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ORIGINAL ARTICLE

Effect of Restoration on Physical and Chemical Peat Properties in Previously Drained Boreal Peatlands

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Abstract

There is a societal demand to restore drained boreal peatlands for purposes of improving water quality and biodiversity and lowering emissions of greenhouse gases. Restoration measures are costly and neither the effects of drainage nor restoration on biogeochemical processes in the peat, and in downstream environments are well understood. This study assesses how 60–100 years of drainage followed by 6–9 years of restored conditions have changed the physical and chemical peat properties in restored boreal peatlands. Eight pairs of restored and natural peatlands were sampled down to 50 cm (n = 3 for each site). Each of the 50 cm peat cores was sliced into 25 two-centimetre discs, generating high-resolution records of the dry bulk density (BD), organic matter content (OM), C- and N- content, $\delta^{13}C$, and $\delta^{15}N$. Peat from the restored sites showed significantly higher BD and lower C:N ratio and OM content than the reference sites. Furthermore, peat from restored peatlands was systematically depleted in $\delta^{13}C$, and the OM was enriched in C and N. Long-term drainage could cause increased peat decomposition, leaving altered physical and chemical peat properties. For example, the C content in OM increases as the residual peat is enriched in aromatic and aliphatic moieties following decomposition. For the same reason, degraded peat can be $\delta^{13}C$ depleted. Interestingly, differences between the restored and pristine sites were mainly found at 20–50 cm depth. Given the low peat formation rates in nutrient-poor peatlands, the superficial 20 cm peat was potentially recovering from drainage even before restoration.

Key words: Restored peatlands; Peatland rewetting; Boreal peatlands; Carbon cycle; Nitrogen cycle; Peat properties; Peat decomposition.

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Highlights

- Up to a century of drained conditions drastically changes the peat properties
- Peatland rewetting does not restore the properties of previously drained peat
- Clogging of drainage ditches could render peat formation

Introduction

Boreal peatlands are vital in long-term carbon (C) storage and contribute significantly to atmospheric methane (CH_4) concentrations (Frolking and Roulet 2007; Nilsson and others 2008). They also provide other essential ecosystem services, such as water retention and biodiversity (Calvin and others 2023). At northern latitudes, peatlands store more C than forests, with an estimated C stock of 450 ± 150 Pg (Hugelius and others 2020; Beaulne and others 2021). This unique feature of peatlands is due to the millennial time scales of C storage. The waterlogged conditions in these wetlands prevent plant material from fully decomposing, leading to a persistent accumulation of C in peat (Ivanov and others 1981; Clymo 1984; Yu 2012). Despite concurrent CH_4 emissions, undisturbed peatlands have a net-cooling effect on the climate radiative forcing on centennial and millennial time scales (Frolking and Roulet 2007).

During the last century, many boreal peatlands were drained for the purpose of agriculture, forestry, horticulture, and peat extraction (Päivänen and Hånell 2012). The exposure of peat to oxic conditions may lead to increased degradation rates, resulting in a net loss of peat (Simola and others 2012) that sometimes can be substantial (He and others 2016). However, it has also been observed that soil C can continue to increase even after drainage (Turetsky and others 2011; Minkkinen and others 2018). In addition, drainage can promote the establishment and growth of trees, which significantly increases C-sequestration and storage at an ecosystem level (Lohila and others 2011; Meyer and others 2013; Ojanen and others 2013; Tong and others 2024).

To counteract drainage-induced losses of peatlands and their ecosystem services, many national governments and the EU have invested large sums of money to restore disturbed peatlands to their pre-drainage state (European Parliament 2024). However, a century of drained conditions irreversibly changes the soil properties (Leifeld and others 2020), making it challenging to predict whether restoration measures also restore biogeochemical processes and related functions to pre-drained conditions. The long-term effects of restoration on surface peat physical and chemical properties are uncertain, and few studies have examined the extent to which biogeochemical and physical processes in restored peatlands return to pre-drained conditions (Glatzel and others 2004; Lavoie and others 2005; Kreyling and others 2021). Understanding these effects is vital to reducing the uncertainty for restoration responses on ecosystem services.

