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Ditches show systematic impacts on soil and vegetation properties across the Swedish forest landscape

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ABSTRACT

Novel mapping methods using AI have led to improved mapping of the extent of drainage systems, but the full scope of the effects of drainage on ecosystems has yet to be understood. By combining ditches mapped with remote sensing and AI methods with soil data from the Swedish Forest Soil Inventory, and vegetation data from the National Forest Inventory we identified 4 126 survey plots within 100 m of a ditch. The inventory data span across three biomes; the northern boreal zone, the hemiboreal zone, and the temperate zone. We explored if soils and vegetation close to ditches were indeed different from the surrounding landscape. The large number of plots spread widely across the Swedish forest landscape spanning different physiographic regions, climates, topography, soils, and vegetation made it possible to identify the general effect of drainage on soil properties, tree productivity, and plant species composition. We found a surprisingly large amount of ditches on mineral soils (50–70%, depending on the definition of peatlands). Forest growth was affected, with higher growth rates of trees closer to ditches, particularly Norway spruce. *Sphagnum* mosses – a key indicator of wet soils - were less common near ditches, where they were replaced by feather mosses. The soil bulk density was higher closer to ditches, as was the concentration of metals that are typically associated with organic matter (Al), while concentrations of metals with a lower affinity for organic material decreased toward ditches (Na, K, Mg). The results from mineral soils and peat soils often differed. For example, N and tree volume increased toward ditches, but on different levels for peat and mineral soils, while the thickness of the humus layer and *Pleurozium schreberi* cover showed opposite patterns for the different soils. Clearly, ditches have affected the entire Swedish forest landscape, driving it towards a drier, more spruce-dominated productive forested ecosystem and away from wetland ecosystems like mires and littoral areas along streams. Furthermore, the biogeochemistry of the soils and understory species cover near ditches have changed, potentially irreversibly, at least within human time frames, and have implications for restoration goals and the future of forestry.

1. Introduction

Soil drainage has been a common practice across northern Europe and parts of North America for centuries (Jakobsson, 2013). While ditching for agricultural purposes dates back to the medieval era (Jakobsson, 2013; Jacks, 2019), the first intense forest drainage period across Fennoscandia was in the 1930s when most of the ditches were hand-dug, followed by a second intense ditching period from the 1960s to the 1980s (Lindholm and Heikkilä, 2006) when ditches were dug using machinery (Peltomaa, 2007; Jacks, 2019). After the mid-1980s, drainage of new wetlands was essentially banned in the Nordic countries (Päivänen and Hånell, 2012). The forestry-related drainage has been particularly pronounced in Europe, impacting a minimum of 20% of peatland regions (Rydin and Jeglum, 2013). The most extensive drainage activities for forestry purposes have been observed in Russia and the Baltic States, resulting in the ditching of more than 13.5 million hectares of wetlands (Paavilainen and Päivänen, 1995). An estimated total of 1 410 000 ha had been drained for forestry in Sweden; two-thirds were classified as peatlands and one-third as wet mineral soils (Hånell, 1990) while in Finland, 5.5 million ha of forest land were drained, of which 4.5 million ha were peatlands (Peltomaa, 2007). Thus, in many northern countries, one of the most widespread forest management activities has been the drainage of wet soils to increase forest productivity (Laudon et al., 2022). In a recent survey of 11 study areas across Sweden (Paul et al., 2023) found that 87% of the channel length in the Swedish forest landscape were ditches, and when scaled up to the country level,

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their accumulated channel length was estimated to be approximately 1.2 million km (equivalent to 28 times around the world) (Laudon et al., 2022). The extent of these man-made systems has engineered our current "natural" landscapes, and they are now likely important components of the landscape in and of themselves. However, their potential for providing functions other than drainage is relatively underexplored and likely underestimated as traditionally, most research and conservation work focuses on natural habitats (Clifford and Heffernan, 2018; Koschorreck et al., 2020). However, with ditches dominating the makeup of the channel length in many boreal landscapes today, we can no longer ignore the potential importance of these constructed waterways. These drainage systems remain in the landscape in various functional states following centuries of land use management, mostly for forestry. Future management of these ditches could cause further impact regardless of whether they are improved by ditch cleaning, abandoned in a non- or semi-functioning state, or blocked to restore wetlands (Lõhmus et al., 2015; Bring et al., 2022). Nonetheless, it is unclear to what extent this drainage has impacted ecosystems on a landscape scale and what future management might do to cause other long-term effects (Laudon et al., 2022).

Most studies on the effects of drainage have been conducted at just one or a few sites, and even larger studies only include, at most, 50 sites (Laine et al., 1995a, Minkkinen et al., 1999, Nieminen et al., 2022). This has in part led to contradictory research results, which can be seen in the light of the great diversity of peatlands and wetlands (Laine et al., 1995b) as each site is unique in its own way, with different soils, topography, nutrient status, and vegetation (Laine et al., 1995a). In addition, of the studies that investigate forest drainage most have focused on peatland drainage while only a few studies focused on drained mineral soils (Sikström and Hökkä, 2016). Therefore, less is known about how the organic surface horizons on mineral soils have been affected by drainage. The purpose of forest drainage was to lower groundwater levels and improve soil aeration to enable afforestation of soils previously too wet for commercial tree species, increase forest growth in previously unproductive wet forests, enable reforestation following harvesting due to higher groundwater levels when transpiring trees are removed, or be used to stabilize forest roads (Lõhmus et al., 2015). A recent meta-analysis on the hydrological effects of ditching in previously glaciated terrain in temperate and boreal climates shows that the water table drawdown of a ditch at 1 m from the ditch was on average 43 cm (95% confidence interval 51 - 34 cm). However, the drawdown effect decreased exponentially with distance from the ditch and was reduced to 50% after 21 m (95% confidence interval: 11 - 64 m) (Bring et al., 2022). So, in essence, half of the drainage effect occurs within ca 20 m of a ditch. The change in hydrology has been shown in isolated case studies to impact soil morphology, soil chemistry, redox potentials, soil water chemistry, erosion, and ecology impacting the overall ecosystem function (Hayes and Vepraskas, 2000; Holden et al., 2004). In similar studies, ditching has also been found to change the plant species composition of the drained sites (Minkkinen et al., 1999, Lõhmus et al., 2015). Water table drawdown can also lead to compaction of the soils and peat subsidence (Minkkinen and Laine, 1998). The increased oxygen levels can increase organic matter mineralization, resulting in increased loadings of DOC and nutrients in waters draining ditched peatlands and increased terrestrial greenhouse gas (GHG) emissions (Nieminen et al., 2017; Asmala et al., 2019; Evans et al., 2021; Finer et al., 2021). Thus, how we choose to manage ditches today will have long-term effects on the hydrology, biogeochemistry, ecology, and greenhouse gas balance of the forest landscape (Laudon et al., 2022). But to what extent these patterns hold over across biomes and wide ranges in latitude as well as and can be generalized across peat soils and mineral soils, is unclear.

Previously, large-scale analysis of ditches could not be performed since ditch distribution could not be assessed at regional or country levels. For example, in Sweden, only 22% of the ditches were mapped on topographical maps (Flyckt et al., 2022). However, a novel way of mapping small-scale water channels (<6 m wide) using a deep neural network (Lidberg et al., 2023) was recently applied to map channels across all of Sweden (Laudon et al., 2022), most of which are ditches (87%; (Paul et al., 2023)). In this article, we use the entire country of Sweden to investigate if soil properties, plant species composition, and tree productivity close to ditches were different from the surrounding landscape and test if it was possible to detect the effects of ditches across different physiographic regions, with different climates, topography, soils, and vegetation. We combine channels mapped by remote sensing and AI with two national surveys in order to answer the following questions; 1) which soil types do ditches drain across the Swedish forest landscape? Do characteristics of 2) soil properties, 3) tree productivity, and 4) plant species composition close to ditches differ from the surrounding landscape?

2. Materials and methods

2.1. Study site – Sweden

Sweden encompasses three biomes across 15 degrees of latitude and 14 degrees of longitude (55–70° N, 11–25° E), from the boreal biome in the north to the hemiboreal transition zone and the temperate biome in the south of Sweden (Gustafsson et al., 2015). The climate is classified as warm summer continental or hemiboreal climates (Dfb) and subarctic or boreal climates (Dfc) (Beck et al., 2018). The country has an elevation and precipitation gradient from north to south, and from east to west, with annual precipitation ranging from 400 to 2100 mm (1961–1990). According to satellite data, the land cover in Sweden is dominated by forest, covering 69% of the country, followed by agricultural land (9%), open peatland (9%), grassland (8%), rock outcrops (5%), and urban land (3%) (Schöllin and Daher, 2019). The Quaternary deposits in Sweden are till soils 53%, thin soils and rock outcrops 18%, coarse sediments (sand–gravel–boulders) 8%, fine sediments (clay–silt) 6%, and other (ice, fillings, etc.) 1% (Ågren et al., 2022). Of the forested landscape, peat soils cover 22% (±4% depending on the definition) (Ågren et al., 2022). The dominating soil type across the country is Podzols, but more complex distributions of Histosols, Gleysols, Arenosols, and Regosols are also common (Olsson, 1999). The topogenous fens are the most prevalent wetland types in Sweden, followed by string mixed mires and string flark fens (Gunnarsson and Löfroth, 2009).

2.2. Remote sensing data

We utilized a novel digital ditch map available as open data (Laudon et al., 2022) to calculate the proximity to a ditch. The map shows ditches across all of Sweden extracted with a deep neural network, an Xception Unet (Lidberg et al., 2023). The deep learning model was trained on airborne laser scanning data with a last return density of 0.5–2 points m^{-2} and 1607 km of manually digitized ditches (Paul et al., 2023). A national digital elevation model with a resolution of 1 m (Terrain Model Download, grid 1 + (Lantmäteriet, 2023)) was used as input for the deep learning model. The ditch model had a recall of 82% and a precision of 63% with a Matthews correlation coefficient (MCC) of 0.72. This means that the ditch map used here contains 82% of the ditches in Sweden and that 63% of the ditch pixels belong to ditch channels (Lidberg et al., 2022). The detected ditch pixels were skeletonized into vector lines from which the Euclidian distance to the center of each survey plot was calculated (see Section 2.3 for national survey data).

To investigate our first question, 1) which soil types ditches drain, we investigated the Swedish Forest Soil Inventory plots within 20 m distance from ditches ($n = 867$) because previous studies found that half of the drainage effect occurs within ca 20 m from a ditch (Bring et al., 2022). To study the effect of the proximity to a ditch on 2) soil properties, 3) tree productivity, and 4) plant species composition we extracted field-inventoried plots from the databases with a distance to ditch ≤ 100 m ($n = 4\,126$). We limited ourselves to this distance because the hydrological drawdown effect of ditches has been shown to generally decrease exponentially with distance from the ditch and the effect of blocking of ditches on hydrology extends up to 80 m from the ditch (Bring et al., 2022). Hence, we classified areas in the range of $>$ 100 m away from ditches as the undrained, surrounding landscape and did not include them in our analysis; the resulting dataset of plots covers the whole Swedish forest landscape (Fig. 1).

