens of km²).

- The importance of topography in determining soil moisture conditions in boreal forests was shown in the analyses presented in Paper I. The results highlighted the importance of within-study validation when predicting soil moisture conditions using terrain indices, in particular, the potentially differential effects of DEM resolution and landscape type on various metrics.
- The research presented in Paper II provided valuable insights concerning variation in soil chemical properties on a landscape scale by revealing a wide range of soil C/N ratios that were characterised by considerable variation. Although many environmental factors remain similar or constant across the studied landscape, e.g., climate, the results showed large variation in soil properties. The result highlights the complexity of interactions among various environmental factors, which influence forest soils in different ways.

- In Paper III, soil moisture was shown to be a key driver of C stocks and partitioning. The total C stock increased rapidly with soil moisture conditions, with the largest increase observed for the organic layer C pool. The overall size and reported ranges of the SOC pool were similar to what has been observed in areas around Sweden in previous studies; this shows the importance of understanding what environmental factors have the largest effect on carbon accumulation at landscape levels.

- In Paper IV, site quality was estimated using an age-independent model approach, which showed large variation across the study area. Areas with high soil moisture showed significantly lower site quality values. Furthermore, there was a tendency for lower site quality in the driest sites, however only on plot-level.

6. Final remarks and future perspectives

The ambitious soil and forest survey that was conducted within this thesis has generated an extensive data set that has great potential to provide further insight into the variation in boreal forest ecosystems at a smaller landscape. Standing alone, this survey fills an important gap in the current research area, due to the study scale, which was 68 km², in combination with the large amount of survey plots. Adding to the value of this survey is its particular setting, by adding to the unique research infrastructure that is the Krycklan catchment study and the Svartberget experimental forests. The research infrastructure includes long-term climate and hydrological measurements, atmospheric observatory systems, forest management trials and much more. The combined soil and forest survey adds an important missing piece both outside and within this setting, offering valuable empirical field data for testing and validating models. Because of the same sampling methods as the Swedish national forest soil inventory, there are now great possibilities for studies testing results and relationships found also at the national scale. However, on a national scale, climate is a main driver of the variation in many soil properties, which can overshadow other important factors. By combining the data from the Krycklan landscape and national scale, we can begin to evaluate the challenges associated with scaling and extrapolating relationships identified from plot or stand scales to larger, regional scales. Hence, this work can provide an important setting for testing results found on both larger and smaller scales. The Papers included in this thesis are only the first initial steps using this data, which has potential to further test various hypotheses. For instance, additional chemical analyses focusing on pH and base saturation, could provide valuable insight furthering our understanding of the nutrient accumulation, while other analysis of the huge sample archive can answer many other important questions in the future.

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Populärvetenskaplig sammanfattning

Skogen bidrar med en mängd viktiga ekosystemtjänster som i sin tur varierar i betydelse beroende på var i landskapet man befinner sig. Skogslandskapets förmåga att binda och lagra koldioxid gör att den är en viktig motståndskraft mot den globala uppvärmningen. Kol lagras in bland annat i träden, men framför allt i marken. Variationen i kolinlagringens storlek styrs av olika miljöfaktorer som varierar i betydelse beroende på en mängd olika faktorer. På global och regional skala spelar klimatet en stor roll, oftast kopplat till skillnader i temperatur och nederbörd. På en lokal landskapsskala (tiotals kvadratkilometer) är det andra faktorer som driver variationen. Topografi styr vattnets rörelse genom landskapet och har därför stor påverkan på markfuktighet. Markfuktigheten i sin tur, har stor inverkan på skogsmarkens egenskaper, så som dess förmåga att lagra kol, mängden näring som finns tillgänglig och hur snabbt träden växer. I denna avhandling undersökte jag därför markfuktighetens effekt på näringstillgång, kolförråd och skogens tillväxt. Analyserna baserades på omfattande inventeringar av både skog och mark inom ett 68 km² stort skogslandskap i Västerbotten. Genom att relatera mätningar och prover från inventeringen till högupplösta markfuktighetskartor och fjärranalys kunde jag undersöka markfuktighetens betydelse som miljöfaktor. Resultaten visade att markfuktighet spelade en viktig roll för näringsförhållanden i marken, som ökade ju blötare det var. Dessutom så ökade det totala kolförrådet markant vid högre markfuktighet, vilket var främst kopplat till en ökning av kolinlagring i markens organiska lager. Genom att mäta skillnaden i trädhöjder i fält innan och efter en femårsperiod, i kombination med fjärranalys kunde jag dessutom beräkna variationen i tillväxtförhållanden över hela det studerade landskapet. Resultaten visade på en tydlig minskning av tillväxtpotential i landskapets blötaste områden. Sammantaget visar jag i min avhandling på markfuktighetens stora betydelse för variationer i näringsförhållanden, kolförråd och skogstillväxt.



Photo: Andreas Palmén

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P.S. Don’t forget to read at least the abstract before this thesis gets put in the bookshelf for the next 20 years. Thank you!



Predicting soil moisture conditions across a heterogeneous boreal catchment using terrain indices

Johannes Larson, William Lidberg, Anneli M. Ågren, and Hjalmar Laudon

Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, 901 83, Sweden

Correspondence: Johannes Larson (johannes.larson@slu.se)

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Abstract. Soil moisture has important implications for drought and flooding forecasting, forest fire prediction and water supply management. However, mapping soil moisture has remained a scientific challenge due to forest canopy cover and small-scale variations in soil moisture conditions. When accurately scaled, terrain indices constitute a good candidate for modelling the spatial variation of soil moisture conditions in many landscapes. In this study, we evaluated seven different terrain indices at varying digital elevation model (DEM) resolutions and user-defined thresholds as well as two available soil moisture maps, using an extensive field dataset (398 plots) of soil moisture conditions registered in five classes from a survey covering a (68 km²) boreal landscape. We found that the variation in soil moisture conditions could be explained by terrain indices, and the best predictors within the studied landscape were the depth to water index (DTW) and a machine-learning-generated map. Furthermore, this study showed a large difference between terrain indices in the effects of changing DEM resolution and user-defined thresholds, which severely affected the performance of the predictions. For example, the commonly used topographic wetness index (TWI) performed best on a resolution of 16 m, while TWI calculated on DEM resolutions higher than 4 m gave inaccurate results. In contrast, depth to water (DTW) and elevation above stream (EAS) were more stable and performed best on 1–2 m DEM resolution. None of the terrain indices performed best on the highest DEM resolution of 0.5 m. In addition, this study highlights the challenges caused by heterogeneous soil types within the study area and shows the need of local knowledge when interpreting the modelled results. The results from this study clearly demonstrate that when using terrain indices to represent soil moisture conditions, modelled results need to be validated,

as selecting an unsuitable DEM resolution or user-defined threshold can give ambiguous and even incorrect results.

1 Introduction

Soil moisture represents plant-available water at the land surface that is not derived from groundwater, rivers and lakes but instead in the pores of the soil. It consists of unsaturated soil, affected by variable temporal and spatial dynamics that regulate fundamental ecosystem functions such as plant growth, nutrient cycling and carbon accumulation (Olsson et al., 2009; Högberg et al., 2017; Wang et al., 2019). Soil moisture also has important implications for drought and flooding forecasting, forest fire prediction and water supply management (Koster et al., 2010; Robock, 2015; O et al., 2020). While temporal variability in soil moisture is largely determined by precipitation, temperature and soil characteristics, topography acts as a first-order control of spatial variation in soil moisture within most landscapes (Florinsky, 2016).

Predicting soil moisture patterns across space and time remains an important scientific challenge, limited by large temporal variability, small-scale heterogeneous responses to precipitation inputs and local soil properties. While small-scale spatial variability often limits the use of empirical measurements for upscaling, temporal dynamics superimposed on such heterogeneous patterns create an additional challenge. Due to the effect that topography has on the spatial variation in soil moisture conditions, such information is a fundamental part of soil moisture modelling. A digital elevation model (DEM) is a digital representation of a terrain surface, often generated using remote-sensing techniques such as photogrammetry or airborne light detection

and ranging (lidar). Terrain indices extracted from DEMs have become widely used in soil and hydrologic sciences predicting surface water and groundwater flow paths and soil moisture conditions.

An early and successful approach to modelling soil moisture conditions was the topographic wetness index (TWI) developed by Beven and Kirkby (1979). TWI is a function of both the slope and upslope contributing area and is still widely used in landscape modelling. TWI has been shown to be sensitive to DEM resolution (Western et al., 1999; Sørensen and Seibert, 2007; Lin et al., 2010) and the specific flow algorithms used (Sørensen et al., 2006; Kopecký et al., 2021). TWI has been followed by several other terrain indices based on similar approaches such as the downslope index (DI) (Hjerdt et al., 2004) and the Wetness Index based on Landscape position and Topography (WILT) (Meles et al., 2020).

Some topography-based indices use stream networks in the calculations, which are derived from flow accumulation grids such as the depth to water index (DTW) (Murphy et al., 2008) and elevation above stream (EAS) (Rennó et al., 2008). Using this approach, streams are defined with a so-called stream initiation threshold, which is the accumulated area required to form surface water. Selecting an appropriate stream initiation threshold has proven to be difficult due to temporal dynamics (Ågren et al., 2015) and soil textures (Ågren et al., 2014). Thresholds, such as stream initiation, used in terrain indices can be as, or even more, important as selecting the correct DEM resolution for the soil moisture modelling.

The use of airborne lidar has increased both the accuracy and resolution of DEMs and, as a result, soil moisture modelling (Murphy et al., 2011; Ågren et al., 2014; Leach et al., 2017; Kopecký et al., 2021). However, the resolutions of DEMs used for hydrological modelling must reflect topographic features that are key elements in the hydrological response (Quinn et al., 1995). This means that higher resolutions do not necessarily result in better predictions, as the microtopography does not always control hydrological flow paths. Hence, there is a concern that the development of lidar-derived high-resolution DEMs has changed resolutions from being too coarse for small-scale hydrological modelling to being too high for many applications. With the use of terrain indices, there is often an optimal resolution depending on landscape type and specific feature of interest (Gillin et al., 2015). Despite rapid lidar development, finding the optimal DEM resolution of terrain indices has remained relatively unexplored, with only a few exceptions (Seibert et al., 2007; Lin et al., 2010; Ågren et al., 2014).

In addition to DEM resolutions and user-defined thresholds, soil moisture modelling using terrain indices must take the local variations in soils and landforms into consideration. Across former glaciated landscapes, soil hydraulic properties are often relatively consistent with unconsolidated ablation till overlaying basal till and/or bedrock. This means that hydro-

drological pathways are significantly affected by the topography, resulting in soil moisture conditions in neighbouring areas differing greatly within short distances because of the local topography (Rodhe, 1987). The topographical effect on hydrological pathways is less pronounced in flat sorted sediment areas due to often low topographic variation and soils with consistent hydrological conductivity at depth (Bachmair and Weiler, 2011). In landscapes with varying quaternary deposits, accurate soil moisture predictions become more challenging (Güntner et al., 2004; Grabs et al., 2009; Zhu and Lin, 2011; Ågren et al., 2014), with consideration of these factors becoming important when interpreting modelled soil moisture.

Recent promising approaches for accounting for landscape and soil variations have combined multiple terrain indices and other mapped information. One example of such an effort is the Swedish soil moisture index (SMI) that combines DTW and the soil topographic wetness index (STI) (Buchanan et al., 2014) and accounts for soil transmissivity estimated from the quaternary deposit maps. An alternative is to use machine learning (Abowarda et al., 2021). Ågren et al. (2021) adjusted the soil moisture maps to local conditions over the whole of Sweden by training the model on field data from 16 000 plots and information from 28 maps. Key to this work were high-resolution terrain indices calculated for different resolutions and thresholds. However, while machine learning is an excellent way of generating predictive models, it is difficult to interpret how the model combines indices with multiple resolutions and thresholds for different landscape types. Due to the large applications, wide uses and availability of terrain indices there is a need of understanding the underlying effects that DEM resolution, user-defined thresholds and landscape types have on the modelled results. Using terrain indices to model soil moisture conditions on inappropriate scales and landscape types may result in inaccurate predictions.