Several physical and chemical peat characteristics can be used as state factors for assessing drainage impact on peatlands and associated biogeochemical functions driving, for example, decomposition rates and greenhouse gas exchange (Biester and others 2014; Järveoja and others 2016). In drained peatlands, the dry bulk density (BD) may increase due to peat subsidence if pores in the peat matrix collapse as the pore water is drained (Minkkinen and Laine 1998). The BD increase at superficial peat levels might also bring indirect effects, such as peat compaction deeper into the soil column (Szajdak and others 2020). An increased degree of decomposition can also increase BD (Bohlin and others 1989). Furthermore, the plant species composition influences peat BD and may increase if, for example, *Sphagnum* spp. are replaced by vascular plants after drainage (Minkkinen and others 2018).

Peatland drainage also affects the organic matter content and the C and N content in the peat (Reddy and others 2022; Serk and others 2022). The initial drainage phase and increased aerobic conditions can be associated with a loss of high-quality organic matter, and the C and N abundance in the remaining organic matter is expected to increase (Reddy and others 2022; Serk and others 2022). Organic polymers preferably degraded by microorganisms, for example, carbohydrate polymers, have a relatively low C content compared to more recalcitrant C-rich polymers, such as aromatic- and lipid-based polymers (Reddy and others 2022; Serk and others 2022). Increased peat recalcitrance, therefore, results in an increased C content in the residual organic matter (Serk and others 2022).

Nitrogen (N) is retained to a higher degree than C during the initial decomposition of labile organic matter (Leifeld and others 2020). The N-availability in oligotrophic and mesotrophic peatlands is low, further retaining N (Eriksson and others 2010). This leads to a relative increase in peat N content and decreased C:N ratios when peatlands degrade (Moore and Basiliko 2006; Leifeld and others 2020).

The fractionation of the stable isotopes δ^{13}C and δ^{15}N is a tool for assessing the degree of peat decomposition (Biester and others 2014; Krüger and others 2015). The δ^{13}C and δ^{15}N signatures of peat-forming vegetation result from photosynthetic C fixation and plant N uptake (Rice and Giles 1996; Ménot and Burns 2001). In peat, isotopic signatures also reflect the hydrological history of peatlands and associated peat decomposition (Krüger and others 2016; Groß-Schmölders and others 2021; Serk and others 2022). Microbial peat decomposition preferentially depletes readily degradable polymers, leaving behind more complex ^{12}C-enriched polymers, containing more aromatic and aliphatic moieties (Benner and others 1987; Serk and others 2022).

This study assesses how drainage, followed by six to nine years of rewetted conditions, has changed the physical and chemical properties of a set of peatlands. Eight boreal peatlands covering oligotrophic to mesotrophic nutrient conditions were sampled. These peatland types represent the vast majority of boreal peatlands. For each restored peatland, an adjacent pristine (natural) reference peatland was sampled to represent similar but undisturbed conditions. A grand total of 54 peat cores of 54 cm depth were sampled and analysed for BD, organic matter content, C, N, δ^{13}C, and δ^{15}N at a two-centimetre vertical resolution. Our results give insights into the effect of both the initial drainage, the active restoration, and what happened in the period between those two interventions.

Methods

Site Description

In the summer of 2021, we sampled 16 peatlands organised into eight pairs of natural and restored sites. Five peatland pairs were sampled between latitudes 62 and 63 in northern Sweden, while the remaining three pairs were located at latitudes 57–58 (Fig. 1; Table S1). The sites represent minerogenic and ombrogenic boreal peatlands with oligotrophic to mesotrophic nutrient status. The sites were ditched initially between the late nineteenth century and the 1960s for various land-use purposes (see below). At the time of restoration, the sites had been set aside for natural conservation purposes.

The sites Store Mosse (SM), Anderstorps Stormosse (AS), and Bredsjömossen (BM) are all located in the southern part of Sweden (latitude 57°N-58°N; Tables 1, S1). AS is an ombrotrophic peatland (bog) with vegetation dominated by *Sphagnum*, sedges (*Eriophorum vaginatum, Carex sp.),* and ericaceous shrubs (*Calluna vulgaris, Erica tetralix*). The shrubs are more common in the restored parts than in the pristine area of the peatland. AS was drained during the 1940s for peat extraction. The peat cores collected at the restored parts of the site were collected within the previously drained area but outside of the former peat extraction site. Restoration of AS was done between 2012 and 2013.