2.3. National survey data

We used the most recent data available from the Swedish Forest Soil Inventory (SFSI) and the National Forest Inventory (NFI). Each plot is inventoried once every 10 years by the SFSI and every 5 years by the NFI (Stendahl et al., 2017). In our study, we used soil data collected between 2010 and 2019 and tree data collected between 2015 and 2019. If the whole plot was homogeneous, the center coordinate of the plot was used to establish the proximity to the ditch. For divided plots (when two or more distinct "land or forest types" are found within a plot and all are sampled) the centroid coordinate of the sub-plots was used for geolocation, for improved precision.

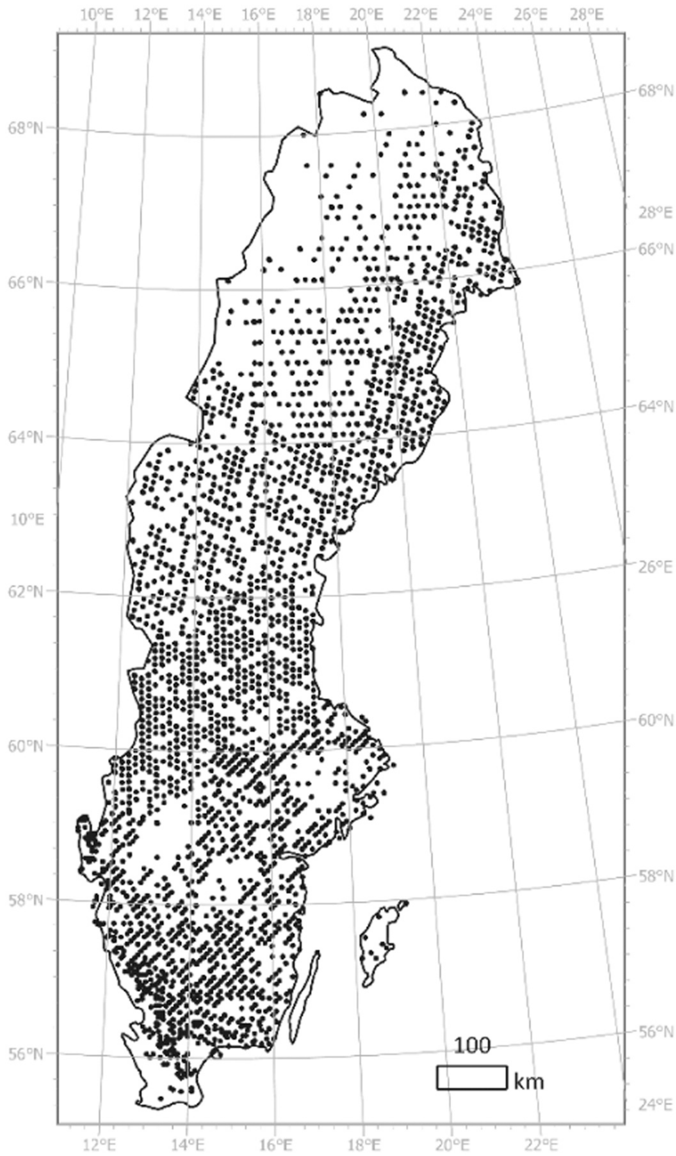

Fig. 1. Distribution of plots across Sweden that had both an H30 sample collected (see Section 2.3.1 for definition) and were located within 100 m of a ditch (n = 4 126).

2.3.1. Swedish Forest Soil Inventory (SFSI)

In this study, we focus on the organic soils, but we include both soils classified as strictly "peatlands" and the organic layer from mineral soil sites. Specifically, we selected all sites where a "humus sample 30 cm" (H30) had been collected from the database of sites (SLU, 2021). H30 samples were collected volumetrically with a humus corer (ca 100 mm in diameter - each corer is measured individually to control for any small variability in diameter) and were collected on half of all the NFI plots. The H30 sample is taken where the humus form is mor (type 1 and 2), moder, peaty mor, or peat and it is taken from the ground surface (excluding loose litter) to the depth of the humus layer but maximum 30 cm (SLU, 2019). For each site, soil characteristics were registered in the field and the thickness of the organic layer was measured. Quaternary deposits are generally determined at 20 cm depth in the mineral soil and divided into five classes; sediment with a high degree of sorting, sediment with a low degree of sorting, till, rock outcrop if no soil exists, or peat if the organic surface layer was thicker than 50 cm (SLU, 2019). Soil type was determined according to the international standard (WRB, 2015) in eight classes; Histosol, Leptosol, Gleysol, Podzol, Umbrisol, Arenosol, Cambisol, and Regosol. Humus form was classified according to depths of the H, Of, and Oh horizons in five classes; Mor type 1 is dominated by the Of horizon, while Mor type 2 is dominated by the Oh horizon, i.e., is more decomposed compared with Mor type 1 (SLU, 2019). If Oh-layer is $\geq$ 75% it is classified as Moder, a transition between mor humus and mull humus. Humus form is peat or peaty mor when the organic soils are wet and decomposition is low, usually dominated by the genus *Sphagnum*, brown mosses (*Amblystegiaceae* family) or *Polytrichum commune*. If the organic layer thickness was $\geq$ 30.5 cm it is classified as peat, otherwise it is peaty mor (SLU, 2019).

For the H30 samples, several samples from the same plot (up to a maximum of 9 samples) are mixed into one sample. Stones and larger roots ($>$ 2 mm) are removed, and the rest is ground and then sorted into coarse ($>$ 2 mm) and fine fraction ($<$2 mm), of which the fine fraction is analyzed. Lab analyses are conducted for bulk density and extensive soil chemical data resulting in 16 soil characteristics measured or calculated per plot; total carbon (C), total nitrogen (N), pH measured in water suspension (1:5–1:25 depending on bulk density), exchangeable Ca, Mg, K, Na, Mn, and Al as well as total acidity (Stendahl et al., 2017). Exchangeable cations are measured using ICP extracted using 1 M NH_4-acetate, except Al which was extracted using 1 M KCl. C and N were measured by combustion using LECO CNS-1000. Total acidity was determined by titration of 1 M NH_4-acetate (pH=7) with an automated system from Metrohm (Titrino 719 S and 721 Net Titrino) controlled by the program TiNet 2.1.

The total cation exchange (CEC_t) is determined at pH 7, but since Swedish organic soils often have a much lower pH, we instead calculated the effective cation exchange capacity at the soil pH (CEC_{eff} (mekv kg ds^{-1})) as suggested by the SFSI:

$$CEC_{eff} = \sum(Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, Al^{3+}) \qquad \text{Eq. 1)}$$

The effective base saturation (BS_{eff} (%)) equals the base saturation at the soil pH and SFSI uses the following equation as a proxy for BS_{eff}:

$$BS_{eff} = \frac{100 \times \sum(Ca^{2+}, Mg^{2+}, K^{+}, Na^{+})}{\sum(Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, Al^{3+})} \qquad \text{Eq. 2)}$$

The relative importance of aluminum in the effective cation exchange was calculated by the ratio:

$$\frac{Al}{CEC_{eff}} = \frac{Al^{3+}}{\sum(Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, Al^{3+})} \qquad \text{Eq. 3)}$$

2.3.2. National forest inventory (NFI)

To understand how tree productivity and plant species composition are influenced by drainage across the Swedish landscape, we used data collected from the National Forest Inventory (NFI) (SLU, 2021). Fifteen characteristics of tree species coverage or growth, and percent cover of 65 understory plant species cover were used in our analyses (Appendix 1). Trees were inventoried on plots with a 10 m radius. The diameter of trees at breast height (1.3 m) was calipered (within 3.5 m from the center, each tree ≥ 4.4 cm is calipered, outside of that radius, each tree ≥ 10 cm is calipered), and the average height of the trees for the plot is estimated based on a random number of measurements in the plot. From the diameters, the basal area was calculated, defined as the total cross-sectional area of all stems in the 10 m plot measured at breast height (1.3 m). Volume was calculated using the correlation between diameter and height, and volume for each tree species. The age of the trees was estimated by coring nearby representative trees for the plot and counting the tree rings. Growth ($m^3\ ha^{-1}\ yr^{-1}$) was calculated based on the annual tree ring measurement data.

In addition to the tree species, the understory plant species composition was included in our analyses. The understory species data are inventoried on the same plots with the same center as the tree inventory but use a circle with a radius of 5.65 m, which gives 100 m^2. For each species, or group of species, the areal cover of the species in the understory layer was calculated as the percent coverage of the plot (or subplot, where applicable). For the bottom layer - 11 species/groups were registered, for the field layer - 53 species/groups were registered, and for the shrub layer - one species was recorded. A complete list of inventoried understory species is found in Appendix 1, (in the results, we only report the species with a significant change with proximity to ditch).

2.4. Statistical analysis

As the hydrological drawdown effect of the ditches has been shown to be exponential in relation to the distance from the ditch (Bring et al., 2022) we assumed that any effect on soils and surrounding vegetation would follow this relationship. Hence, we used the curve estimation procedure in IBM SPSS Statistics 27 and selected a logarithmic model whose equation was $Y = C + (B1 * \ln(x))$. Where Y was our different response variable (e.g., percent cover of *Sphagnum* spp.), C and B1 are constants and x was the proximity to ditch (m). In total, we tested the relationship between proximity to ditch and 96 response variables that included 16 soil properties, 15 tree productivity characteristics, and 65 plant species coverage variables. When we separated these by soil types, we performed 1248 regression analyses in total. In 186 cases, there was a significant logarithmic relationship with distance to ditch ($p \leq 0.05$). Some relationships were not reported because there were fewer than 200 observations from the analysis and these proved to be sensitive to outliers; specifically, we did not include results for soil types that were; moder, rock outcrops, Gleysol, Umbrisol, Arenosol, and Cambisol.

While we present the regression lines for all 186 individual significant relationships (Figs. 3–5), in the text we will aggregate the results and mostly discuss 'peat soils' and 'forest soils', respectively. By 'peat soil' we mean any of the four investigated peat definitions: 1) Peat according to the Geological Survey of Swedens's quaternary deposit classification if the organic layer is ≥ 50 cm (n = 850). 2) Histosol according to (WRB, 2015) if the organic layer is ≥ 40 cm (n = 1006). Peat according to humus form if the organic layer is ≥ 30.5 cm (n = 1028). 4) Peaty mor according to humus form if the humus layer is peat-like but ≤ 30.5 cm (n = 526). By 'forest soils' we mean any of the definitions of the organic layer of the mineral soils i.e., divided by quaternary deposits into; till (n = 2188), sediment with high (n = 560) and low (n = 332) degree of sorting. Humus type; mor 1 (n = 1813) & 2 (n = 530) and soil type WRB; Podsol (n = 1261), Leptosol (n = 299) and Regosol (n = 1228).