The aim of this study was, therefore, to evaluate how DEM resolution, thresholds and landscape types affect soil moisture predictions from a range of readily available terrain indices. We did this by examining which digital terrain index provided the best prediction of field-determined soil moisture classes within a heterogeneous but well-studied landscape in the boreal region, the Krycklan catchment study (Laudon et al., 2021). Using a detailed forest and soil survey that covered the entire catchment allowed for a test and performance evaluation of different terrain indices, in order to find the optimal resolutions and thresholds for modelling soil moisture.

2 Methods

2.1 Site description

The 68 km² Krycklan study catchment is situated in the northern part of Sweden (lat. 64°23' N, long. 19°78' E)

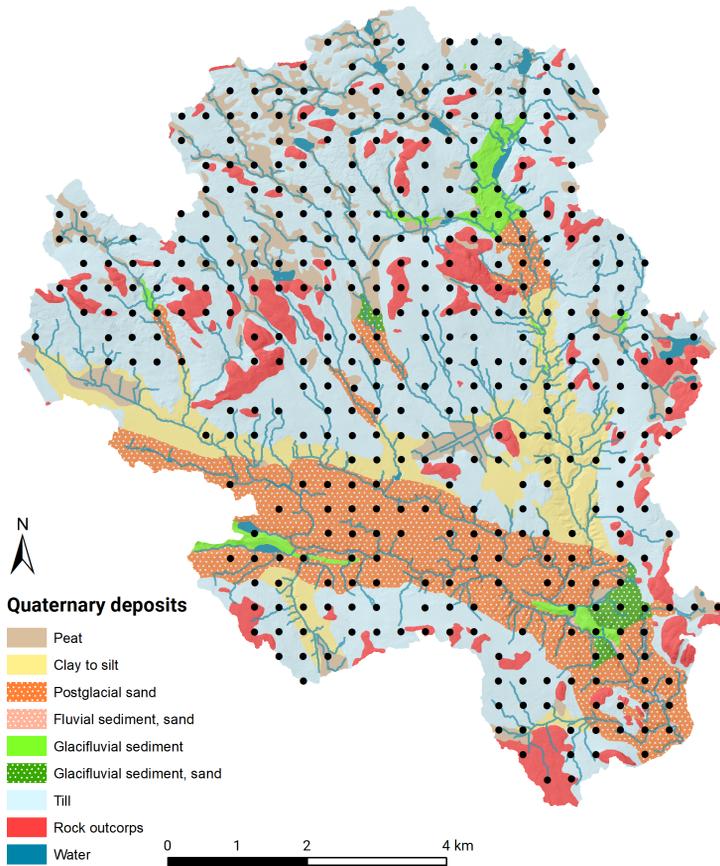


Figure 1. The Krycklan catchment showing the quaternary deposits survey and plots as black circles.

(Fig. 1). The catchment has a gentle topography, with a poorly weathered gneissic bedrock and elevations ranging from 127 to 372 m a.s.l. The highest postglacial relict coastline crosses the area at around 257 m a.s.l. The upper parts are dominated by glacial till, while the lower parts are dominated by sorted sediments of sand and silt. The climate is characterized as a cold temperate humid type with persistent snow cover during the winter season (Laudon et al., 2021). The 30-year mean annual temperature (1986–2015) is 2.1 °C, with the highest monthly mean temperature in July and lowest in January (14.6 and –8.6 respectively). The mean annual precipitation equals 619 mm where more than 30 % falls as snow. Land cover is dominated by forest (87 %) and a mosaic of mires (9 %) and lakes. Due to forest management, Krycklan is a complex mosaic of forest stands of different age classes and species composition. Forests are dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea*

Abies (L.) H. Kartst.), covering 63 % and 26 % respectively. Understorey vegetation is dominated by ericaceous shrubs, consisting mostly of bilberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitis-idaea*) covering moss mats of *Hylocomium splendens* and *Pleurozium schreberi*. Peatlands and wet areas have a vegetation dominated by *Sphagnum* species (Laudon et al., 2013). Forest soils are dominated by well-developed iron podzol. In addition to analysis over the entire catchment area, Krycklan was divided into two sub-areas (till and sorted sediment) according to the quaternary deposits map, in order to analyse the effects of landscape types (Fig. 1).

2.2 Forest survey

A forest survey grid was established in 2014, consisting of 500 10 m radius survey plots (314.15 m²) covering the en-

tire Krycklan catchment, with each plot spaced 350 m apart. The survey plot locations were calculated using a randomly chosen origin and oriented along the coordinate axis of the SWEREF 99 TM projection. Each nominal plot location was located in the field using a Garmin GPS 62stc GNSS receiver, and plot centres were marked with an aluminium profile. During a revisit, high-accuracy centre positions were placed in the field using a Trimble GeoXTR DGPS receiver. Plots without high-precision GPS locations, plots located on or outside the catchment boundaries, arable land, lakes and roads were excluded in this study. In total, soil moisture classifications were made for 398 plots during the autumn of 2014 and the spring of 2015.

2.3 Soil moisture field classification

Soil moisture classes were registered in the field following the protocol of the Swedish national forest inventory (NFI) (Fridman et al., 2014), based on an estimation of each plot's average depth to groundwater level during the vegetation period estimated from its position in the landscape, vegetation patterns and soil type. This approach reduces the discrepancies caused by seasonal variation and provides an indicator of the general soil moisture conditions, which is the focus of this study. Survey plots were categorized in five classes – dry, mesic, mesic–moist, moist and wet – which are described and presented below and can be found in more detail in the field instruction (Swedish NFI, 2014).

- Dry soils have an average groundwater table more than 2 m below the soil surface. Dry areas tend to be coarse-textured and can be found on the top of hills, ridges and eskers. The soils are mainly Leptosols, Arenosols, Regosols or Podzols (with thin organic and bleached horizons).
- Mesic soils have an average groundwater table between 1–2 m below the soil surface. Podzol is the dominating soil type with a thin fairly thin (4–10 cm) organic mor layer covered mainly by dryland mosses (e.g. *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum scoparium*). They can be walked on dry-footed even directly after rain or shortly after snowmelt.
- Mesic–moist soils have an average groundwater table depth less than 1 m. Mesic–moist areas are often located on flat ground in lower-lying areas or lower parts of hillslopes. The soils tend to wet up on a seasonal basis. Whether you can cross in shoes and keep your feet dry depends on the season and the time since the last heavy rain or snowmelt event. Patches of wetland mosses (e.g. *Sphagnum* sp., *Polytrichum commune*) are common, and trees commonly tend to grow on humps. Podzols are commonly found but often with a thicker organic layer compared to mesic sites. The organic layer is often classified as peaty mor.
- Moist soils have an average groundwater table depth less than 1 m below the soil surface. The groundwater table is often visible in depressions within the plot. Areas classified as moist are found at lower grounds, at the lowest parts of slopes and flat areas below larger ranges. One can cross in shoes and keep one's feet dry by utilizing tussocks and higher-lying areas. When stepping in depressions, water should form around the feet even after dry spells. The vegetation includes wetland mosses (e.g. *Sphagnum* sp., *Polytrichum commune*, *Polytrichum formosum*). Trees often grow on small mounds, and the soil type is most often Histosol, Regosol or Gleysol.
- Wet soils are areas where the ground water table is close to the soil surface, and permanent pools of surface water are common. These areas are often located on open peatlands. Drainage conditions are very bad, and it is not possible to cross these areas in shoes without ending up with wet feet. Coniferous trees seldom develop into stands. The soil type is most often Histosol or Gleysol.

2.4 Digital terrain indices

The study utilized a lidar-based digital elevation model (DEM) created from an airborne laser scanning in August 2015. A 0.5 × 0.5 m DEM was generated from a point cloud with 10 points per square metre. Horizontal and vertical errors were 0.1 and 0.3 m, respectively. The DEM was resampled from 0.5 m to resolutions of 1, 2, 4, 8, 16, 32 and 64 m. Nine commonly used digital terrain indices were calculated using DEMs with eight resolutions of 0.5, 1, 2, 4, 8, 16, 32 and 64 m (Table 1). The indices depth to water (DTW) and elevation above stream (EAS) use extracted stream networks in their calculations, with the size of the stream network being set by the stream initiation threshold. For each resolution, DTW and EAS were calculated for the stream initiation thresholds 1, 2, 4, 8, 16 and 32 ha, which is the range of the expected variability in the study region. The downslope index (DI) was calculated with vertical distances of 2 and 4 m. A total of 146 terrain indices maps of soil moisture were produced. Field plot centre values for all indices maps were extracted for evaluation. All of the digital terrain indices were calculated using Whitebox Tools (Lindsay, 2016b), an open-source program developed at the University of Guelph, Canada. The code for aggregating the DEM and the Python code for the calculations can be found in the “Code and data availability” section. In addition to the terrain indices that we calculated from the DEM, we also used two soil moisture maps downloaded from external sources: the SLU soil moisture map (Ågren et al., 2021) and a soil moisture index map (SMI) developed by the Swedish Environmental Protection Agency (Naturvårdsverket, 2021).

Table 1. All indices calculated in this study. Calculations were made for resolutions of 0.5, 1, 2, 4, 8, 16, 32 and 64 m. ¹ Calculations were also done for stream initiation thresholds of 1, 2, 4, 8, 16 and 32 ha. ² Calculated with vertical distances of 2 and 4 m. All GIS calculations were carried out using Whitebox Tools (Lindsay, 2016b), except for SLU soil moisture map and SMI, which were downloaded from other sources.

Digital terrain indices	Abbreviation	Total number of layers
Topographic wetness index	TWI	8
Depth to water	DTW ¹	48
Elevation above stream	EAS ¹	48
Downslope index	DI ²	16
Wetness Index based on Landscape position and Topography	WILT	8
Relative topographic position	RTP	8
Plan curvature	PlanC	8
SLU soil moisture map	SLU	1
SMI	SMI	1

2.5 DEM preprocessing and extraction of stream networks

Prior to hydrological modelling, the DEM was preprocessed to make it hydrologically accurate using the two-step breaching approach suggested by Lidberg et al. (2017). This approach works by first carving a short path into the DEM at locations where culverts and previously mapped streams intersect road embankments. Remaining depressions were resolved by a complete breaching approach using the tool Breach depressions in Whitebox Tools (Lindsay, 2016a). Two flow pointer grids and flow accumulation (FA) grids were extracted from the hydrologically corrected DEM using the *D*-infinity flow routing algorithm (*D*∞) (Tarboton, 1997) and the multiple flow direction algorithm (MD∞) (Seibert and McGlynn, 2007). D8 (O’Callaghan and Mark, 1984) and *D*∞ (Tarboton, 1997) are both commonly used and widely implemented flow routing algorithms. MD∞ is an attempt to combine these two approaches and disperses flow like *D*∞ up to a user-defined threshold (aiming to simulate diffuse groundwater flows), after which it switches to operate like D8 without dispersion (aiming to simulate channelized flow of surface waters). Stream networks were extracted from the flow accumulation raster using stream initiation thresholds 1, 2, 4, 8, 16 and 32 ha. Streams during different conditions can be mapped by varying the stream initiation thresholds. Larger stream initiation thresholds represent streams during low flow conditions, while smaller thresholds represent conditions at high flow rates.

2.5.1 Topographic wetness index (TWI)

TWI predicts soil moisture based on local slope and the area’s specific catchment area (Eq. 1), where α is the specific catchment area, and β is the slope of the grid cells in degrees (Beven and Kirkby, 1979).

$$TWI = \ln(\alpha / \tan \beta) \tag{1}$$

This was calculated using the *D*∞ flow algorithm for all eight DEM resolutions.

2.5.2 Depth to water (DTW)

The depth to water index predicts soil moisture using the surface water source grid (stream network) and the surrounding landscape (Murphy et al., 2008). The DTW index refers to the least-cost path from any cell in the landscape to the nearest surface water cell (DTW = 0) channel. DTW is expressed as Eq. (2), where dz_i and dx_i represent the vertical distance between two cells.

$$DTW = \left[\sum \frac{dz_i}{dx_i} a \right] x_c \tag{2}$$

The constant α is equal to 1 if the path between the cells connects parallel to the cell boundaries or $\sqrt{2}$ if it connects the cell diagonally; x_c is the size of the raster cells. Cells located far away or at higher elevation from the flow channels will have high DTW values, meaning that the cells are drier. Stream cells were calculated using the source layers with extracted streams from the (MD∞) pointer described above. DTW was calculated for each of the six stream initiation thresholds and eight DEM resolutions.