Store Mosse is a bog with vegetation dominated by *Sphagnum* spp. Sedges (*Rhynchospora alba, Eriophorum spp.),* ericaceous shrubs (*Andromeda sp., Vaccinium spp., Calluna vulgaris, Erica tetralix*), and lichens (*Cladonia spp.*) also occur at SM (Ryberg and others 2022). The restored part of SM was used as a peat extraction site during the first half of the twentieth century. The peatland was restored between 2013 and 2015 by damming the previously established drainage ditches.

Bredsjömossen (BM) is classified as a minerotrophic mire (fen) with vegetation dominated by *Sphagnum* spp. and ericaceous shrubs (*Emporium nigrum, Calluna vulgaris*) (SEPA 2013). BM was originally drained during the sixteenth century to lead water from the peatland to the nearby ironworks. The four-metre-wide ditch was kept open and acted as a small stream to an adjacent lake until damming in the spring of 2014.

Two peatland areas were sampled in western Sweden, close to the Scandinavian Mountains: Ånnsjön peatland (AN) and Öjsjömyrarna (OA; Table 1, 2). Peatlands in the AN and OA areas were most commonly drained in the late nineteenth century for fodder and hay production, and it is likely that both peatlands were drained for this purpose. AN is a fen at a relatively high altitude (533 m.a.s.l.). The vegetation predominantly consists of *Sphagnum* spp., brown mosses (*Amblystegiaceae* family), and shrubs (for example, *Calluna vulgaris*).

The second peatland sampled in western Sweden, OA, also has a relatively high altitude (459 m.a.s.l.). OA is a fen with vegetation dominated by *Sphagnum* spp. and brown mosses (*Amblystegiaceae* family). The site was restored in 2012.

Three sampling sites were located close to the Gulf of Bothnia between latitudes 62°N and 63°N: Stensjöflon (SF), Sör-Lappmyran (SL), and Mossaträsk (MT; Tables 1, S1). SF is a fen with vegetation dominated by *Sphagnum* spp., sedges (*Eriophorum vaginatum, Carex pauciflora*), shrubs (*Betula nana, Empetrum nigrum, Andromeda polifolia*),