3. Results

3.1. Which soil types do ditches drain across the Swedish forest landscape?

Between 30–50% of the study plots occurred on peat soils depending on the definition of 'peat,' with the remainder draining mineral soils, or what we here call 'forest soils' (Fig. 2). If peat is defined according to quaternary deposits (i.e. ≥ 50 cm organic layer thickness) 30% of the ditches drain peat, but if it is defined as the soil type Histosol (i.e. ≥ 40 cm organic layer thickness) 35% of the ditches drain peat. If peat is defined as humus forming peat and peaty mor (no thickness restriction) 50% of the ditches drain peat, meaning that 50–70% of the ditches drain what has typically been named mineral soils, what we here call 'forest soils' (Fig. 2).

3.2. Do soil properties close to ditches differ from the surrounding landscape?

Proximity to ditch explained between 0.03–9.9% of the total landscape variability of soil properties (Table A. 1–4). Soil properties near ditches were significantly different compared to the surrounding landscape for all soils (black, total line) except for Ca, Mg, TA, and CEC_{eff} (Table A. 1). The thickness of the organic layer decreased towards the ditch on 'peat soil', while it increased on the 'forest soils' and for the ditches in general (Fig. 3a). The bulk density increased toward ditches; both 'peat soils' and 'forest soils' show the same pattern, though the bulk density was lower for 'peat soils' than for the 'forest soils' (Fig. 3b). C:N ratio decreased toward ditches, for both 'peat soils' and 'forest soils' (Fig. 3c). The carbon content decreased toward ditches mostly on 'forest soils' (Fig. 3d), while the nitrogen content increased toward ditches on both 'peat soils' and 'forest soils' (Fig. 3e). pH increased (Fig. 3f) while the total acidity (Fig. 3g) decreased towards ditches on 'forest soils'. The different cations showed diverse patterns. K decreased toward ditches for 'peat soils' and 'forest soils' (Fig. 3h), while Mn (Fig. 3i) and Mg (Fig. 3j) decreased toward ditches on 'peat soils' and Na (Fig. 3k) decreased toward ditches on 'forest soils'. Al (Fig. 3l) was the only cation that increased toward ditches, and only on 'peat soils'. Ca and the effective cation capacity (CEC_{eff}) did not show a significant relationship with distance to ditch and is not shown in Fig. 3. The effective base saturation (BS_{eff}) decreased towards ditches (Fig. 3m) for the total dataset (black line) and on 'peat soils', while the relative importance of Al in the effective cation exchange increased for the total dataset (black line) and on 'peat soils' (Fig. 3n).

3.3. Does tree productivity close to ditches differ from the surrounding landscape?

Total basal area ($m^2\ ha^{-1}$) (Fig. 4a), total volume ($m^3\ ha^{-1}$) (Fig. 4b) and total growth of all trees ($m^3\ ha^{-1}\ yr^{-1}$) (Fig. 4c) of the 10 m plot increased toward ditches, on both 'peat soils' and 'forest soils', while the average tree height (m) only increased on 'peat soils' (Fig. 4d) and tree age (yr) (Fig. 4e) decreased on 'peat soils'. When looking at the individual tree species the results differed. The results for Scots pine (*Pinus sylvestris*) indicated a decrease in volume (Fig. 4f) and growth (Fig. 4g) toward ditches on 'forest soils'. Norway spruce (*Picea abies*) showed an increase in volume (Fig. 4h) on 'forest soils' and an increase in growth toward ditches on both 'peat' and 'forest soils' (Fig. 4i). Birch (*Betula pendula, Betula pubescens*) showed an increase in volume (Fig. 4j) and growth (Fig. 4k) toward ditches on both 'peat soils' and 'forest soils'. For other broadleaves (aspen, oak, beech etc.) the results indicate an increased volume (Fig. 4l) and growth (Fig. 4m) closer to ditches on 'forest soils'. Only the volume and growth of the non-native Lodgepole pine (*Pinus contorta*) did not display a significant relationship with distance to ditch and is not shown in Fig. 4.

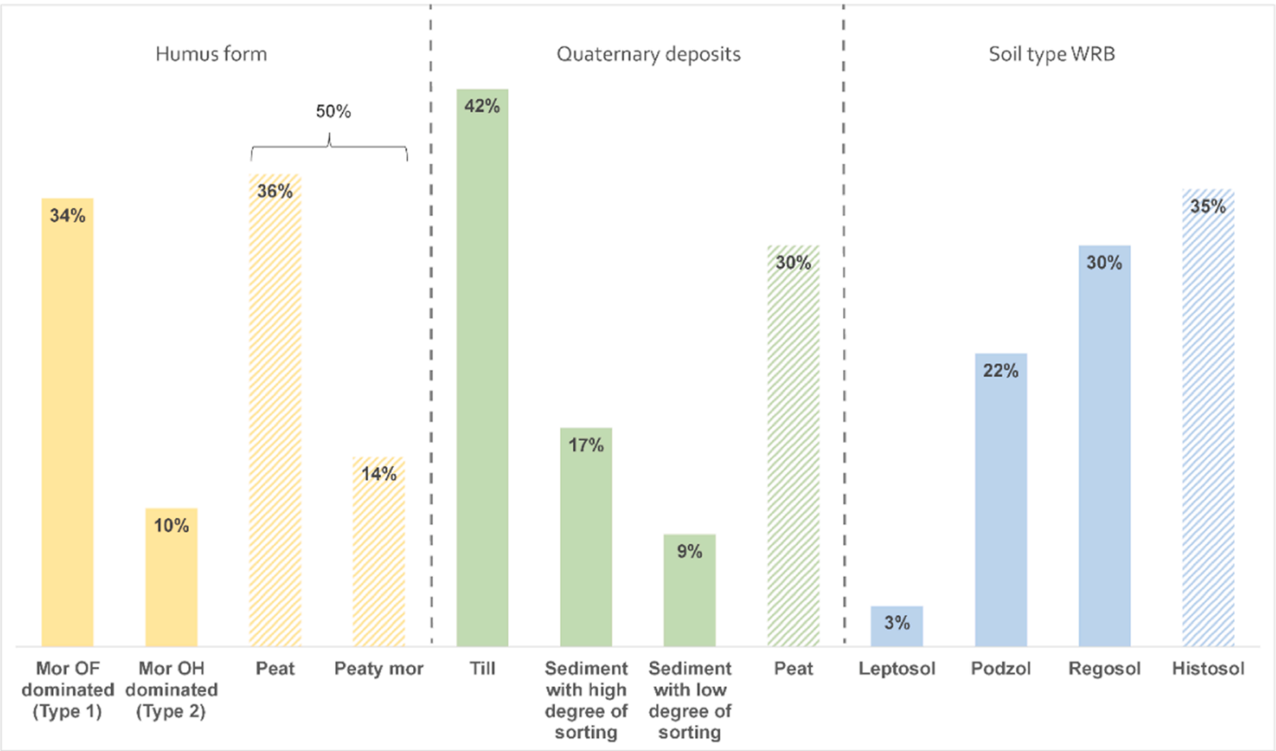

Fig. 2. Relative distribution of sites within 20 m of a ditch (n = 867), grouped by different soil classifications. The 'peat' soils are indicated by dashed bars. The soil classification in the left panel includes all humus forming peat and peaty mor (no thickness restriction), the middle panel is the quaternary deposits definition (≥50 cm organic layer thickness) and in the right panel are the World Reference Base (WRB) for soil resources definitions (≥40 cm organic layer thickness).

3.4. Does understory species coverage close to ditches differ from the surrounding landscape?

Of the investigated 65 understory species (listed on the first page of the Appendix 1), only eight showed significant changes with proximity to ditches, of which four were moss species. *Sphagnum* spp. showed the largest change in species coverage with distance to ditch, which on 'peat soils' decreased from ca 65% coverage 100 m from a ditch to < 20% coverage close to ditches (Fig. 5a). The other mosses showed diverse patterns; *Hylocomnium splendens* decreased towards ditches on 'forest soils' (Fig. 5b). *Polytrichum commune* increased towards ditches on both 'peat soils' and some 'forest soils' (Fig. 5c). *Pleurozium schreberi* increased towards ditches on 'peat soils' while it decreased towards ditches on 'forest soil' (Fig. 5d).

Two berries showed opposite patterns, bilberries (*Vaccinium myrtillus*) decreased towards ditches on 'forest soils' (Fig. 5e) while raspberry (*Rubus ideaus*) increased towards ditches on 'forest soils' (Fig. 5f). Grasses (broad-leafed *Poaceae spp.)* increased towards ditches on 'peaty mor' (Fig. 5g) and the group NMLWS = "Non-Moisture Loving short Wood-rush (*Luzula*) and Sedges (*Carex)*" increased towards the ditches on 'forest soils' (Fig. 5h).

4. Discussion

4.1. Study design

Despite the fact that the ditches range in age, depth, and functioning state and that each ditch is draining its unique landscape with different soils, topography, nutrient status, vegetation, and land management, the sheer number of study sites (n = 4 126) across the whole Swedish forest landscape made it possible to identify the general effect of ditches on soils and vegetation. However, it should be noted that even if the proximity to ditch can only explain about 0.03–9.9% of the total landscape variability of the evaluated variables (Table A. 1–4), this can be seen as substantial given the geographical coverage and vast variability in the underlying data. A commonly used approach to studying ditches is to compare ditched sites with nearby non-ditched sites (Laine et al., 1995a; Maanavilja et al., 2014), usually in a pairwise approach. Ditched sites and non-ditched sites that are close to each other are likely to have similar environmental and edaphic conditions, which reduces the potential for confounding factors. However, here we study systematic changes with distance to ditch environmental and edaphic conditions. While it is likely that such effects are due to the drainage effect of ditches, there could also be confounding effects that the drainage ditches were placed in different landscape types than sites further away from ditches. However, including localized effects within just 100 m and weighing sites closer to ditches more (using the logarithmic relationship), we minimize the risk of such confounding effects, while accounting for the large random variance induced by the large spatial scale.