2.5.3 Elevation above stream (EAS)

EAS indicates soil moisture using the source layer with extracted streams described above and the original DEM (Rennó et al., 2008). EAS is calculated from the elevation difference between a grid cell in the landscape and the nearest stream cell calculated from the nearest flow path from the (MD∞) pointer grid. EAS was calculated for each of the six stream initiation thresholds and eight DEM resolutions.

2.5.4 Downslope index

The downslope index represents the length of a flow path required to drop a given vertical distance d (m) (Eqs. 3 and 4) (Hjerdt et al., 2004). The algorithm calculates the distance downslope required to travel in order to descend d m. The downslope index can be reported both as a distance d and a gradient, $\tan\alpha_d$, where the horizontal distance to the point d m below follows the steepest directional flow path.

$$\tan\alpha_d = \frac{d}{L_d} \quad (3)$$

Local linear interpolation is used between the two points to calculate the value of L_d . The slope angle between the starting point and the target point is represented by α_d . For elevation differences approaching zero, the values of $\tan\alpha_d$ approach the local ground surface gradient, $\tan\beta$:

$$\tan\alpha_d = \tan\beta. \quad (4)$$

The downslope index was calculated for 2 and 4 m as the given vertical distances.

2.5.5 Wetness Index based on Landscape position and Topography (WILT)

WILT assumes that soil moisture is inversely proportional to ΔX and ΔZ in a groundwater-dominated landscape, where ΔZ is the depth to groundwater, and ΔX is the horizontal distance to the nearest surface water feature (Eq. 5) (Meles et al., 2020). WILT is a modification of TWI, obtained by dividing the upslope contribution area A by ΔX and ΔZ :

$$\text{WILT} = \ln\left(\frac{A}{\Delta X \cdot \Delta Z \cdot \tan\beta}\right). \quad (5)$$

In this study, we calculated WILT, where A was the upslope source area using $D\infty$ flow accumulation, as with the TWI calculations. ΔX was derived from the downslope distance to stream and lakes using surface waters. ΔZ was the elevation difference between the DEM and modelled groundwater, represented by a DTW calculated for the property map.

2.5.6 Relative topographic position (RTP)

RTP is an index for the local position of a point in the landscape relative to its surroundings, which accounts for elevation distribution (Eq. 6). Within a user-specified local neighbourhood size, the RTP function uses the central elevation relative to the minimum (z_{\min}), mean (μ) and maximum elevation (z_{\max}):

$$\text{RTP} = \frac{(z_0 - \mu)}{(\mu - z_{\min})}, \text{ if } z_0 < \mu \text{ or}$$

$$\text{RTP} = \frac{(z_0 - \mu)}{(\mu - z_{\max})}, \text{ if } z_0 \geq \mu. \quad (6)$$

RTP index is bound by the interval of $[-1, 1]$, indicating whether the cell is above or below the filtered mean (Newman et al., 2018).

2.5.7 Plan curvature (PlanC)

The plan curvature represents the curvature of the surface perpendicular to the direction of the slope direction (Wilson and Gallant, 2000). This index shows the divergence and convergence of slopes, where values are positive for convergent areas and negative for divergent ridges. The plan curvature was chosen for its influence on the downslope convergence and divergence of water flow paths.

2.5.8 Soil moisture index (SMI)

We also included an SMI from the national land cover database of the Swedish Environmental Protection Agency (Naturvårdsverket, 2021). This SMI was calculated as

$$\text{SMI} = \left(0.7 \times \frac{1}{\text{DTW}}\right) + (0.3 \times \text{STWI}). \quad (7)$$

This is a weighted map combining DTW and a modified TWI calculation, the Soil Topographic Wetness Index (STWI) (Buchanan et al., 2014), which accounts for soil transmissivity estimated from the quaternary deposit maps. The SMI map has a resolution of 10 m.

2.5.9 SLU soil moisture map

A recent development in soil moisture mapping has been the use of machine learning to combine multiple soil moisture indices into one map (Lidberg et al., 2019; Abowarda et al., 2021; Ågren et al., 2021). Ågren et al. (2021) developed a new soil moisture map of Sweden by utilizing a variety of nationwide information, including the above-mentioned terrain indices, climate data and quaternary deposits. Training data consisted of nearly 16 000 field plots spread across the Swedish forested landscape from the national forest inventory. The final map showed the probability (0%–100%) of a soil being wet. The SLU soil moisture map was produced at 2 m resolution, while the input digital terrain indices were calculated in multiple scales.

2.6 Statistics

2.6.1 Orthogonal Projections to Latent Structures (OPLS)

To ascertain which digital terrain index provides the best prediction of soil moisture within this heterogeneous landscape, we used Orthogonal Projections to Latent Structures (OPLS) analysis. Field classifications of soil moisture at each plot were used to evaluate the terrain indices through direct plot by plot comparison. OPLS was carried out on the entire

catchment. The OPLS was carried out using the multivariate statistical program SIMCA 16.0, Umetrics, Umeå. The method of OPLS is a modification of partial least-squares regression (PLS) (Eriksson et al., 2006). In OPLS, the systematic variation in the predictors (X) is divided into two parts: one part that is predictive for the determinant (Y) (in this case, the field-determined soil moisture classes) and the orthogonal, i.e. not related to Y . OPLS produces a model with improved interpretability compared to the ordinary PLS method. The method is used to identify important variables for predicting Y and singling out less important variables containing “noise”. High positive or negative loadings on the predictive axis (pq[1]) indicate variables that are, respectively, positively or negatively correlated with Y , with increased correlation further away from origin. The orthogonal axis shows how much of the variation for each variable was not correlated with the determinant (Y). Before analysis, all variables were transformed to fit normality using a log transformation in SIMCA. SIMCA 16.0 also calculates the influence of each X variable in the model called “variable importance on projection” (VIP). VIP components of an OPLS model are VIP predictive and VIP orthogonal as well as VIP total component. The VIP values are regularized such that if all X variables had the same importance for the model, they would all take the value 1. VIP values larger than 1 for either VIP component indicate X variables that are important for that part of the model (Eriksson et al., 2006). Analysis was carried out in SIMCA 16.0, and figures were produced using R version 4.0.2 (R Core Team, 2020) and the package ggplot2 (Wickham, 2016).

2.6.2 Confusion matrix

To evaluate the effects of landscape type, i.e. sorted sediment and till soils within the catchment, we used the terrain index that performed best in the OPLS analyses and its correspondence to the two wettest soil moisture classes (wet and moist). The overall conformance of the best terrain index with the combined wet and moist classes was assessed using confusion matrixes, accuracy (ACC) (Eq. 8) and the Matthews correlation coefficient (MCC) (Eq. 9). The confusion matrix consists of true positives (TP) values, so accurately predicted wet plots, and false positive (FP) values where dry plots were predicted wet, true negative (TN) values, where the map correctly predicted dry plots, and false negative (FN) values, where the map predicted dry areas on wet plots. Accuracy (ACC) was assessed for each of the plots by

$$\text{ACC} = \frac{\text{TP} + \text{TN}}{\text{TP} + \text{TN} + \text{FP} + \text{FN}}. \quad (8)$$

The confusion matrix was further evaluated using the Matthews correlation coefficient (MCC), for which a value of 1 indicates a perfect fit, 0 no better than random predic-

Table 2. Percentage of observations in the five soil moisture classes for the entire Krycklan catchment and divided into till and sorted sediment areas.

Soil moisture class	Soil moisture classes					Plots (n)
	Dry	Mesic	Mesic–moist	Moist	Wet	
Entire catchment	10 %	60 %	15 %	8 %	8 %	398
Till	9 %	57 %	15 %	10 %	10 %	293
Sorted sediment	12 %	69 %	13 %	3 %	3 %	105

tions and -1 a perfect negative correlation. MCC was calculated as

$$\text{MCC} = \frac{\text{TP} \times \text{TN} - \text{FP} \times \text{FN}}{\sqrt{(\text{TP} + \text{FP})(\text{TP} + \text{FN})(\text{TN} + \text{FP})(\text{TN} + \text{FN})}}. \quad (9)$$

For unbalanced datasets such as this, MCC is the best measure of model performance (Boughorbel et al., 2017).

3 Results

3.1 Field data

The field survey showed that the dominant soil moisture class was mesic, making up 60 % of the survey plots in the catchment (Table 2). Mesic–moist was the second largest class with 15 % of the plots; the moist and wet classes each made up 8 %. The driest class (dry) made up 10 % of the total plots in the catchment. Dividing the catchment into till and sorted sediment areas using the quaternary deposit map (Fig. 1), the proportion of classes became substantially different. Only 6 % of the plots in the sorted sediment area were classified as moist or wet, compared to 20 % in the till areas. A larger percentage (12 %) of plots were found in the driest class in the sorted sediment areas compared to the till areas (9 %).

3.2 OPLS analysis

The OPLS analysis loading plot showed large variation in performance within and between terrain indices (Fig. 2). Figure 2 only shows the variable names from the best resolution for each digital terrain index and threshold based on the $\text{VIP}_{\text{predictive}}$ value shown in Fig. 3, as the graph would be too cluttered if all 146 variable names were displayed. There is an interactive plot in the “Code and data availability” section where the name of each variable can be found. The general patterns of the effects of scale and threshold are indicated by the size and colour of the dots in the OPLS loading plot (Fig. 2). In order to help the reader to visualize the effects of scales and resolution, the indices and thresholds have been grouped together using coloured guides to connect terrain indices moving from high to low resolutions.

The OPLS analysis demonstrates that the DTW was a strong predictor of soil moisture classes (Fig. 3) but only if

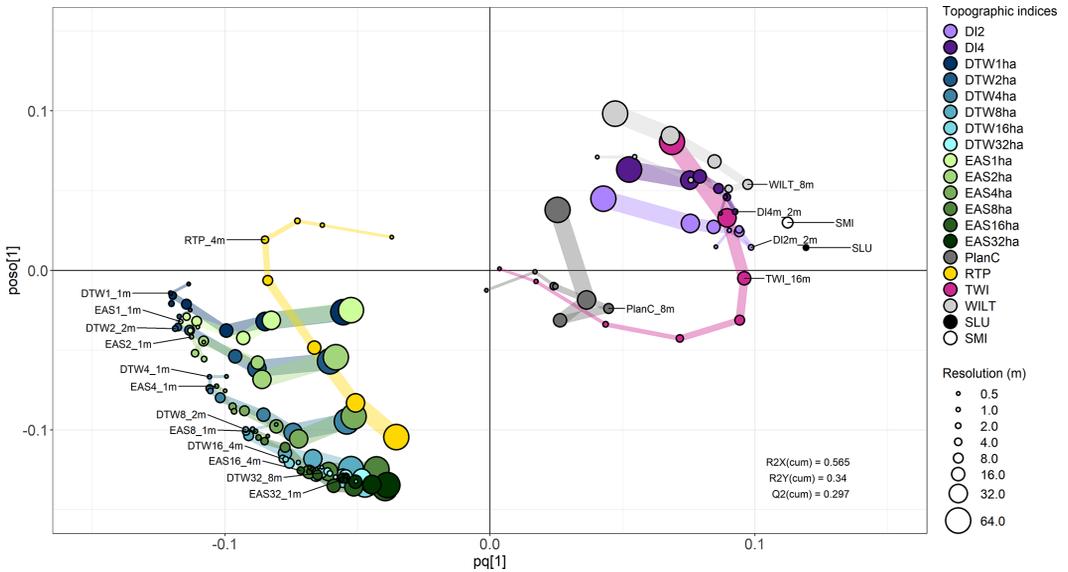


Figure 2. OPLS loading plots for the Krycklan catchment and DEM-derived terrain indices in respect of soil moisture predictions. Variables that cluster closely within the same neighbourhood along the far sides of the horizontal axis are the more robust soil moisture predictors across DEM scales. Coloured guides connect terrain indices moving from small to large resolutions as depicted by the symbol size. In the loading plot, predictive performance increases with increased distance from 0 on the predictive axis (pq[1]). Negative and positive values on the (pq[1]) axis correspond to negative and positive correlations with *Y*. The orthogonal axis (poso[1]) represents how much of the variation for each variable was not correlated with the determinant (*Y*). For the reader who is interested in the details, we have published an electronic version of this graph where all labels are visible by moving the cursor over each circle (“Code and data availability” section).