The uncertainty in the AI-detected ditches underlying this study was reported on a pixel-by-pixel level (Lidberg et al., 2022). This means that parts of the uncertainty are due to uncertainties of which pixels along the sides of the ditches should be marked as ditches, while other uncertainties include misclassification of streams, gullies, and tracks as ditches. By skeletonizing the ditches into vectors, and systematically calculating the distances to the center of the ditch, we can disregard the uncertainty along the borders. Hence, on a "ditch level", the map captures more of the drainage systems than the numbers reported suggest. So while some of the detected channels may be mislabeled natural channels, or potentially modified natural channels, we believe these are too few to affect the overall results. Hence we assume that the general patterns found in this article are representative of how ditching has affected the forest landscape.

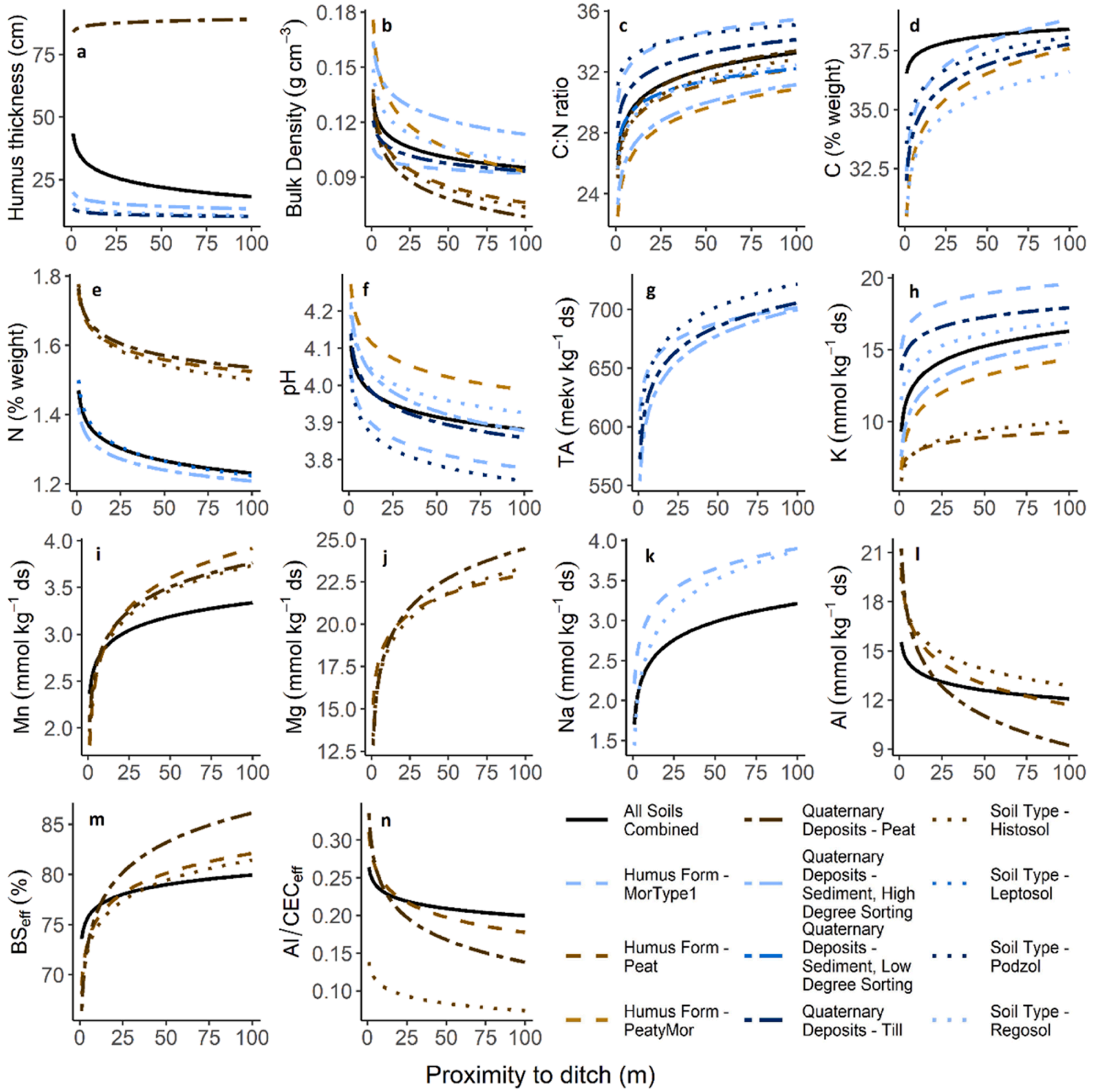

Fig. 3. Relationship of the 14 significant soil properties (a-n) with proximity to ditch, separated by soil types. 'Peat soils' are colored in brown hues and 'forest soils' are colored in blue hues. If a soil type is not shown on a given panel, it was tested, but not statistically significant ($p \leq 0.05$). The statistics for Fig. 3 are found in (Table A. 1–4).

4.2. Which soil types do ditches drain across the Swedish forest landscape?

Between 50–70% of the drainage ditches are found in 'forest soils,' which are mineral soils (Fig. 2), depending on the definition of 'peat soils.' This number is higher than reported by (Hånell, 1990) who claimed that just one-third of the drained soils in Sweden are wet mineral soils. By the end of the 1920s, there was already systematic research on the drainage of mires for forest production. For peatlands, it was established that the nutrient status determined the success of drainage from a forest production perspective. In practice, nutrient status was often determined by inspection of the surface vegetation, the peat type, and the mineralogical composition and biological structure of the surrounding solid ground. The slope of the peat and the thickness of the peat were also considered for selecting sites suitable for transitioning peatland into forest land. Malmström (1928) argued for dividing peatlands into minerogenic, ombrogenic and soligenic peatlands according to von Post and Granlund (1926). Peat margins with more shallow peat layers represented peat with higher nutrient availability (Ehnvall et al., 2023) and better physical root support from the underlying mineral soil with biotic and abiotic immobilization of plant nutrients; such areas were therefore drained to a higher degree (Korpela and Reinikainen,

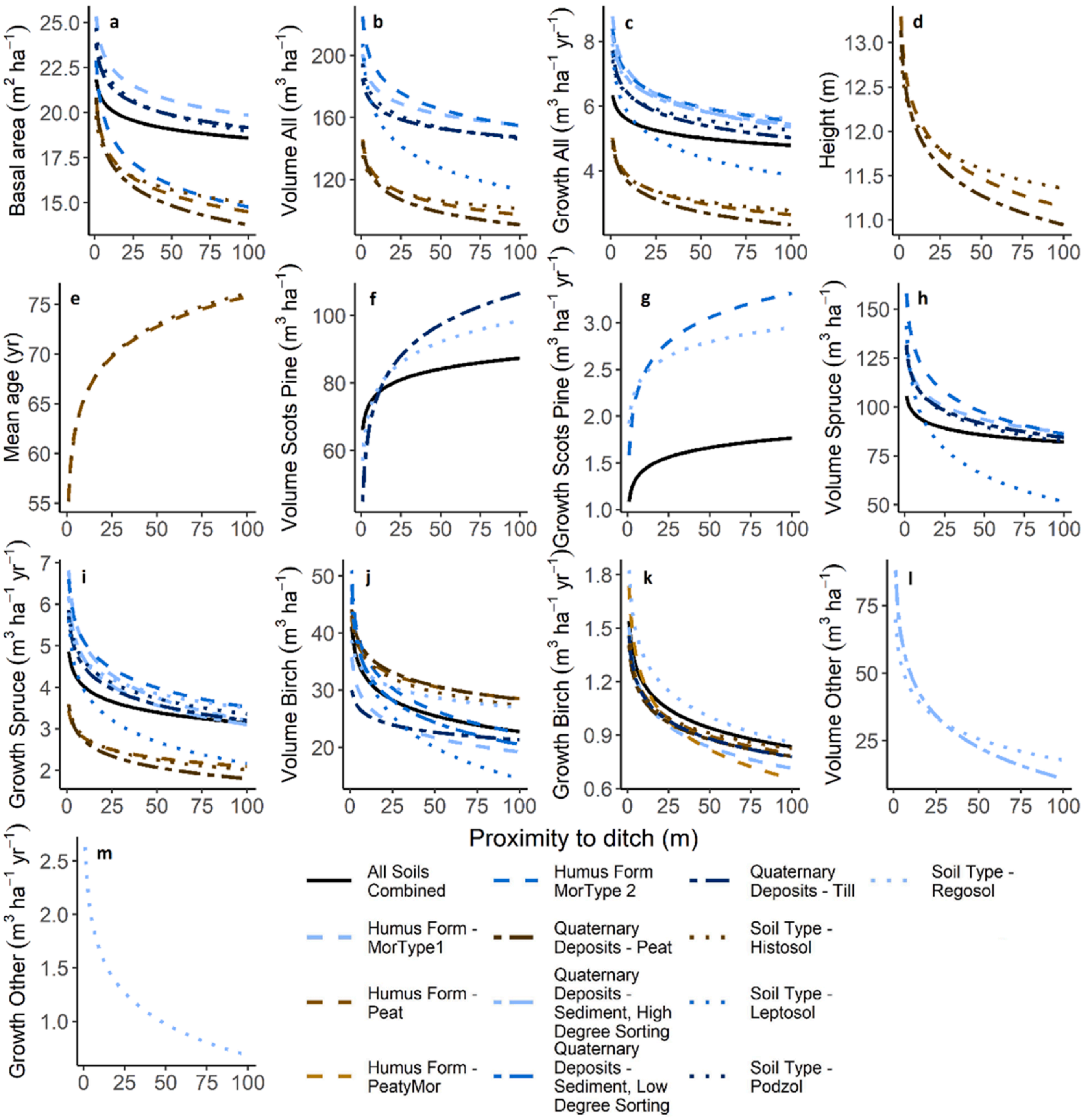

Fig. 4. Relationship of the 13 significant tree properties and growth with proximity to ditch (a-m), separated by soil types. 'Peat soils' are colored in brown hues and 'forest soils' are colored in blue hues. If a soil type is not shown on a given panel, it was tested, but not statistically significant ($p \leq 0.05$). The statistics for Fig. 4 are found in (Table A. 1–4).

1996). This could potentially explain why, on average (Fig. 3a), ditches were found where the organic layer thickness was ca. 50 cm. The 'forest soils' drained were the wetter soils with lower decomposition and, relatively speaking, thicker organic layers (Ågren et al., 2022) but the 'peat soils' that were drained were the shallower peatlands and edges of peatlands (Fig. 3a).