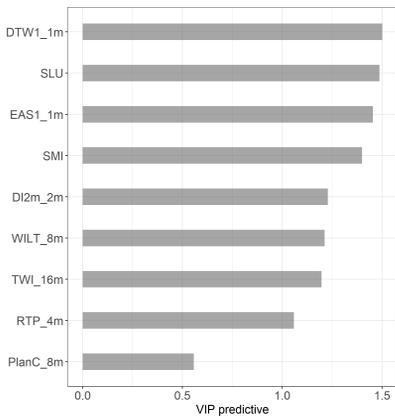


Figure 3. VIP_{predictive} values for the best-performing variable for each terrain index. In OPLS, VIP_{predictive} < 1 are variables that are better at explaining *Y*.

the optimal resolution and stream initiation threshold were used (Fig. 2). DTW loadings were located below zero on the predictive axis due to a negative relationship to soil moisture classes. Generally, the DTW variables were clustered together according to thresholds, with decreasing performance for coarser DEM resolutions. The loading of EAS followed the pattern of DTW, and both terrain indices had the highest predictive performance at stream initiation thresholds of 1 and 2 ha in DEM resolutions of 1–4 m. The highest resolutions of 0.5 m had a lower predictive performance (Fig. 2). Increased stream initiation thresholds above 2 ha lowered the predictive performance and added noise, as shown on the orthogonal axis (poso[1]).

The SLU soil moisture and SMI maps both performed well and were the second and fourth best terrain indices, respectively, for predicting soil moisture classes (Fig. 3). SMI scored lower on the predictive axis (pq[1]) and had slightly higher variation not related to the soil moisture classes compared to the SLU soil moisture map (Fig. 2). The SLU soil moisture map and DTW were the best-performing soil moisture predictors and had a very similar VIP_{predictive} value (Fig. 3).

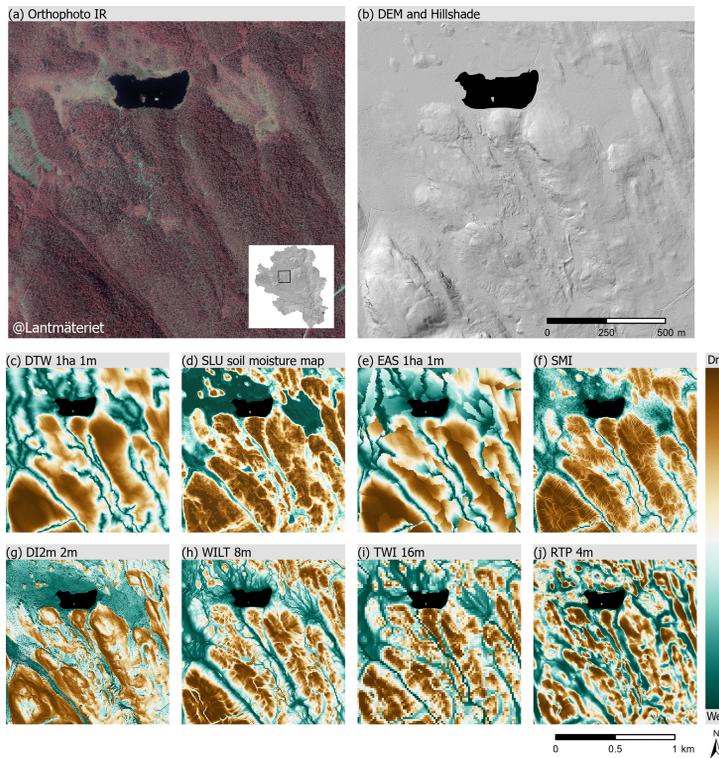


Figure 4. Orthophoto (© Lantmäteriet) (a) and hill-shaded DEM (b) covering a till area within the Krycklan catchment. Below, maps of the highest-performing maps of different terrain indices in order of $VIP_{\text{predictive}}$ with simplified common symbology for terrain indices (c–j) based on value distribution for the visual comparison.

The downslope index (DI) was shown to be a good soil moisture class predictor. DI was positively correlated to soil moisture classes and therefore located on the positive $pq[1]$ axis. DI2m ($d=2$ m) performed better than DI4m ($d=4$ m) with higher loading on the predictive axis and lower loading on the orthogonal axis. For both DI2m and DI4m, a resolution of 2 m had the highest predictive performance ($pq[1]$) with the lowest noise. Resolutions below 2 m and above 8 m reduced the performance of the predictions substantially.

The performance of TWI was highly sensitive to the resolution of the DEM; too fine or too coarse resolutions gave nonsensical results. For this landscape, 16 m was found to be the optimal resolution for TWI calculations (Fig. 3).

WILT showed the highest value on the positive predictive axis at 8 and 4 m resolution, which was also true for RTP. The WILT loadings were slightly higher than the best-performing TWI on the predictive axis ($pq[1]$) but also much higher on the orthogonal axis, indicating a large variation not related to soil moisture (Fig. 2). RTP showed no clear clustering,

similar to TWI, and performed worse compared to the above-mentioned terrain indices (Fig. 3). Plan curvature scored low on the horizontal axis, indicating that this variable was not a good soil moisture predictor for this landscape, something also confirmed by the $VIP_{\text{predictive}}$ value being below 1.

3.3 Visual evaluation

Wet and moist soil conditions within the catchment are mostly found on mires or as riparian soils along streams, as shown in Fig. 4. In the IR orthophoto (Fig. 4a), mires can be seen in the flatter areas (Fig. 4b) in the northern parts of the selected area. Several small stream channels in the bottoms of valleys drain the area from northwest to southeast, which borders onto wet riparian soils. Modelled soil moisture conditions of the best-performing indices showed similar but varied agreement with natural features when visualized (Fig. 4), with DTW and SLU soil moisture maps clearly delineating the mire in the northwest corner and around the lake, as well as the drier hilltops in the southeast cor-

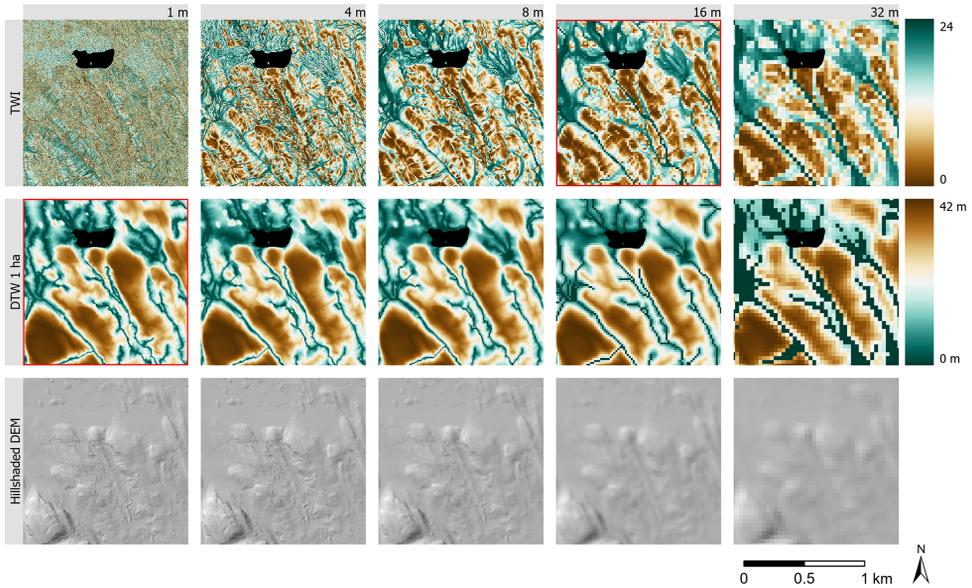


Figure 5. Maps of TWI, DTW and hill-shaded DEM at 1, 4, 8, 16 and 32 m resolution. Best-performing rasters in the OPLS analysis are outlined in red.

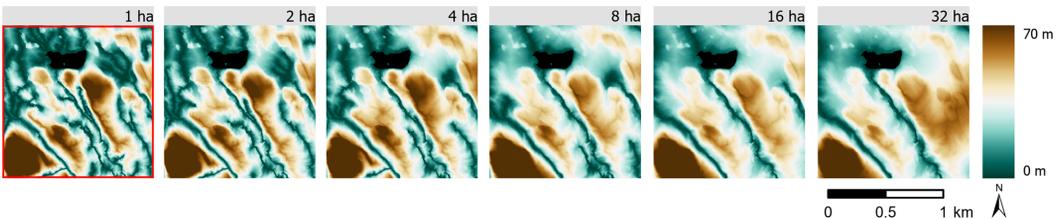


Figure 6. Maps of DTW at 1 m resolution with stream initiation thresholds from 1 to 32 ha.

ner (Fig. 4). With the appropriate resolution and thresholds, many of the terrain indices were able to represent the variation of soil moisture conditions in more or less accurate ways after visual comparison. RTP had a poor performance in the OPLS, which is in line with the results demonstrated in Fig. 4j, where it predicted dry areas within the mire.

Figure 5 illustrates differences in the effects of increased DEM resolution represented by modelled results for TWI and DTW with a 1 ha streamflow initiation threshold. Varying DEM resolution had larger effects on the spatial variation of soil moisture conditions using TWI compared to DTW, which was less affected; this is illustrated by the large differences moving from TWI at 1 m resolution to 32 m. The distribution of wet areas was not affected by DEM resolution for DTW compared to TWI. To visualize the effects of different user-defined stream initiation thresholds, DTW maps calcu-

lated for 1, 2, 4, 8, 16 and 32 ha stream networks were created (Fig. 6). Increasing the streamflow initiation threshold shortens the stream network, resulting in a drier landscape model, and decreasing the streamflow initiation threshold models a wetter landscape.

3.4 Confusion matrix

The overall agreement of DTW 1 m 1 ha values ($DTW < 1$) in relation to wet and moist soil classes was further tested using a confusion matrix (Table 3). Over the entire catchment area, the accuracy was 77 %, with a MCC of 0.42. Dividing the catchment into till and sorted sediment areas revealed significant differences in conformance. On the till area of the catchment, the DTW accuracy was higher with an accuracy of 78 % and a MCC of 0.50. On the sorted sediment area of

Table 3. Confusion matrix of true positive (TP), true negative (TN), false positive (FP) and false negative (FN) values, representing wet (positive) and dry (negative) plots predicted by DTW 1 ha at 1 m resolution and the SLU soil moisture map, as well as prediction accuracy (ACC, %) and the Matthews correlation coefficient (MCC, %). Confusion matrices and statistics were calculated for the entire catchment and divided into till and sorted sediment areas.

	Area	Plots (<i>n</i>)	TP	TN	FP	FN	ACC (%)	MCC
DTW	Entire catchment	398	61	245	61	31	77	0.42
	Till	293	53	176	49	15	78	0.50
	Sorted sediment	105	8	69	12	16	73	0.20
SLU	Entire catchment	398	78	255	21	44	84	0.60
	Till	293	69	180	11	33	85	0.66
	Sorted sediment	105	9	75	10	11	80	0.34

the catchment, DTW falsely predicted a large proportion of the dry plots as wet (FP). Only a third of the wet plots were predicted as wet (TP). The overall accuracy was better for the SLU soil moisture map but showed the same pattern as DTW in the sorted sediment area, with a low MCC value of 0.34 %.

4 Discussion

Modelling the spatial patterns of soil moisture remains an important scientific challenge and terrain indices are potentially a useful tool. As the availability and resolution of DEMs have increased, so have the uses of terrain indices for modelling hydrological, environmental and soil properties. However, the predictive performance of terrain indices is highly dependent on identifying the optimal spatial scales and user-defined thresholds for modelling soil moisture (Sørensen and Seibert, 2007; Lin et al., 2010; Ågren et al., 2014). The aim of this study was, therefore, to evaluate how DEM resolution, user-defined thresholds and landscape types affect soil moisture predictions from a range of readily available terrain indices in relation to field-classified soil moisture conditions across a boreal catchment. Our results demonstrate the potential of terrain indices for modelling soil moisture when the optimal DEM resolutions and user-defined thresholds are selected. No previous study has been able to provide such detailed data at catchment level or this large amount of terrain indices in combination with an extensive field survey, which clearly demonstrates the importance of selection of terrain indices, DEM resolution and index-specific thresholds.

Several terrain indices were able to predict the spatial variation of soil moisture classes within our study area; however our results revealed a large variation in the predictive performance within, and between, terrain indices at different DEM resolutions and index-specific thresholds (Fig. 3). The general agreement of appropriately scaled terrain indices with field classified soil moisture conditions (Fig. 2) and visual-

ized maps (Fig. 4) supports the underlying assumption that topography acts as the main driver of spatially varying soil moisture conditions. This is in line with many previous studies relating terrain indices to soil moisture conditions (Lin et al., 2010; Seibert et al., 2007; Grabs et al., 2009; Murphy et al., 2011; Ågren et al., 2014) and groundwater levels (Rinderer et al., 2014).

Ground truthing is required to evaluate the performance of different terrain indices, to prevent inappropriate choices of resolution and user-defined thresholds, resulting in non-representative predictions of soil moisture. As its ground truth, this study used a uniquely extensive and high-precision field survey within a well-studied landscape. We used field-mapped soil moisture classes based on estimated depth to groundwater from the soil surface guided by surrounding topography and vegetation patterns as a proxy for average soil moisture conditions, thus reducing the uncertainty associated with the large temporal and small-scale spatial variability of soil moisture (Murphy et al., 2011; Oltean et al., 2016; Beucher et al., 2019; Lidberg et al., 2019). The position in the landscape and the vegetation patterns that form the basis for the classifications stay constant over time. In contrast, more direct soil moisture measurements using values such as soil water content and time domain reflectometry (TDR) are greatly affected by the specific weather conditions before, and at the moment of, measurement. On the other hand, using soil moisture classes as the ground truth, we only evaluate the “average” soil moisture conditions for each site and thereby focus on the spatial variability of relative soil moisture conditions within the landscape. We do, however, acknowledge that soil moisture varies greatly with season and depends on regional weather conditions, causing stream networks and wet soils to expand and shrink during the year (Ågren et al., 2015).

Our results highlight that the optimum DEM resolution for soil moisture predictions differed depending on terrain index and further demonstrated the large effects of DEM resolution within certain terrain indices (Fig. 5). In line with previous studies, TWI was greatly affected by DEM resolution and was shown to perform best with a coarser 16 m resolution while performing poorly with high-resolution DEMs. This agrees well with previous studies both within Sørensen and Seibert (2007) and Ågren et al. (2014) and outside the study area (Lin et al., 2010; Murphy et al., 2011). However, this is in contrast to a recent study by Riihimäki et al. (2021), where they thoroughly investigated the effect of DEM resolution and flow accumulation algorithms on TWI calculations in a 300 ha area of the northwestern Fennoscandian mountain tundra. Their conclusion was that the *D*-infinity flow routing algorithm reached its maximum explanatory power at 3 m resolution. This highlights that the optimal DEM resolution for predicting soil moisture conditions using TWI cannot just be taken from literature as it varies from site to site, and it is necessary to investigate the optimal resolution for each landscape. While this has previously been shown in the

literature, a concern with the rapidly increasing numbers of high-resolution DEMs worldwide is that researchers will use the most commonly used terrain index TWI and disregard its poor performance with high-resolution DEMs. Other indices, such as DTW, EAS and DI, had the best performance for resolutions between 1 and 4 m and were stable within this range, as shown for DTW in Fig. 5. When using high-resolution DEMs, the importance of selecting the optimal method for the preprocessing step (the hydrological corrections of depressions) increases. The impoundments caused by road banks (that are captured in high-resolution DEMs) otherwise cause problems for the subsequent steps of modelling the flow paths in the landscape (Woodrow et al., 2016; Leach et al., 2017). Studies have shown that it is better to preprocess the DEM using breaching rather than filling functions (Wang et al., 2019; Lidberg et al., 2017). In this study, we used the protocol suggested by Lidberg et al. (2017), as that study was carried out on similar glaciated catchments in Sweden. The highest resolution of DEM did not perform optimally for any of the evaluated terrain indices. This has been highlighted by previous studies to be caused by small-scale variations in surface topography that do not affect the overall hydrological pathways (Gillin et al., 2015). The dependency of DEM resolution is important for any type of digital soil mapping, and the optimum resolutions have been shown to be different, depending on landscape and the spatial scale of the environmental phenomena and processes involved in the soil property of interest (Cavazzi et al., 2013).

This study also demonstrated the effects of adjusting user-defined thresholds associated with certain indices calculations (Figs. 2 and 6). In line with a previous study modelling the spatial extent of wet areas, DI calculated with a 2 m given vertical distance (d) (Eq. 3) performed best (Hjerdt et al., 2004). DTW and EAS were among the best-performing terrain indices (Fig. 3); however the overall predictive performance was dependent on the chosen stream initiation thresholds (Fig. 2). The best performance was achieved at 1 ha followed by 2 ha streamflow initiation threshold, much in line with previous results from the studied catchment area (Ågren et al., 2014) and from other study areas (Oltean et al., 2016). However, that only means that those thresholds might work well for glaciated catchments: in other regions, these thresholds might need to be adjusted. Again, our study highlights the need for ground truthing of the digital terrain indices, as the quality of the generated maps is so dependent on the selected thresholds. The substantial effects of varied user-defined thresholds for DTW and EAS highlight the importance of caution when selecting terrain indices.

The unique setting of the Krycklan catchment, with its heterogeneous soils, made it possible for this study to demonstrate the challenges raised from variable landform types, where the assumption of topography acting as a first-order control of soil moisture becomes less valid. In the sorted sediment areas of the Krycklan catchment, topographic variation is low and hydraulic conductivity high, allowing for

deeper infiltration of water, which decreases the topographical control of groundwater flows compared to the upper till which dominates parts of the catchment (Jutebring Sterte et al., 2021). The layout of the study did not allow for separate analysis of the different land form classes due to the limited number of field plots and low variation of soil moisture classes in the sorted sediment area (Table 1). However, using a confusion matrix of the classified best-performing terrain index (DTW < 1 m) from the OPLS in conformance with wet and dry soils, this study demonstrated a large difference in the MCC values between the sorted sediment (0.20) and till (0.50) parts of the catchment. The attempts of combining terrain indices and other mapped information to tackle the challenges of soil moisture modelling faced by landscape heterogeneity did not outperform the more basic terrain indices at the entire catchment level. The confusion matrix using the SLU map and DTW's overall conformance clearly showed the challenges caused by the sorted sediment areas of the catchment (Table 3). This study highlights the necessity of adapting soil moisture predictions to local soil conditions. These underlying factors need to be taken into consideration when modelling soil moisture conditions on any level from catchment, regional and national scale. One such attempt was the SLU soil moisture map which was constructed for the entire country of Sweden using vast amounts of field data from 16 000 field plots across the country as training data and several digital terrain indices at multiple resolutions and thresholds. Even so, when evaluated on the Krycklan catchment, the SLU soil moisture map ranked second among the top predictors for soil moisture (Figs. 2 and 3) and did not outperform several of the more simple terrain indices.

The results from this study demonstrate the potential of terrain indices for modelling soil moisture across the landscape when the optimal scales and thresholds are selected for the calculations. Terrain indices have been related to soil properties (Seibert et al., 2007; Zajíčová and Chuman, 2021), ecological studies (Zinko et al., 2005; Bartels et al., 2018) and site productivity (Mohamedou et al., 2017; Bjelanovic et al., 2018) and will likely develop further as a useful tool within many fields of study. However, it should be recognized that the predictive power of terrain indices is limited by the non-topographical drivers of the spatial variation in soil moisture, which will always be significant and rarely less than 50% (Western et al., 1999). Such drivers are, for example, soil depth, texture, hydrological conductivity, permeability and vegetation (Gwak and Kim, 2017). With an increasing demand for high-resolution spatial and temporal soil moisture models for climate, hydrology and soil modelling, it is important to understand the underlying covariate factors used to build them.

5 Conclusion

This study was designed to test, demonstrate and visualize the importance of appropriate scaling when modelling soil moisture conditions using terrain indices. Although some previous studies have drawn similar conclusions, there is still a tendency within many fields to use the highest DEM resolution available when using terrain indices to represent soil moisture conditions as a covariate. However, one size – or resolution in this case – does not fit all. Due to the differences in climate, landscape types and soil texture, terrain indices must be adapted to local conditions and calculated at appropriate scales and thresholds. Heterogeneous landscape types remain a challenge for predicting soil moisture conditions and should be taken into account when interpreting modelled results. We, therefore, stress the importance of evaluating the modelled terrain index results for the area of interest and not to extrapolate the optimum terrain indices for our study areas directly or to blindly use the DEM of highest resolution available.

Code and data availability. The code and data used in this study for aggregating the DEM and generating the different terrain indices are available at <https://doi.org/10.17632/dg64p8wmj9.1> (Larson et al., 2022) in addition to an interactive/electronic version of Fig. 2.

Author contributions. All authors were responsible for the conceptualization of the study and evaluation of results. WL was responsible for the data curation, and JL performed the analysis. JL prepared the manuscript and figures and led the writing of the paper, with contributions from all the co-authors.

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OPEN Soil moisture controls the partitioning of carbon stocks across a managed boreal forest landscape

Johannes Larson¹, Jörgen Wallerman², Matthias Peichl¹ & Hjalmar Laudon¹

Boreal forests sequester and store vast carbon (C) pools that may be subject to significant feedback effects induced by climatic warming. The boreal landscape consists of a mosaic of forests and peatlands with wide variation in total C stocks, making it important to understand the factors controlling C pool sizes in different ecosystems. We therefore quantified the total C stocks in the organic layer, mineral soil, and tree biomass in 430 plots across a 68 km² boreal catchment. The organic layer held the largest C pool, accounting for 39% of the total C storage; tree and mineral C pools accounted for 38% and 23%, respectively. The size of the soil C pool was positively related to modelled soil moisture conditions, especially in the organic soil layer ($R^2 = 0.50$). Conversely, the tree C pool exhibited a unimodal relationship: storage was highest under intermediate wetness conditions. The magnitude and variation in the total soil C stocks observed in this work were comparable to those found at the national level in Sweden, suggesting that C accumulation in boreal landscapes is more sensitive to local variation resulting primarily from differences in soil moisture conditions than to regional differences in climate, nitrogen deposition, and parent material.

Forests provide many life-sustaining ecosystem services. It has been suggested that management interventions in forest ecosystems could be among the most effective nature-based solutions combating climate change^{1,2} because forests play critical roles in global carbon (C) sequestration and long-term carbon storage³. Boreal forest landscapes store approximately one third of the entire terrestrial C pool⁴, with the majority of this C being stored below ground as soil organic carbon (SOC)⁵. Various biomass components including tree trunks, branches, roots, foliage, and deadwood also hold large C pools⁶. However, the relative sizes of these above- and belowground C pools within boreal landscapes are rather poorly constrained. Global, national, and regional estimates of boreal forest C stocks are often associated with large uncertainties⁷, which are typically attributed to under-sampled regions, a lack of remote sensing data, and differences in sampling methods and intensities between studies⁴. This limits our ability to develop strategies for improving the carbon sequestration potential of forest landscapes.

It is well established that soil forming factors are sensitive to climate, time, organisms, parent material and topography⁸, all of which by extension influence the development of the SOC pool. Several studies have identified climate as a key driver of SOC accumulation on global and regional scales, mainly because of its impact on temperature and precipitation^{9,10}. However, on smaller landscape scales (up to several tens of km²), site-specific soil-forming factors such as local topography may be more important because some of the factors mentioned above can be considered constant and are thus controlled for in small scale observational studies¹¹. For example, in mountainous landscapes where the parent material can be assumed to be constant, the spatial variation in the SOC stock is largely regulated by differences in altitude and aspect that have large control on climatic variability¹².

The central role of local topography as a primary controlling factor of soil moisture conditions is particularly evident in boreal landscapes, which are often dominated by unsorted glacial till with limited variation in hydrological properties^{13–15}. Soil moisture is a major factor governing SOC accumulation^{16–18} because it influences the input of organic carbon via its effects on plant production and also controls decomposition rates. The accumulation of the aboveground C stock in boreal landscapes is also sensitive to disturbances such as fires and forest management¹⁹, while forest productivity is tightly constrained by climate, nutrient availability, and water levels^{20,21}. Specifically, tree growth in dry sites is often limited by water and nutrient availability²², whereas

¹Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden. ²Department of Forest Resource Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.  email: Johannes.larson@slu.se

excessive wetness leads to soil saturation and limits tree growth by creating anoxic conditions that are often associated with increased organic layer thickness^{23,24}.