4.3. Do soil properties close to ditches differ from the surrounding landscape?

Another explanation of the observed pattern of more shallow peat layers closer to ditches (Fig. 3a) is peat subsidence (Hillman, 1992). Rapid peat subsidence in the short term after drainage is caused by drainage, peat compaction, shrinkage, and consolidation, while long-term effects (>20 years) are caused by the oxidation of organic materials (Liu et al., 2020). This subsidence, regardless of cause, may explain the observed increase in bulk density (BD), which was observed

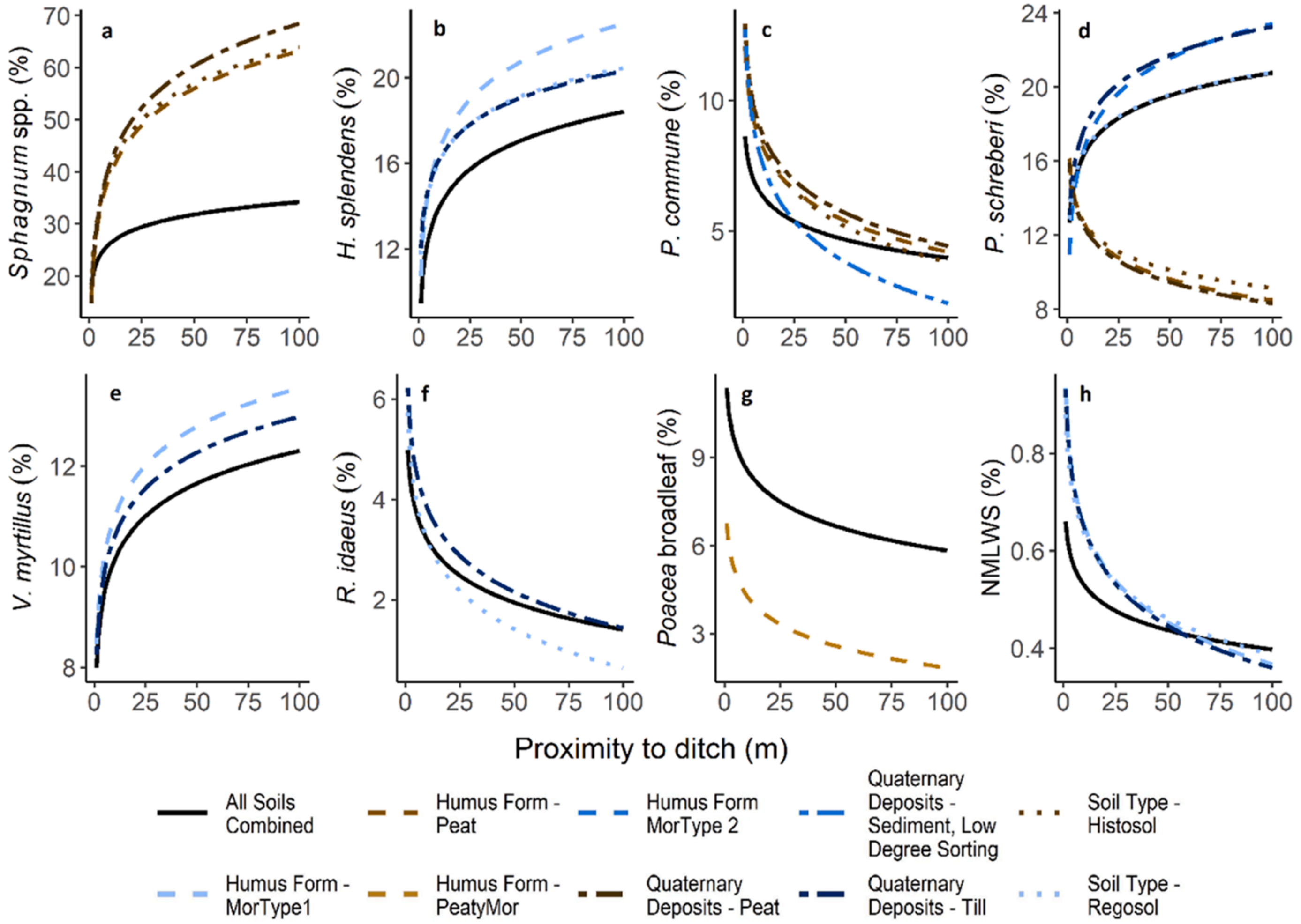

Fig. 5. Relationship of plant species coverage (percent cover) with proximity to ditch for the 8 significant species/groups (a-h), separated by soil types. Specifically, we show mosses (Sphagnum spp., Hylocomnium splendens, Polytrichum commune, Pleurozium schreberi), broad leafed grasses (Poaceae spp.), * NMLWS = "Non-Moisture Loving short Wood-rush (Luzula) and Sedges (Carex) species", bilberries (Vaccinium myrtillus) and raspberry (Rubus ideaus). 'Peat soils' are colored in brown hues and 'forest soils' are colored in blue hues. If a soil type is not shown on a given panel, it was tested, but not statistically significant ($p \leq 0.05$). The statistics for Fig. 5 are found in (Table A. 1–4).

for both 'peat soils' and 'forest soils' (Fig. 3b). Farthest from the ditch, peat BD was ca 0.07 g cm^{-3}, similar to the BD of undrained peatlands 0.09 ± 0.03 g cm^{-3} found by Liu et al. (2020). While close to ditches, BD was 0.13 g cm^{-3}. The BD of forest soils was generally higher ranging from ca 0.10 to 0.16 g cm^{-3}. However, we believe that one should be careful in interpreting the results of the changes in the thickness of the organic layer and BD as purely a result of subsidence through compaction and oxidation of organic material. For example, an increase in organic matter inputs reflecting increased productivity and plant functional types may also result in increased peat BD (Minkkinen et al., 1999, Laiho, 2006). Also, according to a national field inventory of ditches across all of Sweden (n = 2188), the mean depth of a ditch was 58 ± 44 cm (Flyckt et al., 2022). With an average thickness of the organic layer near ditches in the order of 45 cm (Fig. 3a), many ditches were thus dug through the organic layer and into the mineral soil. The heavier mineral soil particles would have been placed on the side of the ditches on top of the organic soils, and over time, has likely been incorporated into the organic soils. Also, after the ditches were dug, hydrological disturbances such as flooding and ice scour effects could have contributed to more mineral particles in the organic layer closer to ditches (Luke et al., 2007). Collectively, a number of different processes can explain the higher BD of organic soils near ditches (especially since we fit a logarithmic relationship with larger changes closer to ditches), but the broad scale of our data does not allow for distinguishing this further.

Further evidence that suggests that mineral soil has been mixed into the peat or humus layer close to ditch is the comparably low C-contents. Peat and soil organic matter typically have a C content of 50–65% (Öquist et al., 2009; Loisel et al., 2014), depending on the degree of oxidation, although pure Sphagnum peat may have C contents of 46% (± 4%) (Loisel et al., 2014). Our observed C-contents were consistently below 40%, and in some cases as low as 30% (Fig. 3d), further indicating a fairly large proportion of mineral soil particles in the H30 samples. However, the overall regression line for C-content is comparably high and the significant regression lines are dominated by sites on mineral soils and peaty mor, with systematically lower C contents compared to the overall average. Consequently, the significant decrease in C content observed in site classes belonging to our "forest soil" classification may not be relevant for, e.g. histosols or peat matrixes in general, which did not show significant relationships across the transects. Even if it is tempting to interpret reduced C-contents in humus layers and peat adjacent to drainage ditches as indicative of increased decomposition rates and loss of soil C, this pattern can be caused and is easily confounded by other variables.

Gradients of increasing concentrations of N from upland areas towards channels and streams are frequently observed in forested catchments (Blackburn et al., 2017). This may be attributed to, for example, the relocation of nutrients from upland areas to riparian zones. Drainage of inundated areas with organic soils may release N due to increased mineralization exacerbating this effect due to drainage. Consequently, the increased N closer to the ditches on both ‘peat soils’ and ‘forest soils’ (Fig. 3e), is a likely driver of the increased productivity observed for many plant species.

N_2O is the strongest greenhouse gas from organic soils. Land use has a strong effect on N_2O emissions, where cropland and agricultural soils have the highest emissions (Leppelt et al., 2014). In the forest landscape, emissions from drained peatlands have been found to increase exponentially for nutrient-rich peatlands (at C:N ratios below 20), and the highest emissions were found on previous agricultural soils (Klemedtsson et al., 2005). The best management practice for rewetting peatlands is therefore to restore nutrient-rich sites, where N_2O emissions can decrease to even below undrained levels during the first 20 years after restoration (Minkkinen et al., 2020). An interesting observation in our study is that the C:N ratios decreased toward ditches, for both ‘peat soils’ and ‘forest soils’ (the black total curve decreased from 33 to 26) (Fig. 3c). Varying groundwater levels near ditches during drying/-rewetting events can create “hot moments” and “hot-spots” for N_2O emissions (Leppelt et al., 2014; Minkkinen et al., 2020). Whether the detected local increase in nutrient status near ditches (indicated by the decrease in C:N ratio) contributes to this local effect of “hot-spots” and “hot moments” in the same way as naturally nutrient-rich peatlands or fertilized sites (Minkkinen et al., 2020), or, if there are other controlling mechanisms, needs to be investigated further.

The fact that pH increased towards ditches (Fig. 3f) while the effective base saturation (BS_{eff}) decreased towards ditches (Fig. 3m), can seem counterintuitive. However, $Al(OH)_3$ is not stable and weathers into soluble Al^{3+} (Löfgren et al., 2015) under the pH levels of Swedish ‘forest soils’ and ‘peat soils’ that are on average 3.8–4.2 (Fig. 3f). The organically bound Al^{3+} can be considered to be a non-acidic cation having similar properties to base cations, and will act as a base at these pHs instead of an acid (Skyllberg, 1999; Skyllberg et al., 2001). Hence, cation exchange with Al^{3+} could be responsible for driving the increase in pH (Fig. 3f). The fact that the relative importance of Al in the effective cation exchange (Fig. 3n) increases toward the ditches lends support to this idea. However, while these patterns were true for the total dataset, the division of ‘forest soils’ and ‘peatland soils’ show discrepancies (Fig. 3f, l, n). High exchangeable Al and low base cations have also been found in other organic soils in Sweden (Skyllberg, 1994) and Norway (Mulder et al., 1991). However, the increase in pH towards ditches could also be related to the changes in litter composition and tree species planting experiments have shown that e.g. Scots pine litter induces more acidic conditions as compared to birch (Segura et al., 2019). The increased tree volume close to ditches (Fig. 4b) also means that soils near ditches receive more litter input from trees. A Finnish study has shown that tree litter input on drained soils changes the litter type composition and can greatly change its chemical quality at the community level, over decades (Straková et al., 2010).

Al originates from the weathering of mineral soils. Two simultaneous processes likely explain the increase in Al toward ditches on ‘peat soils’ (Fig. 3l). One is local weathering from the suggested higher degree of mixing of mineral soils into the organic soils close to ditches as discussed above. Secondly, this is controlled by the different metals’ affinity for organic material which is essential for understanding their transport and spatial variability in the boreal landscape (Lidman et al., 2014). The increase in Al (Fig. 3l) and the decrease in other metals such as K, Na, Mg & Mn (Fig. 3h-k) towards ditches can be explained by the high affinity of Al (ca 70%) and the low affinity (ca 0.1–4%) of K, Na, Mg leading to different biogeochemical enrichment or removal processes by water draining toward the ditches (Lidman et al., 2017). Hence, the increase in Al (Fig. 3l) could also be due to an enrichment in the organic materials (Fig. 3a) with a strong affinity for Al^{3+}, where the Al originates either from local weathering (Skyllberg, 1994, 1999), or has been laterally transported from upland soils (Lidman et al., 2017). It has been suggested that plant-fungi communities may also actively use Al alkalinity in organic soils to increase pH to stimulate microbial degradation of soil organic matter in order to increase bioavailable N in forest soils (Clarholm and Skyllberg, 2013). This is in line with the biogeochemical changes in soils closer to ditches (Fig. 3). In addition, the patterns for Mn (Fig. 3i) could also be driven by redox potentials as Mn is sensitive to this (Lidman et al., 2014). Some drained sites may also have been fertilized, likely with NPK in the north and PK in the south where N mineralization is faster (Sundström et al., 2000), or using biofuel ash (Hånell and Magnusson, 2005). To summarize, soil properties in drained areas across Sweden have likely been influenced by a combination of soil mixing when the ditches were dug into mineral soils, subsidence, increased decomposition, changes in tree species and understory species which affect litter quality, different management strategies including potential fertilization of peatlands, but, it is difficult to evaluate the relative importance of these processes.

4.4. Does tree productivity close to ditches differ from the surrounding landscape?

Forest ditches were dug with the primary goal of increasing forest volume and growth, and Swedish ditches have been successful. Malmström (1923) predicted that ditching of forested wet soils (“sumpskogar” in Swedish) could increase the growth by 3–4 m^3 ha^{-1} yr^{-1}. According to Swedish NFI data there has been a steady increase in tree growth from an estimated 3.2 m^3 ha^{-1} yr^{-1} in 1923 to 5.2 m^3 ha^{-1} yr^{-1} in 1992 (Elfving et al., 1996), which continued to increase until 2010 (Roberge et al., 2023). Our study showed that as of the last NFI measurement, tree growth increased from 2.0 to 2.4 m^3 ha^{-1} yr^{-1} towards ditches on ‘peat soils’, and increased from 2.1 to 3.8 m^3 ha^{-1} yr^{-1} towards ditches on ‘forest soils’ (Fig. 4c). This suggests that ditching of the Swedish forest landscape can explain a substantial part his overall increase in growth over time. In addition, the standing volume also increased towards ditches, from ca 100 to 140 and 160 to 200 (m^3 ha^{-1}) on ‘peat soils’ and ‘forest soil’, respectively (Fig. 4b), likely as a result of the increased growth. All species except for Scots pine had higher volume and growth closer to ditches. Norway spruce had the highest volumes (Fig. 4h) and the highest increases in growth toward ditches (Fig. 4i), which supports the concept of ‘sprucification’ of the Swedish landscape (Kritzberg et al., 2020), found during 1926–2015 when Norway Spruce dominated the total volume of trees in Sweden (Roberge et al., 2023). Furthermore, nitrogen concentrations were higher closer to ditches, suggesting increased net mineralization rates of nutrients (Fig. 3e). This is similar to results from Nieminen et al. (2022) who found that tree stand volume was positively correlated with the N and P concentrations discharged from particularly sites with deep peat (>50 cm). The lowered soil water levels due to a combination of the drainage effect of the ditch combined with the higher tree volume leading to more evapotranspiration results in lowered soil water levels, likely leading to enhanced aerobic mineralization of the organic soils (Nieminen et al., 2022). However, whether the higher N concentrations closer to ditches (Fig. 3e) reflects bioavailable N is unknown as the N cycling of the boreal forests (Sponseller et al., 2016) and boreal peatlands (Limpens et al., 2006) are complex. The million km of ditches in Sweden have likely drastically changed stand-level conditions controlling tree growth and thus the forest of the entire landscape, but mainly within 20–25 m of the ditches, as the hydrological drawdown effect of ditches is highest within those distances (Bring et al., 2022). The fact that the growth and volume of Scots pine decreased towards ditches on mineral soils (Fig. 4f, g) is a bit surprising. On peatland soils, Scots pine forests have been shown to grow better after ditching or ditch cleaning (Ahti et al., 2008). Conceivably, our results could be an effect of increased shading from other trees (Fig. 4h, j, l), other controls by soils and ground vegetation (Kuuluvainen et al., 1993), or different forest management practices around thinning and planting, but these are not possible to determine in our present study. Scotts Pine has surpassed Norway Spruce as the dominating tree species in Sweden today (measured as total volume) (Roberge et al., 2023). Given our results that

Pine showed a decrease in growth and volume towards ditches on mineral soils, perhaps this implies a reduced overall need for protective ditching and ditch cleaning on such soils in the future. But, this needs to be verified with other studies before we can draw clear conclusions. Future research should explore to what extent drainage in itself or in combination with forest management has driven the growth trends for spruce and pine.

4.5. Does understory species coverage close to ditches differ from the surrounding landscape?

Similar to other studies, the largest species cover change with distance to ditch occurs in the moss layer (Paal et al., 2016). The *Sphagnum* mosses showed the largest change in species coverage with the distance to ditch, decreasing from ca. 65% to < 20% coverage on 'peat soils' (Fig. 5a). This is to be expected as most *Sphagnum* spp. are highly specialized to growing on mires with a high water table (Paal et al., 2016), *Sphagnum* is sensitive to the groundwater level and drainage has been shown to decrease the *Sphagnum* coverage while rewetting has been shown to increase the *Sphagnum* coverage (Maanavilja et al., 2014). In agreement with other peatland drainage studies in Finland, *Sphagnum* mosses in drained areas get replaced by feather mosses, characteristic of the forest landscape such as *Polytrichum commune* (Fig. 5c), *Pleurozium schreberi* (Fig. 5d) (Laine et al., 1995a; Jaatinen et al., 2007; Kangas et al., 2014) on 'peat soils'. *Hylocomium splendens* have also been shown to increase on drained fen mires (Laine et al., 1995a; Kangas et al., 2014), however, in our study, we saw no increase in *H. splendens* on 'peat soils'. Instead we observed a decrease in both *P. schreberi and H. splendens* on 'forest soils' (Fig. 5d, b), which is surprising as *H. splendens* prefer the more shaded areas provided by a denser canopy (Tamm, 1964) and as the volume of trees, and thus shading, increase near ditches (Fig. 4b), this should be suitable habitat. Both of the feather mosses, *P. schreberi* and *H. splendens* can fixate nitrogen (Zackrisson et al., 2009; Stuiver et al., 2015), and the increase in *P. schreberi* towards ditches on 'peat soils' (Fig. 5d) could help explain the increasing N towards ditches on 'peat soils' (Fig. 3e). Some *Sphagnum* species can also fixate nitrogen (Leppänen et al., 2015) under certain conditions, but, since *Sphagnum* is not registered at a species level, we cannot say if this process also contributes to the observed N increase towards ditches. On peaty mor, which constitutes shallow organic peat soils with a high connectivity to the mineral soils, grasses (broad leafed Poaceae) increased towards ditches (Fig. 5g), while on 'forest soils' the group NMLWS = "Non-Moisture Loving short Wood-rush (*Luzula*) and Sedges (*Carex*) species" increased towards the ditches (Fig. 5h).Table A. 2.

While it has been known for a long time that bilberry (*Vaccinium myrtillus*) suffers after nitrogen fertilization and clearcutting (Veijalainen, 1976), the effect of ditches was not studied until recently when it was found that ditching increased the coverage of bilberry on bogs in Estonia (Lõhmus and Remm, 2017). Our study differs from theirs in that across Sweden, we could find no significant effect on bilberry coverage on peatlands while we observed a decrease toward ditches on 'forest soils' (Fig. 5h). Raspberry (*Rubus idaeus*) on the other hand, increased towards ditches on 'forest soils' (Fig. 5f), in agreement with a Finnish study claiming that after forest ditching in spruce forested peatlands *R. idaeus* appears soon after and gives a very good yield for many years (Veijalainen, 1976). Table A. 3,Table A. 4.

5. Conclusions

Swedish soils were drained more than 100 years ago with the primary goal of increasing forest volume and growth. Our results show a significant increase in forest growth, particularly Norway spruce, closer to ditch channels, a relationship that was only speculated in previous studies. Depending on the definition of 'peat soils' (i.e. from ≥ 50 cm organic layer to no thickness restriction), between 50–70% of the drainage ditches are found in 'forest soils,' i.e. mineral soils. Further, our results show that *Sphagnum* mosses in drained areas are being replaced by feather mosses. We also observed a pattern of more shallow peat layers closer to ditch channels and metals with a high affinity for organic matter (Al) increased in concentrations near ditches. Other elements such as K and Na decreased closer to ditches, which suggests removal processes by water draining toward ditch channels. The response in soil biogeochemistry, tree productivity, and understory species coverage to drainage generally differed between 'peat soils' and 'forest soils'. Finally, considering our results it is clear that how we choose to manage drained areas today will have long-term effects on the hydrology, biogeochemistry, ecology and GHG-balance of the boreal forest landscape. Forest management that continues to maintain ditches could exacerbate 'sprucification' of Swedish forests and the cascading effects that has on ecosystems, while blocking of ditches to restore historic conditions would reduce forest growth. Increasing broadleaf trees in drained areas has the potential to mitigate some of potentially negative effects of drainage, but more research needs to be done to understand if this is a reasonable management option.

CRediT authorship contribution statement

Hasselquist Eliza Maher: Writing – review & editing. **Öquist Mats:** Writing – review & editing. **Ågren Anneli M.:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Lidberg William:** Formal analysis, Writing – review & editing. **Anderson Olivia:** Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. This declaration of interests concern the submission of an original research article to Forest Ecology and Management by A. M. Ågren, O. Anderson, W. Lidberg, M. Öquist, and E. M. Hasselquist with the title 'Ditches show systematic impacts on soil and vegetation properties across the Swedish forest landscape'.

Data Availability

The ditch map and code do derive it is open data, the NFI and SFSI data are available for research purposes upon request.

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Appendix 1

List A. 1. Complete list of understory species inventoried in the National Forest Inventory.

To save space and make the tables easier to read we only present the 8 significant understory species/groups in the tables below, but all of the 65 species/groups in this list were evaluated.