Managed boreal landscapes are particularly heterogeneous in terms of vegetation structure and composition, which can enhance variation in C stocks across smaller spatial scales. However, the lack of spatially extensive soil moisture data means that the landscape-scale effects of management on C stocks are poorly constrained¹¹. This is a significant problem because climatic change is likely to change the water balance in boreal landscapes and thereby affect soil moisture conditions. Consequently, there is a clear need to improve our understanding of the size and distribution of C stocks on the landscape scale and to identify the factors governing them in order to develop sustainable forest management strategies.

To address these needs, we conducted a comprehensive forest and soil survey across a 68 km² managed boreal forest catchment in Northern Sweden with the aim of quantifying the magnitude and variation of forest ecosystem C stocks. We sampled 430 plots, obtaining detailed soil profile descriptions of organic and inorganic soils down to 50 cm in the mineral soil and performing chemical analyses of samples from fixed soil depths. The soil survey was combined with an extensive forest survey using the same survey grid and a high resolution airborne laser scanning (ALS) dataset. Recent advances in ALS have made it possible to retrieve various forest biophysical properties²⁵ and acquire high resolution topographic information, opening up new approaches to soil moisture modelling and digital soil mapping. For example, in Sweden ALS-derived topographical information has been combined with additional geographical datasets to model soil moisture conditions at a spatial resolution of 2 m using machine learning algorithms²⁶. This approach was shown to accurately delineate peat soils²⁷. Furthermore, high resolution estimates of above- and belowground biomass have been obtained by combining ALS and forest survey data^{28–30}. These developments offer new ways to identify factors controlling the magnitude and variation of above- and below-ground forest ecosystem carbon stocks.

The specific objectives of this study were to (i) estimate the size and spatial variation of C stocks in soil and trees in a managed boreal forest landscape, (ii) characterize the relationships between the sizes of these C stocks and soil moisture conditions (iii) and produce high-resolution wall-to-wall estimates of soil and tree C stocks within the landscape. We hypothesised that (i) soil C is the largest and most variable C pool across the landscape, (ii) soil moisture conditions control SOC levels at the landscape scale, with increased soil moisture being associated with larger SOC stocks, and (iii) soil moisture effects on the organic layer C pool are a key determinant of the studied landscape's total C stock.

Methods

Site description. This study was conducted in the Krycklan catchment, situated in northern Sweden (Lat. 64°23'N, Long. 19°78'E)³¹. The catchment has a cold temperate humid climate with a 30 year (1991–2020) mean annual air temperature of 2.4 ± 0.3 °C and a mean annual precipitation of 638 ± 40 mm, of which 35% falls as snow. The catchment spans 68 km² and has a gentle topography, with elevations ranging from 127 to 372 m.a.s.l. and a poorly weathered gneiss bedrock. The soils of the upper parts are dominated by unsorted glacial till while those of the lower parts consist primarily of sorted sediments of sand and silt. Approximately 25% of the catchment has been protected for research since 1922; ownership of the remaining area is divided among private owners and forest companies. The catchment's land cover is dominated by forests, which account for 87% of its total area and consist primarily of Scots pine (*Pinus sylvestris* L.) (63%) and Norway spruce (*Picea abies* (L.) H. Karst.) (26%). Forests in the non-protected areas are managed by conventional rotation forestry and are predominantly even-aged, artificially regenerated, and thinned. The forest soils are dominated by well-developed iron podzols³². Mires and lakes cover 9% and 1% of the landscape, respectively, while arable land covers 2%.

Field data. The survey grid covers the entire catchment area and consists of 500 plots that each have a radius of 10 m and an area of 314 m², with a spacing of 350 m between adjacent plots (Fig. 1). The survey grid is densified in a 1500 × 1500 m area around an eddy covariance tower in the centre of the study area, where the spacing between adjacent plots is 175 m. Plot locations were established in 2015 using a randomly chosen origin and were oriented along the coordinate axis of the Sweroff 99 TM projection. The centre of each plot was located in the field using a Trimble GeoXTR GNSS receiver.

Soil survey. The soil survey was conducted during the snow-free seasons of 2019 and 2020, following the methods of the Swedish National Forest Soil Inventory (SFSI; <http://www-ris.slu.se>). Soil profile descriptions and site variables such as soil moisture classes (described below), humus form, organic layer thickness, and soil texture were determined, measured, or recorded for each plot. The organic layer was sampled volumetrically using a 10 cm diameter corer to the full depth of the O-horizons or to a maximum depth of 30 cm after removing the litter layer and bottom layer of mosses and carefully separating them from the mineral soil below. Samples were collected from 1 to 9 sampling points until the target sample volume of ca 1.5 L was obtained. These points were distributed within a 3.14 m² subplot close to the survey plot's centre. Mineral soil was sampled to a depth of 65 cm (or to bedrock or boulder depth) at fixed intervals of 0–10, 10–20, and 55–65 cm. Total C was analysed on the fine fraction (<2 mm) after samples had been dried at 65 °C, ground to a fine powder and homogenised. A total of 1500 individual samples were analysed for soil C concentration by mass spectrometry using a Delta IRMS instrument coupled to a Flash EA 2000 analyzer (Thermo Fischer Scientific, Bremen, Germany). Analyses were performed with 5–50 mg soil material depending on the organic matter content. Organic layer C stocks were calculated by multiplying each sample's C concentration by its dry weight and then dividing the result by the total sampled area. Mineral soil C stocks in each sampled layer (0–10, 10–20, and 55–65 cm) were calculated based on the C concentration, bulk density (g/cm³), soil layer thickness (cm) and the volume percentage of stones and boulders using the following expression:

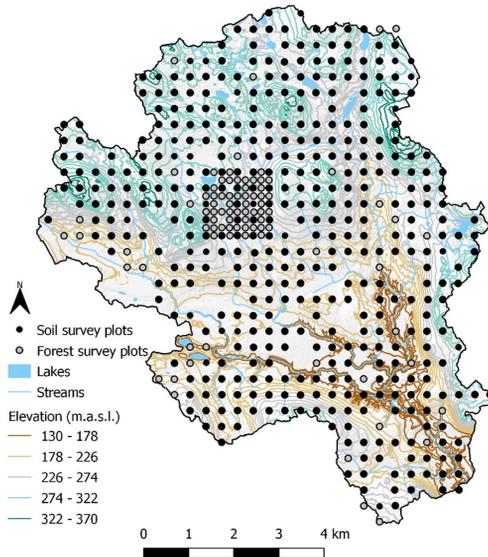


Figure 1. Topography of the Krycklan catchment and locations of soil and forest survey plots (represented as black and grey dots, respectively). Forest surveys were also conducted on soil survey plots. Most plots are located on the vertices of a 350×350 m grid but there is a densified 175×175 m grid around an Eddy covariance tower in the catchment's centre. The map was created using Esri ArcGIS Pro 3.0.2, <https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview>.

$$\text{Storage} = \text{Concentration} (\%) \times \text{BulkDens} \times \text{LayerThickness} \times (100 - \text{StoneVol})/100 \quad (1)$$

The bulk density of the mineral soil horizons was calculated using the SFSI procedure, which is based on a pedotransfer function that depends on the C concentration and depth (cm)^{10,33}.

$$\text{BulkDens} = 1.5463 \times \text{EXP}(-0.3130 \times \text{CarbonConc}^{0.5}) + 0.0027 \times \text{Depth} \quad (2)$$

The volume of stones and boulders in each plot was estimated using the stoniness index, which is determined by driving a 1 cm diameter metal rod into the soil using a small sledge hammer (2 kg) until the rod cannot penetrate further. The penetration depth (max 30 cm) is then measured from the top of the mineral soil surface. Measurements were done at 12 predetermined locations across each plot and the volume percentage was then calculated using a transfer function^{34,35}. The total SOC stock was calculated as the sum of the organic and mineral C pools. For plots with peat soils where the organic layer thickness was > 30 cm, the total C stock was calculated to a maximum depth of 1 m from the organic layer surface. In these plots, the C stock of the organic layer was estimated by collecting samples to a maximum depth of 30 cm and extrapolating downwards.

Forest survey. The forest survey was conducted in the late fall of 2019 and the early spring of 2020. A total of 488 plots were surveyed, of which 430 were also included in the soil survey (Fig. 1). All trees within each 10 m radius plot were measured and the stem diameter at breast height (DBH; 1.3 m) of trees with DBH > 4 cm was recorded along with the heights of saplings. In regenerating/young forests and some other stands with very high stem densities, the plot radius was reduced to 5 m to limit the time needed for surveying. Species and DBH were recorded for all trees and tree heights were measured using a laser-guided hypsometer on a subjectively selected sub-sample of at least three trees that were chosen to capture the tree size variation of each species. The height of the remaining trees was estimated using plot-level fixed mixed effects modelling for single trees and then imported into the Heureka system for plot biomass calculations³⁶. The aboveground biomass in each plot was estimated using allometric equations for stumps, stems, bark, dead and living branches, and foliage for Scots pine, Norway spruce, and birch, with tree height and DBH as independent variables³⁷. For Lodgepole pine (*Pinus contorta* Bol.), we used the same functions as for Scots pine; other deciduous species were modelled using the birch functions. Belowground biomass was estimated for individual trees using species-specific allometric equations with DBH as the independent variable and were summarized per plot³⁸. The total tree C pool was calculated by summarizing the above- and belowground biomass for each plot and then converting to Mg C ha⁻¹, assuming a C concentration of 50% in biomass.

Soil moisture classes. Each plot was assigned to one of five soil moisture classes based on its average groundwater table depth, which was estimated from the plot's position in the landscape, soil texture, and vegetation patterns. The five soil moisture classes were: dry (7% of all plots), mesic (73%), mesic-moist (11%), moist (7%) and wet (2%). These classes are described briefly below and at greater length in previous publications³⁹.

- Dry soils have an average groundwater table > 2 m below the soil surface. They tend to be coarse-textured and can be found on hills, ridges, and eskers. Dry soils are mainly Leptosols, Arenosols, Regosols, or Podzols with thin organic and bleached horizons.
- Mesic soils have an average groundwater table between 1 and 2 m below the soil surface. Podzol is the dominating soil type with a fairly thin (4–10 cm) organic mor layer covered mainly by dryland mosses (e.g., *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum scoparium*). They can be walked on dry-footed even directly after rain or shortly after snowmelt.
- Mesic-moist soils have an average groundwater table depth < 1 m below the soil surface and are normally located on flat ground in lower-lying areas or lower parts of hillslopes. The soils become wet seasonally following snowmelt or heavy rain events. The feasibility of crossing with dry feet in normal shoes depends on the season. Peat mosses (e.g., *Sphagnum* sp., *Polytrichum commune*) in patches are common, and trees often grow on humps. Podzols are commonly found but often with a thicker organic layer than in mesic sites. The organic layer is often classified as peaty mor.
- Moist soils have an average groundwater table depth < 1 m below the soil surface and the surface water is commonly visible in depressions within the plot. Moist soils are found at lower altitudes, on the lowest parts of slopes and flat areas below larger ranges. They can be crossed in shoes without getting wet feet by utilizing tussocks and higher-lying areas. The vegetation includes wetland mosses (e.g., *Sphagnum* sp., *Polytrichum commune*, *Polytrichastrum formosum*). When stepping in depressions, water should form around the feet even after dry spells. Trees often grow on small mounds and the soil type is most often Histosol, Regosol, or Gleysol.
- Wet soils have a ground water table close to the soil surface and permanent pools of surface water are common. Soils are typically Histosols or Gleysols. Drainage conditions are very bad and they cannot be crossed in shoes without getting wet feet. Wet areas are often located on open peatlands and coniferous trees seldom develop into stands.

Modelled soil moisture conditions. Soil moisture conditions were modelled using the newly developed SLU machine learning soil moisture map with a resolution of 2 m²⁶. The map was developed using multiple nationwide geographical information datasets including various terrain indices, climate data, and quaternary deposit information. The training and validation data consisted of almost 20,000 field soil moisture classifications (1–5) from the national forest inventory that were spread across the entire Swedish forested landscape. The final model used Extreme Gradient Boosting (XGBoost) to produce a 2-class model in which the depth water index⁴⁰ and topographic wetness index⁴¹ were the most important predictors. The survey grid employed in the present study was used for external validation of the modelled soil moisture, which yielded a kappa value of 0.52²⁶. The model's output is presented as a wetness index map showing the predicted probability (0–100%) of wetness for each pixel and is publicly available (Swedish University of Agricultural Sciences, 2022). Modelled soil moisture conditions for each survey plot were extracted using the coordinates of the plot's centre.

Carbon pool mapping. Data representing all plots included in the forest survey of 2019 were used as ground truth for Tree C pool mapping. ALS data were acquired in August 2019 using a Reigl VQ-1560i-DW 1064 nm (NIR) scanning system with an average point density of 20 points m⁻². The raw ALS data were pre-processed by classifying point returns as ground, unclassified, or noise. A digital terrain model was then generated and the ALS points were normalised to represent the tree canopy height above the ground surface. Finally, metrics were generated from the ALS data to summarize the point-cloud information on the raster cell level using the CloudMetrics program in the Fusion software package⁴². These metrics were calculated for 12.5 × 12.5 m grid cells using methods previously developed to generate ALS estimates on a national scale⁴³. Plots were excluded if the absolute difference between Lorey's mean height and the ALS metric P95 (the 95th percentile of the ALS point cloud's height distribution) was above 5 m. Regression models relating the observed Tree C pool at the plot level to several other explanatory ALS metrics were fitted and extrapolated over the entire study area. The total SOC stocks over the catchment area were mapped using the modelled relationship between plot-level measurements of total SOC stocks and the SLU soil moisture map.

Statistics. Descriptive statistics for the different C pools were generated using the statistical software R⁴⁴. The relationships between modelled soil moisture conditions and C pools were evaluated by linear regression, using polynomial models in some cases. Predictive models with log-transformed dependent variables were back-transformed using smearing estimates⁴⁵ to avoid bias. As no independent data were available to assess the accuracy of the models' C pool predictions, we performed leave-one-out cross-validation⁴⁶ by removing one sample from the model dataset and fitting the selected models on the remaining plots. Model performance was evaluated using R² and RMSE.

Results

Soil carbon pools. The mean total SOC stock down to 50 cm of mineral soil including peat soils was 94 ± 5 (SE) Mg C ha^{-1} (Table 1). Excluding peat soils, the mean total C stock was 67 ± 2 Mg C ha^{-1} . The mean SOC stock in mineral soils was 40 ± 1 Mg C ha^{-1} while that in the organic layer (to a maximum depth of 1 m) was 59 ± 6 Mg C ha^{-1} . Forty-nine plots were classified as peat soils (organic layer thickness > 30 cm); the mean C stock for these plots was 307 ± 29 Mg C ha^{-1} .

Tree carbon pool. The forest age varied between 0 and 272 years with a mean of 79. The mean height and basal area were 13 m and $21 \text{ m}^2 \text{ ha}^{-1}$, respectively (Table 2). The total tree C pool varied from 0 to 228 Mg C ha^{-1} , with a mean of 58 Mg C ha^{-1} . On average, 24% of the Tree C was stored below ground and 76% above ground (Table 3).

Total carbon stock estimates. The total SOC pool accounted for 62% (94 ± 1 Mg C ha^{-1}) of the landscape's total C storage (152 Mg C ha^{-1}), with the remaining 38% (58 ± 2 Mg C ha^{-1}) being stored in the tree C pool. The largest individual C pool was the organic layer (59 ± 6 Mg C ha^{-1}), which comprised 39% of the total C stock on average, while the mineral soil C pool accounted for 23% of the total (35 ± 1 Mg C ha^{-1}). If peat soils were included, the organic soil C pool accounted for 63% of the total SOC pool. However, if peat soils were excluded, the mineral soil C pool comprised 60% of the overall SOC stock.

Soil moisture effects on C allocation. The size of the total C pool differed significantly between soil moisture classes, ranging from 100 Mg C ha^{-1} in the driest class to 270 Mg C ha^{-1} in the wettest (Fig. 2). This relationship was mainly driven by an increase in the size of the organic layer C pool in the mesic-moist to wet soil moisture classes. The C stored in the mineral soil C pool decreased from 37 to 18 Mg C ha^{-1} between the driest and the wettest class; this is mainly due to the greater depth of the organic layer in wetter soils and the fact that sampling was only conducted to a maximum depth of 1 m below the soil surface. The mineral soil C pool depth was therefore reduced or zero in cases where the organic layer thickness was around or above 1 m. The tree C pool increased from 44 Mg C ha^{-1} in the dry class to a maximum of 80 Mg C ha^{-1} in the mesic-moist sites but then decreased as the moisture increased further, falling to 40 Mg C ha^{-1} in the wettest soil class (Fig. 2).

The median proportion of the total C stock in the tree C pool increased from the dry (42%) to mesic (51%) soil moisture classes (Fig. 3). The majority (57%) of the survey plots had over 50% of their total stored C in the soil.

Variable	Case	N	Mean	SD	Median	Min	Max	SE
Total SOC pool	Including peat soils	430	94	109	62	9	959	5
Organic C pool	Including peat soils	430	59	115	21	0	959	6
Mineral C pool	Including peat soils	430	35	23	35	0	171	1
Total SOC pool	Excluding peat soils	381	67	43	58	9	412	2
Organic C pool	Excluding peat soils	381	27	33	19	0	336	2
Mineral C pool	Excluding peat soils	381	40	22	37	0	171	1
Total SOC pool	Only Peat soils	49	307	198	291	21	959	29

Table 1. Soil carbon stocks (Mg C ha^{-1}).

Variable	Mean	SD	Median	Min	Max	SE
Age (years)	79	48	73	0	272	2
Hgv (m)	13	5	14	0	24	0.24
Basal area ($\text{m}^2 \text{ ha}^{-1}$)	21	12	21	0	58	0.5
Volume ($\text{m}^3 \text{ ha}^{-1}$)	156	111	149	0	601	5.0
Number of stems (ha^{-1})	1459	1835	1178	0	33,205	83

Table 2. Field measurements of forest stand variables in the forest survey plots (n = 488).

Variable	Mean	SD	Median	Min	Max	SE
Tree C pool	58	40	55	0	228	2
Above ground	44	30	41	0	170	1
Below ground	14	10	14	0	58	1

Table 3. Tree C pool stocks (Mg C ha^{-1}) in the surveyed plots (n = 488).

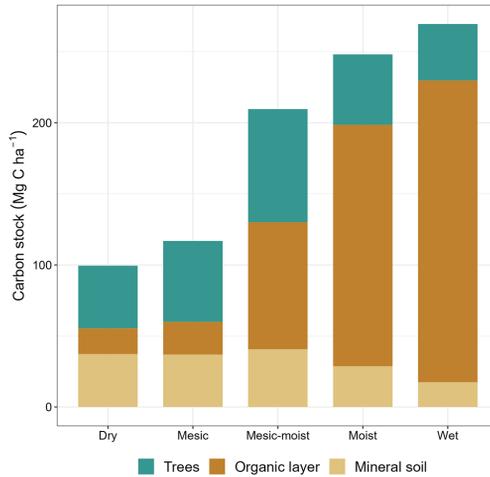


Figure 2. Sizes of the tree, organic layer, and mineral soil carbon pools for different field-classified soil moisture conditions.

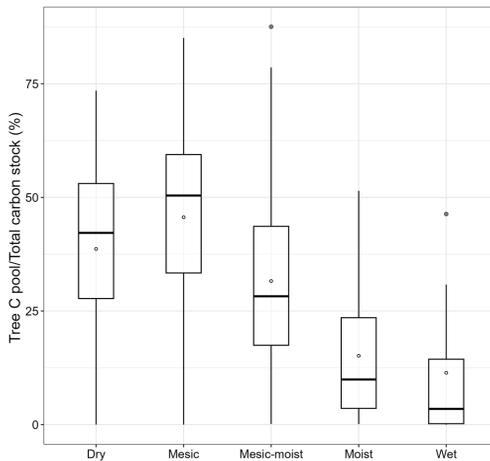


Figure 3. The tree carbon pool as a proportion of the total carbon stock in each of the five soil moisture classes. Mean values are indicated by white circles.

A model to predict C pool sizes based on soil moisture. Upon relating the measured C pools to soil moisture predictions obtained using the SLU soil moisture map, we found that the relationship between the tree C and SOC pools at different soil moisture levels was unimodal (Table 4; Fig. 4), in accordance with the results obtained using the field soil moisture classifications (see Fig. 3). The relationship between the total SOC pool size and the modelled soil moisture was described well by a polynomial regression ($R^2 = 0.40$) (Table 4), which accurately captured the large increase in C stocks with increasing soil moisture (Fig. 4b). This analysis also confirmed that the increase in the total SOC stock was mainly due to an increase in the size of the organic layer C pool ($R^2 = 0.50$). The mineral C pool showed a significant positive linear increase with the soil moisture, but this trend explained only 5% of the total variation in C pool size.

To avoid confounding effects from forest management on the standing biomass across our 430 plots, we also evaluated the relationship between the tree C pool and soil moisture in plots containing only tree stands that were at least 80 years old, representing mature forests ($n = 166$). In this analysis, the tree C pool showed a

Carbon pool	n	Regression	R ²	RMSE	F-stat	p-value
Tree C pool _(stand ages ≥ 80)	166	$y = 80.57 - 129.3x - 165.9x^2$	0.14	40.74	13.09	5.362e-06
Total SOC pool	430	$\log(y) = 4.23 + 8.51x + 3.35x^2$	0.40	90.24	140.3	< 2.2e-16
Organic C pool	430	$\log(y) = 3.32 + 13.87x + 6.12x^2$	0.50	95.73	209.8	< 2.2e-16
Mineral C pool	373	$y = 36.43 + 0.19x$	0.05	20.36	24.82	7.108e-06

Table 4. Results obtained using linear and polynomial regression models of the relationship between carbon pool size and predicted soil moisture (x). RMSE values were calculated by leave-one-out cross validation (LOOCV) in which the Total SOC and Organic SOC stocks were retransformed using SMEAR to avoid logarithmic bias.

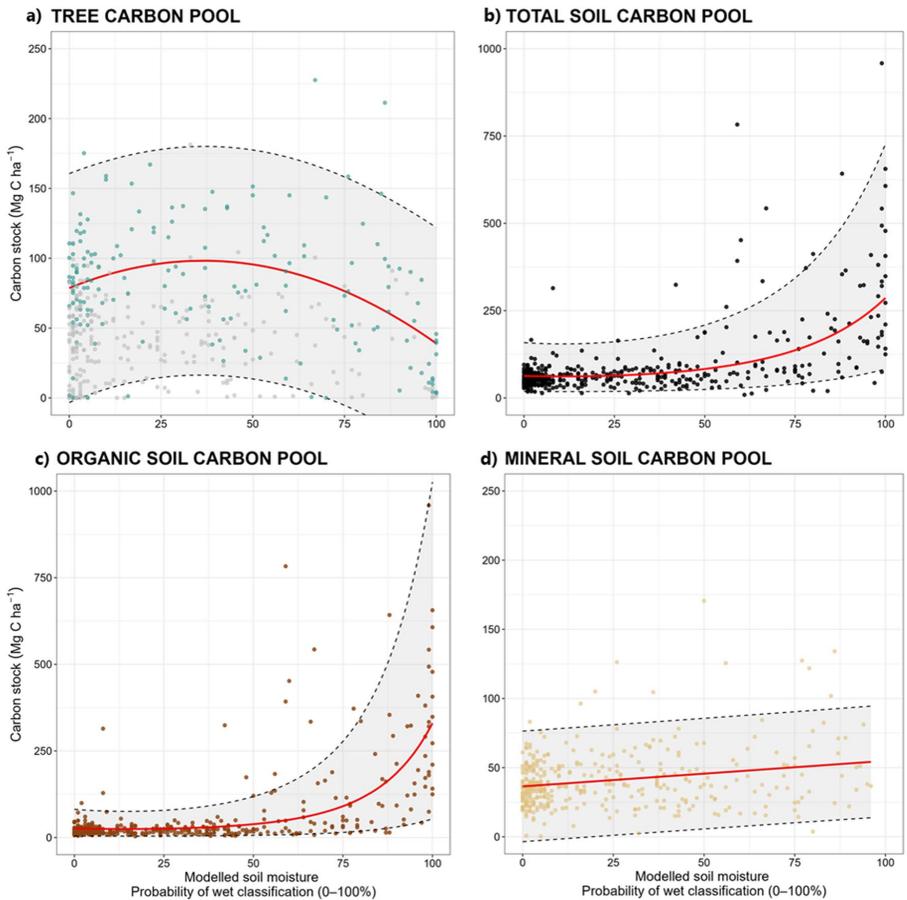


Figure 4. Carbon pool sizes as functions of modelled soil moisture conditions. Regression lines are shown in red and 95% prediction intervals are shown using dashed lines. The modelled soil moisture represents the probability of plots being classified as wet (dry – wet) based on a 2-class XGBoost model. The tree carbon pool modelling results shown in plot (a) are based on data for survey plots with a stand age of 80 years or above (results indicated by blue dots) to reduce the impact of management effects. Results for plots with a mean stand age below 80 years are represented by grey dots.

weak but significant (p -value < 0.01) unimodal relationship with the modelled soil moisture, indicating that the proportion of the total C stock in trees is generally higher in areas with intermediate soil moisture than in those with very low or very high wetness.