'Bottom layer' - 11 registered species/groups; *Cladina spp., Cladonia spp., Hylocomnium splendens,* No Bottom layer, Other lichens, Other mosses, *Pleurozium schreberi, Polytrichum commune, Sphagnum spp., Stereocaulon spp.*

'Field layer' - 53 species/groups; *Aconitum lycoctonum, Actaea spp., Aegopodium podagraria, Andromeda polifolia, Anemone nemorosa, Angelica sylvestris, Anthriscus sylvestris, Arctostaphylos uva-ursi, Calluna vulgaris, Carex globularis, Cicerbita alpina, Cirsium helenioides, Cirsium palustre, Crepis paludosa,* NMLWS**, Empetrum nigrum, Epilobium angustifolium, Equisetum sylvaticum, Erica tetralix, Filipendula ulmaria, Galium odoratum, Geranium sylvaticum, Geum rivale, Gymnocarpium dryopteris, Hepatica nobilis, Lamiastrum galeobdolon, Ledum palustre, Listera ovata, Lycopodiaceae, Maianthemum bifolium, Melampyrum prat.&sylv., Menyanthes trifoliate, Mycelis muralis,* No Field layer, Other Field layer species, *Oxalis acetosella, Paris quadrifolia, Phegopteris connectilis, Poaceae (broad leafed), Poaceae (narrow leafed), Pteridium aquilinum, Rubus chamaemorus, Rumex acetosa, Silene dioica, Stellaria holostea, Stellaria nemorum, Tall brackens, Trollius europaeus, Urtica dioica, Vaccinium myrtillus, Vaccinium oxycoccus & microcarpum, Vaccinium uliginosum, Vaccinium vitis-idaea*.

* NMLWS = "Non-Moisture Loving short Wood-rush (*Luzula*) and Sedges (*Carex)* species". Most common species are *Luzula pilosa, L. campestris, syn. L. vulgaris, L. multiflora ssp. multiflora/frigida, L. pallescens, Carex digitata, C. pilulifera, C. caryophyllea, syn. C. praecox/C. ericetorum/C. montana, C. pallescens C. spicata, syn. C. contigua, C. muricata, spp. lamprocarpa/muricata, syn. C. pairaei C. divulsa, syn. leersii.*

Shrub layer - 1 Species; *Rubus idaeus*.

Table A. 1

Significant ($p \leq 0.05$) logarithmic relationships of the investigated soil and vegetation, for the entire dataset (All soils combined, black line in Figs. 3–5). C is the intercept and B1 is the constant (e.g. the form of the function) and R2 is the explanatory power, and n is the number of observations. Empty cells denote non-significant evaluated relationships. * NMLWS = "Non-Moisture Loving short Wood-rush (Luzula) and Sedges (Carex) species". Most common species are *Luzula pilosa, L. campestris, syn. L. vulgaris, L. multiflora ssp. multiflora/frigida, L. pallescens, Carex digitata, C. pilulifera, C. caryophyllea, syn. C. praecox/C. ericetorum/C. montana, C. pallescens C. spicata, syn. C. contigua, C. muricata, spp. lamprocarpa/muricata, syn. C. pairaei C. divulsa, syn. leersii. Note that for the understory species cover, the non-significat species (n = 57) were excluded from the table to save space.*

Variable/Statistics	C	B1	R2	n
Soil properites				
Humus thickness (cm)	47.393	-5.489	0.022	4124
Bulk Density (g cm^{-3})	0.132	-0.008	0.012	4126
C/N-ratio	26.187	1.534	0.016	4126
C (% weight)	36.532	0.408	0.001	4126
N (% weight)	1.47	-0.052	0.011	4126
pH	4.107	-0.049	0.008	4126
Al (mmol kg^{-1} ds)	15.535	-0.753	0.003	2011
Ca (mmol kg^{-1} ds)				2012
K (mmol kg^{-1} ds)	9.302	1.515	0.028	2012
Mg(mmol kg-1 ds)				2012
Mn (mmol kg^{-1} ds)	2.36	0.212	0.003	2012
Na (mmol kg^{-1} ds)	1.704	0.327	0.006	2012
TA (mekv kg^{-1} ds)				2012
CEC$_{eff}$ (mekv kg ds^{-1})				2011
BS$_{eff}$ (%)	73.567	1.381	0.004	2011
Al/CEC$_{eff}$	0.264	-0.014	0.004	2011
Tree data				
Average height (m)				3805
Basal area (m^2 ha^{-1})	21.835	-0.705	0.003	3805
Mean age (years at breast height, 1.3 m above ground)				3805
Volume All (m^{-3} ha^{-1})				3805
Volume Scots Pine (m^{-3} ha^{-1})	66.058	4.623	0.003	2615
Volume Lodgepole Pine (m^{-3} ha^{-1})				69
Volume Norway Spruce (m^{-3} ha^{-1})	105.531	-5.109	0.002	2772
Volume Birch (m^{-3} ha^{-1})	41.127	-3.992	0.012	2539
Volume Other Broadleaf (m^{-3} ha^{-1})				743
Growth All (m^{-3} ha^{-1} yr^{-1})	6.333	-0.337	0.004	3805
Growth Scots Pine (m^{-3} ha^{-1} yr^{-1})	1.804	0.148	0.003	2615
Growth Lodgepole Pine (m^{-3} ha^{-1} yr^{-1})				69
Growth Norway Spruce (m^{-3} ha^{-1} yr^{-1})	4.86	-0.374	0.006	2772
Growth Birch (m^{-3} ha^{-1} yr^{-1})	1.539	-0.153	0.009	2539
Growth Other Broadleaf (m^{-3} ha^{-1} yr^{-1})				742
Understory species coverage				
Polytrichum commune (% coverage)	8.626	-1.009	0.012	719
Vaccinium myrtillus (% coverage)	7.992	0.937	0.006	1720
Poaceae (broad leafed) (% coverage)	11.37	-1.204	0.008	860
NMLWS* (% coverage)	0.668	-0.057	0.005	806
Rubus idaeus (% coverage)	4.984	-0.777	0.018	350
Hylocomnium splendens (% coverage)	9.448	1.947	0.009	1518
Sphagnum spp. (% coverage)	18.34	3.441	0.011	1126
Pleurozium schreberi (% coverage)	12.657	1.759	0.007	1815

Table A. 2

Results divided by humus forms. Significant relationships ($p \leq 0.05$) are given. Empty cells denote non-significant tested relationships, note that for the understory species cover, the non-significat species ($n = 57$) were excluded from the table to save space *NMLWS = "Non-Moisture Loving short Wood-rush (Luzula) and Sedges (Carex) species". Most common species are Luzula pilosa, L. campestris, syn. L. vulgaris, L. multiflora ssp. multiflora/frigida, L. pallescens, Carex digitata, C. pilulifera, C. caryophyllea, syn. C. praecox/C. ericetorum/C. montana, C. pallescens C. spicata, syn. C. contigua, C. muricata, spp. lamprocarpa/muricata, syn. C. pairaei C. divulsa, syn. leersii.

Humus forms	Mor OF dominated (1)				Mor OH dominated (2)				Peat				Peaty mor			
Variable/Statistics	C	B1	R2	n	C	B1	R2	n	C	B1	R2	n	C	B1	R2	n
Soil properties																
Humus thickness (cm)				1813				530				1028				529
Bulk Density (g cm^{-1})	0.106	-0.003	0.003	1813				530	0.136	-0.013	0.036	1028	0.176	-0.018	0.058	529
C/N-ratio	30.002	1.181	0.008	1813				530	25.590	1.431	0.013	1028	22.506	1.819	0.031	529
C (% weight)	32.384	1.398	0.017	1813				530				1028	30.465	1.549	0.023	529
N (% weight)				1813				530	1.754	-0.050	0.009	1028				529
pH	4.045	-0.058	0.014	1813				530				1028	4.273	-0.062	0.010	529
Al (mmol kg^{-1} ds)				897				279	20.104	-1.825	0.017	441				282
Ca (mmol kg^{-1} ds)				898				279				441				282
K (mmol kg^{-1} ds)	15.052	0.980	0.012	898				279	6.629	0.574	0.012	441	6.645	1.669	0.043	282
Mg (mmol kg^{-1} ds)				898				279	15.247	1.671	0.018	441				282
Mn (mmol kg^{-1} ds)				898				279	1.812	0.457	0.014	441				282
Na (mmol kg^{-1} ds)	2.210	0.367	0.006	898				279				441				282
TA	613.310	19.179	0.007	898				279				441				282
CEC$_{eff}$				898				279				441				282
BS$_{eff}$				989				279	68.881	2.869	0.019	441				282
Al/CEC$_{eff}$				989				279	0.311	-0.029	0.019	441				282
Tree data																
Average height (m)				1722				502	13.296	-0.467	0.01	890				485
Basal area (m^{2} ha^{-1})	25.342	-1.191	0.006	1722	27.907	-1.768	0.014	502	20.762	-1.359	0.014	890				485
Mean tree age (years)				1722				502	55.514	4.401	0.018	890				485
Volume All (m^{-3} ha^{-1})	200.907	-9.952	0.004	1722	225.115	-15.293	0.009	502	145.7	-10.511	0.01	890				485
Volume Scots Pine (m^{-3} ha^{-1})				1237	44.782	13.422	0.019	342				644				283
Volume Contorta (m^{-3} ha^{-1})				44				5				6				10
Volume Norway Spruce (m^{-3} ha^{-1})	130.827	-9.545	0.005	1312	158.08	-15.693	0.012	395				543				381
Volume Birch (m^{-3} ha^{-1})	35.795	-3.609	0.011	1034	48.528	-5.652	0.019	333	42.663	-3.078	0.007	1028				396
Volume Other Broadleaf (m^{-3} ha^{-1})				325				128				115				88
Growth All (m^{-3} ha^{-1} yr^{-1})	8.326	-0.744	0.018	1722	8.777	-0.617	0.012	502	5.015	-0.516	0.02	890				485
Growth Scots Pine (m^{-3} ha^{-1} yr^{-1})				1237	1.581	0.377	0.015	342				644				283
Growth Contorta (m^{-3} ha^{-1} yr^{-1})				44				5				6				10
Growth Norway Spruce (m^{-3} ha^{-1} yr^{-1})	6.819	-0.784	0.019	1312	6.605	-0.669	0.017	395	3.436	-0.291	0.008	543				381
Growth Birch (m^{-3} ha^{-1} yr^{-1})	1.506	-0.172	0.013	1034				333	1.459	-0.144	0.01	1028	1.738	-0.235	0.02	396
Growth Other Broadleaf (m^{-3} ha^{-1} yr^{-1})				325				128				115				88
Understory species cover																
Polytrichum commune (% coverage)				270				83	12.078	-1.709	0.031	182				149
Vaccinium myrtillus (% coverage)	8.458	1.107	0.005	841				221				357				213
Poaceae (broad leafed) (% coverage)				741				200				142	6.757	-1.069	0.033	154
NMLWS* (% coverage)	0.934	-0.123	0.02	462				125				75				75
Rubus idaeus (% coverage)				132				64				60				46
Hylocomnium splendens (% coverage)	10.718	2.565	0.012	768				212				264				190
Sphagnum spp. (% coverage)				320				112	15.789	10.277	0.099	452				211
Pleurozium schreberi (% coverage)				859	10.96	2.705	0.02	221	16.145	-1.664	0.016	424				214

Table A. 3

Results divided by Quaternary deposits. Only significant relationships ($p \leq 0.05$) are given. Note that for the understory species cover, the non-significat species (n = 57) were excluded from the table to save space. *NMLWS = "Non-Moisture Loving short Wood-rush (Luzula) and Sedges (Carex) species". Most common species are Luzula pilosa, L. campestris, syn. L. vulgaris, L. multiflora ssp. multiflora/frigida, L. pallescens, Carex digitata, C. pilulifera, C. caryophyllea, syn. C. praecox/C. ericetorum/C. montana, C. pallescens C. spicata, syn. C. contigua, C. muricata, spp. lamprocarpa/muricata, syn. C. pairaei C. divulsa, syn. leersii.

Quaternary deposits	**Till**				**Sediment with high degree of sorting**				**Sediment with low degree of sorting**				**Peat**			
Variable/Statistics	**C**	**B1**	**R2**	**n**	**C**	**B1**	**R2**	**n**	**C**	**B1**	**R2**	**n**	**C**	**B1**	**R2**	**n**
Soil properties																
Humus thickness (cm)	13.33	-0.68	0.004	2188	20.07	-1.478	0.014	560				332	84.065	1.629	0.009	850
Bulk Density (g cm^{-1})	0.121	-0.006	0.006	2188	0.164	-0.011	0.021	560				332	0.133	-0.014	0.045	850
C/N-ratio	28.322	1.259	0.01	2188	23.272	1.714	0.029	560	26.879	1.158	0.015	332	25.673	1.673	0.016	850
C (% weight)	31.981	1.348	0.013	2188				560				332				850
N (% weight)				2188	1.42	-0.046	0.01	560				332	1.766	-0.05	0.009	850
pH	4.14	-0.061	0.012	2188	4.224	-0.075	0.016	560				332				850
Al (mmol kg^{-1} ds)				1100				267				182	21.256	-2.615	0.041	363
Ca (mmol kg^{-1} ds)				1100				267				182				363
K (mmol kg^{-1} ds)	13.547	0.946	0.009	1101	7.553	1.72	0.045	267				182				363
Mg (mmol kg^{-1} ds)				1101				267				182	12.832	2.527	0.04	363
Mn (mmol kg^{-1} ds)				1101				267				182	2.061	0.369	0.014	363
Na (mmol kg^{-1} ds)				1101				267				182				363
TA	572.234	28.976	0.012	1101	553.623	31.757	0.014	267				182				363
CEC$_{eff}$				1101				267				182				363
BS$_{eff}$				1101				267				182	66.392	4.287	0.047	363
Al/CEC$_{eff}$				1101				267				182	0.336	-0.043	0.047	363
Tree data																
Average height (m)				2048				528				315	13.138	-0.476	0.011	728
Basal area (m^{2} ha^{-1})	23.843	-1.014	0.005	2048				528				315	20.845	-1.534	0.019	728
Mean tree age (years)				2048				528				315				728
Volume All (m^{-3} ha^{-1})	185.317	-8.275	0.003	2048				528				315	144.474	-11.643	0.014	728
Volume Scots Pine (m^{-3} ha^{-1})				1364				347				216				538
Volume Contorta (m^{-3} ha^{-1})				508				5				7				6
Volume Norway Spruce (m^{-3} ha^{-1})	130.195	-9.95	0.005	1614				383				240				414
Volume Birch (m^{-3} ha^{-1})	30.005	-1.888	0.003	1342				375	46.175	-5.577	0.034	212	44.173	-3.428	0.008	512
Volume Other Broadleaf (m^{-3} ha^{-1})				406	88.108	-16.77	0.059	114				77				89
Growth All (m^{-3} ha^{-1} yr^{-1})	7.718	-0.586	0.01	2048	8.192	-0.559	0.011	528				315	4.95	-0.57	0.026	728
Growth Scots Pine (m^{-3} ha^{-1} yr^{-1})				1364				347				216				538
Growth Contorta (m^{-3} ha^{-1} yr^{-1})				508				5				7				6
Growth Norway Spruce (m^{-3} ha^{-1} yr^{-1})	5.732	-0.55	0.011	1614	6.193	-0.671	0.018	383				240	3.601	-0.391	0.015	414
Growth Birch (m^{-3} ha^{-1} yr^{-1})	1.455	-0.147	0.007	1342				375				212	1.408	-0.136	0.009	512
Growth Other Broadleaf (m^{-3} ha^{-1} yr^{-1})				406				114				77				89
Understory species cover																
Polytrichum commune (% coverage)				388				124	12.721	-2.275	0.075	55	12.806	-1.818	0.032	131
Vaccinium myrtillus (% coverage)	8.256	1.027	0.005	1025				228				134				282
Poaceae (broad leafed) (% coverage)				891				181				116				94
NMLWS* (% coverage)	0.931	-0.124	0.022	536				125				65				52
Rubus idaeus (% coverage)	6.217	-1.038	0.021	205				58				28				47
Hylocomnium splendens (% coverage)	12.025	1.799	0.007	928				221				120				199
Sphagnum spp. (% coverage)				500				144				75	14.754	11.658	0.135	373
Pleurozium schreberi (% coverage)	12.989	2.23	0.01	1026				256				137	15.918	-1.649	0.015	341

Table A.4
Results divided by Soil Type WRB. Only significant relationships ($p \leq 0.05$) are given and all units are the same as in Table 1 in the article. Note that for the understory species cover, the non-significat species ($n = 57$) were excluded from the table to save space. * NMLWS = "Non-Moisture Loving short Wood-rush (Luzula) and Sedges (Carex) species". Most common species are Luzula pilosa, L. campestris, syn. L. vulgaris, L. multiflora ssp. multiflora/frigida, L. pallescens, Carex digitata, C. pilulifera, C. caryophyllea, syn. C. praecox/C. ericetorum/C. montana, C. pallescens C. spicata, syn. C. contigua, C. muricata, spp. lamprocarpa/muricata, syn. C. pairaei C. divulsa, syn. leersii.

Soil Type WRB	Histosol				Leptosol				Podzol				Regosol			
Variable/Statistics	C	B1	R2	n	C	B1	R2	n	C	B1	R2	n	C	B1	R2	n
Soil properties																
Humus thickness (cm)				1006				299				1261	15.493	-1.073	0.013	1228
Bulk Density (g cm^{-1})	0.138	-0.014	0.041	1006				299				1261	0.149	-0.011	0.021	1228
C/N-ratio	25.029	1.691	0.019	1006				299	31.109	0.864	0.004	1261	25.635	1.483	0.023	1228
C (% weight)				1006				299	33.542	0.984	0.007	1261	30.607	1.301	0.014	1228
N (% weight)	1.777	-0.06	0.013	1006	1.521	-0.06	0.014	299				1261				1228
pH				1006				299	4.028	-0.062	0.016	1261	4.189	-0.057	0.01	1228
Al (mmol kg^{-1} ds)	19.488	-1.435	0.009	446				141				675				561
Ca (mmol kg^{-1} ds)				446				141				675				561
K (mmol kg^{-1} ds)	5.86	0.897	0.027	446				141				675	11.502	1.169	0.016	561
Mg (mmol kg^{-1} ds)	13.369	2.164	0.03	446				141				675				561
Mn (mmol kg^{-1} ds)	1.956	0.386	0.014	446				141				675				561
Na (mmol kg^{-1} ds)				446				141				675	1.438	0.528	0.009	561
TA				446				141	593.862	27.784	0.011	675				561
CEC$_{eff}$				446				141				675				561
BS$_{eff}$	68.02	2.907	0.017	446				141				675				561
Al/CEC$_{eff}$	0.320	-.029	0.017	446				141				675				561
Tree data																
Average height (m)	12.844	-0.323	0.005	876				280				1193				1149
Basal area (m^2 ha^{-1})	19.831	-1.049	0.006	876				280	24.702	-1.245	0.007	1193				1149
Mean tree age (years)	55.135	4.556	0.019	876				280				1193				1149
Volume All (m^{-3} ha^{-1})	135.747	-7.488	0.005	876	207.426	-20.407	0.015	280	194.625	-10.488	0.004	1193				1149
Volume Scots Pine (m^{-3} ha^{-1})				644				223				836	56.963	9.006	0.01	747
Volume Contorta (m^{-3} ha^{-1})				7				1				24				30
Volume Norway Spruce (m^{-3} ha^{-1})				529	141.428	-19.529	0.027	299	131.634	-10.696	0.005	911				923
Volume Birch (m^{-3} ha^{-1})	43.099	-3.425	0.009	621	50.99	-7.922	0.059	150				724	38.804	-3.377	0.008	820
Volume Other Broadleaf (m^{-3} ha^{-1})				116				84				209	69.904	-11.336	0.036	253
Growth All (m^{-3} ha^{-1} yr^{-1})	4.768	-0.435	0.15	876	7.639	-0.821	0.017	280	7.427	-0.471	0.006	1193	7.936	-0.505	0.009	1149
Growth Scots Pine (m^{-3} ha^{-1} yr^{-1})				644				223				836	1.924	0.223	0.006	747
Growth Contorta (m^{-3} ha^{-1} yr^{-1})				7				1				24				30
Growth Norway Spruce (m^{-3} ha^{-1} yr^{-1})	3.594	-0.343	0.012	529	5.632	-0.752	0.024	299	5.864	-0.545	0.008	911	5.798	-0.498	0.01	923
Growth Birch (m^{-3} ha^{-1} yr^{-1})	1.396	-0.124	0.007	621				150				724	1.825	-0.21	0.014	820
Growth Other Broadleaf (m^{-3} ha^{-1} yr^{-1})				116				84				209	2.629	-0.423	0.028	253
Understory species cover																
Polytrichum commune (% coverage)	12.939	-1.983	0.041	163				32				190				261
Vaccinium myrtillus (% coverage)				339				112				564				600
Poaceae (broad leafed) (% coverage)				130				99				497				528
NMLWS* (% coverage)				75				55				227	0.88	-0.107	0.019	353
Rubus idaeus (% coverage)				51				18				85	5.735	-1.105	0.042	152
Hylocomnium splendens (% coverage)				248				105				506	11.721	1.896	0.009	565
Sphagnum spp. (% coverage)	17.314	10.127	0.098	425				58				214				339
Pleurozium schreberi (% coverage)	15.615	-1.402	0.01	401				116				565	12.864	1.719	0.008	617

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