Carbon mapping (wall-to-wall estimates) across the forest landscape. To map the tree C pool (including both the above- and belowground pools) over the entire catchment area, we developed a model based on the relationship between the field tree C data and ALS-derived metrics by adapting the previously-reported area-based method⁴⁷. The final model (Eq. 3) included two dependent ALS variables relating to height distribution (P95 and SD, i.e., the 95th percentile and the standard deviation of ALS point heights above ground, respectively), and one relating to tree canopy density (VR, i.e., the proportion of ALS points reflected in the vegetation).

$$\text{Tree C pool} = 4.94 + 0.02(\text{P95} \times \text{VR})^{1.2} - 3.17\text{HSD} \quad (3)$$

The agreement between the predicted and observed data was good ($R^2 = 0.9$, $p < 0.001$) (Fig. 5), and leave-one-out cross validation indicated an acceptable goodness of fit with a RMSE of $12.4 \text{ Mg C ha}^{-1}$. The model was therefore used to predict the tree C pool for each $12.5 \times 12.5 \text{ m}$ raster cell within the Krycklan catchment (Fig. 6a).

To map the SOC stock across the entire catchment, we applied the polynomial function described in section "A model to predict C pool sizes based on soil moisture" to each 2 m cell based on the modelled soil moisture (Table 4). This revealed a mosaic of clear cuts (white) and mature stands with high tree C stocks, demonstrating the profound effects of forest management on tree C pools within the landscape (Fig. 6a). Total SOC stocks were highest in wetlands (peat) and the riparian zones alongside streams (Fig. 6b). The inverse relationship between high soil C stocks and the size of the tree C pool was particularly pronounced in the wetland areas.

Discussion

Despite the importance of boreal forests for carbon sequestration and climate mitigation, the factors governing C stock variation and its distribution at the landscape scales remain poorly understood. Based on an extensive survey of the tree and SOC pools in > 400 sample plots within a landscape-scale study area, this work provides (i) insights into the magnitude and variation in C stocks across a meso-scale boreal landscape; (ii) empirical evidence of the profound impact of soil moisture conditions on SOC stocks; and (iii) high-resolution estimates of the C stock distribution over a managed boreal forest landscape. Taken together, our results show how the total and individual organic and mineral SOC stocks vary across the boreal landscape and co-vary with the tree C pool.

Although we found that the total C stocks at the plot level are highly variable across a 68 km^2 managed boreal forest landscape catchment, our estimate of the average landscape SOC stock ($94 \pm 3 \text{ Mg C ha}^{-1}$) is similar to previous regional and national SOC stock estimates based on the Swedish national forest soil inventory. For instance, a national study focusing on Swedish podzols (i.e., excluding peat soil) estimated an average total SOC stock¹⁶ of $82 \pm 3 \text{ Mg C ha}^{-1}$. In the same study, Olsson et al. found that the average SOC pool size in the organic layer was 28 Mg C ha^{-1} , which is identical to the value obtained in our analysis when peat soils were excluded. In a regional analysis covering all of northern Sweden, Hounkpatin et al. estimated a mean total SOC stock of 73 Mg C ha^{-1} , which also is consistent with our results. The fact that the average SOC stocks in our boreal catchment are similar to previously reported regional- and national-scale estimates for Sweden suggests that SOC

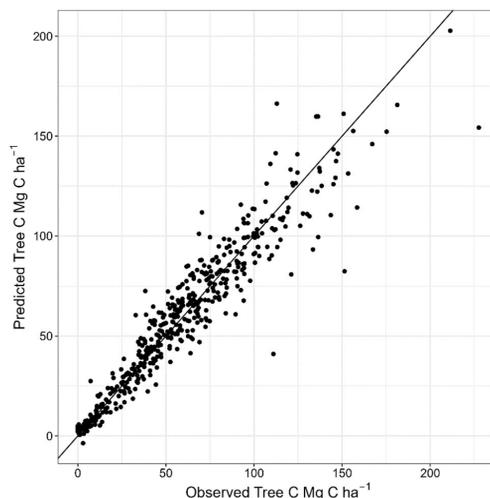


Figure 5. Relationship between ground truth data and the Tree C pool predicted by the ALS model (Eq. 1).

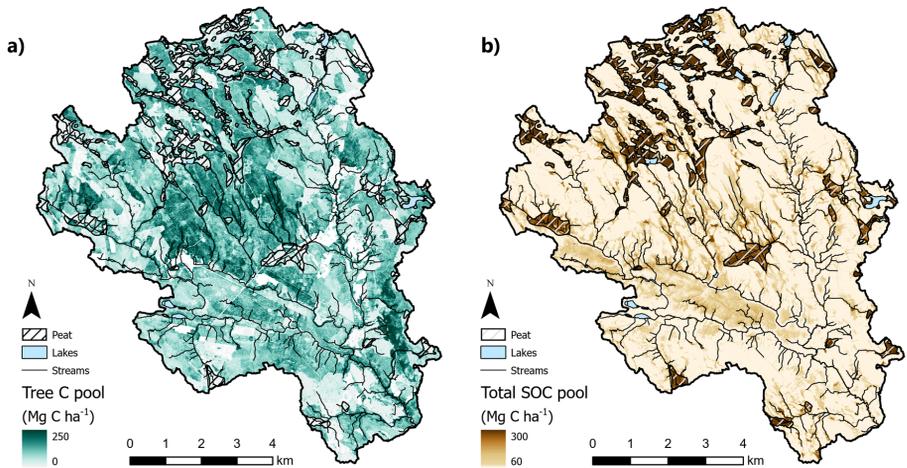


Figure 6. Tree C distribution map derived from ALS data using the area-based method (a) and the total SOC stock distribution derived by regression analysis of soil moisture data (b). Areas shown in white are dominated by clear-cuts and open peatland. The maps were created using Esri ArcGIS Pro 3.0.2, <https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview>.

stocks are far more sensitive to local-scale variation than to differences along the national north–south gradient despite the associated wide variation in climate, nitrogen deposition, and parent material.

In accordance with our first hypothesis, the total C stock increased rapidly with the soil moisture level, primarily because of a large increase in the size of the organic layer C pool (Fig. 2). Findings from other boreal landscapes support our results: multiple studies have concluded that SOC stocks increase with soil moisture levels, whether evaluated on the basis of drainage class or wetness indices^{18,48}. However, this study goes beyond previous works because it is based on a unique high-density soil dataset for a catchment-scale site; the catchment scale has received little attention in previous research. Furthermore, while organic soils often are excluded or considered separately from mineral soils due to differences in soil formation conditions, our work highlights the need to include organic soils to fully understand overall variation in C stocks in high altitude landscapes. Peat soils host a large proportion of the total terrestrial C stock in boreal biomes; our estimates suggest that they account for about one-third of the global SOC stock to a depth of 1 m⁴⁹. Even though only 11% of the plots within this study area were peat soils, they accounted for 37% of the total measured soil C stock.

Forest management practices, particularly clear-cut harvesting, have significantly affected the natural variation of tree C stocks within boreal forest landscapes, reducing the impact of natural disturbances that previously had central roles such as forest fires and wind. The long history of forest management in Sweden has probably obscured the relationship between the tree C pool and soil moisture conditions in a way that may depend on site-specific conditions (Fig. 4). Additionally, the legacy of peatland drainage efforts within the catchment and across Fennoscandia has enhanced forest production in many areas, greatly expanding the tree C pool⁵⁰. Evaluating these impacts can be challenging, but the successful application of our area-based method in this work clearly shows that ALS provides an effective way to systematically collect forest information in order to quantify aboveground carbon stocks on the landscape scale²⁹ while also dealing with confounding factors resulting from forest management interventions (Fig. 6a).

The SOC pool accounted for a large proportion of the total C stock within our studied boreal landscape, highlighting the presence and impact of local C stock hotspots in wet peat soils (Fig. 6b). It is notable that peat soils are not only found in forested and open wetlands but also in the riparian zones lining most streams. The proportion of C stored in trees in these wet areas is substantially lower than in other forested regions, so less common management practices such as continuous-cover forestry may be preferable to ensure the preservation of these large SOC stocks⁵¹. More generally, the presence of large SOC stocks in riparian zones suggests a need for greater caution in forest management when dealing with such near-stream areas⁵².

To better understand the landscape-scale variation in SOC stocks, the effects of factors such as forest productivity, management, tree species, and fire history will have to be studied. Future work should also focus on exploring the combined impacts of different soil forming factors across fine spatial scales, including soil texture, bulk density, soil depth, and chemical properties. Special attention should be given to improving the reliability of bulk density estimates for unsorted sediment soils because quantifying uncertainty in this area is difficult and time-consuming. Following the method of the Swedish national forest inventory, we modelled bulk density in the mineral soil using empirical pedotransfer functions; this represents a notable weakness in our C stock estimates given the limited accuracy of such functions. Furthermore, we chose to focus specifically on testing soil moisture effects by using a state-of-the-art map based on terrain indices and other geographical information in this study²⁶. However to better understand the influence of topography as a soil forming factor we could also consider the C

stock in relation to individual terrain indices such as the commonly used Topographic Wetness Index (TWI)⁴¹ and the associated effects on aboveground productivity and soil chemical properties.

Conclusion

We have presented a unique perspective on the total C stock of a managed boreal forest landscape that emphasizes the importance of soil moisture conditions as a key regulator of the SOC stock distribution. Our results indicate that the total C stock increases when moving from dry to wet areas, but the tree C stock is highest in regions with intermediate soil moisture levels. Landscape-scale soil moisture variation is largely governed by topography because it controls the distribution of water, which determines the spatial distribution of different soil types. To clarify the distribution and dynamics of the above- and belowground C pools, future studies should focus on disentangling the multiple drivers of C accumulation such as ecosystem productivity, species, forest history and other soil forming factors. Our results also indicate that potentially drier future conditions due to climate change might reduce the total landscape C storage and shift its allocation from soils towards tree biomass. This would have important implications for the C pool's protection from disturbances (e.g., fire and wind throw) and associated risk of terrestrial C being emitted to the atmosphere.

Data availability

The dataset generated during the current study is available from the corresponding author on reasonable request.

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Author contributions

J.L. and H.L. designed the study. H.L. provided funding acquisition, project administration, and resources. J.L. led and conducted the majority of the fieldwork. J.L. analysed, interpreted the data. J.W. produced the ALS models. J.L. wrote the manuscript with contributions from all co-authors.

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Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to J.L.

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ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

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This thesis explores the role of soil moisture conditions for controlling nutrient accumulation, carbon storage, and tree growth. Using an extensive soil and forest survey across a boreal forest landscape, the results presented in this thesis show significant decrease in organic layer soil C/N ratios and increased carbon stocks with higher soil moisture conditions. Tree growth potential decreased in the wettest parts of the landscape. This thesis provides a unique insight into the variation of boreal forest landscapes.

Johannes Larson received his doctoral education at the Department of Forest Ecology and Management, SLU, Umeå. He holds a Master of Science degree in Forestry from SLU, Umeå.

Acta Universitatis agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

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