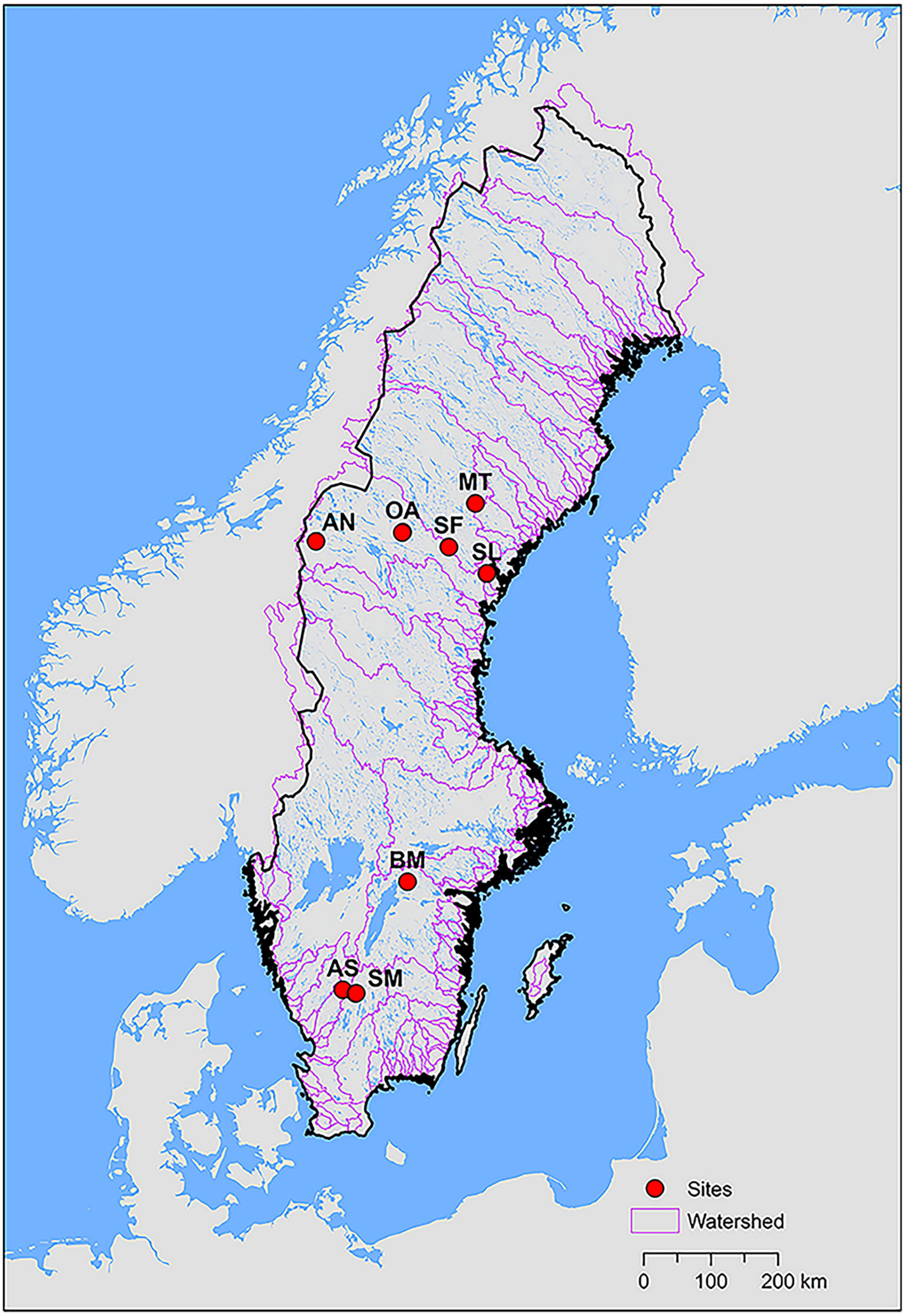

Figure 1. Geographical location of the respective peatland pairs where each marker represents a restored and a natural reference peatland. AS, Anderstorp Stormosse; SM, Store Mosse; BM, Bredsjömossen; AN, Ånnsjön mire; OA, Öjsjömyrarna; SF, Stensjöflon; SL, Sör-Lappmyran; MT, Mossaträsk. See SI for the exact coordinates of each peatland.

and water trefoil (*Menyanthes trifoliata*). The southern part of the SF peatland, where peat cores were sampled, was originally drained in 1926 to increase forest growth in the area. The drainage ditches at SF were dammed in 2012.

Sör-Lappmyran is a fen, and *Sphagnum* spp., sedges (*Eriophorum vaginatum, Carex pauciflora*), and water trefoil (*Menyanthes trifoliata*) dominate the vegetation. The previous drainage ditches in the area originate from the 1950s and 1960s and were

Table 1. Table of Mean Annual Temperature, Precipitation, pH (± SE) for the Paired Natural/Control and Restored Peatlands, Respectively, Köppen Climate Zone Classification, and Bedrock Geology Underlying the Peat Layer

Site ID	Temperature (°C)[a]	Precipitation (mm y^{-1})[a]	pH natural	pH restored	Köppen classification[b]	Bedrock[c]
AN	2.1	898	4.1 ± 0.06	4.5 ± 0.27	Dfb	Carbonate-rich phyllite
OA	3.7	522	5.1 ± 0.05	4.9 ± 0.13	Dfb	Pelite
MT	3.7	583	4.3 ± 0.03	4.3 ± 0.06	Dfa/Dfb	Granite
SF	3.2	577	4.4 ± 0.01	4.4 ± 0.03	Dfa/Dfb	Paragneiss
SL	5.0	743	4.7 ± 0.35	4.9 ± 0.42	Dfa/Dfb	Mica-rich wacke
AS	6.4	773	4.2 ± 0.13	4.2 ± 0.13	Cfb	Granite
SM	6.4	773	4.1 ± 0.06	4.0 ± 0.04	Cfb	Granodioritic gneiss
BM	7.1	565	3.9 ± 0.03	3.9 ± 0.04	Cfb	Mica-rich wacke

[a]*Data acquired from smhi.se.*
[b]*Peel and others (2007).*
[c]*Data acquired from sgu.se.*

dug out to increase forest growth at the peatland. All ditches were covered during the peatland restoration in 2012.

The third peatland sampled in north-eastern Sweden is MT. The peatland is a fen, and the vegetation is dominated by *Sphagnum* spp., sedges (*Carex rostrata, Carex pauciflora, Eriophorum vaginatum*), shrubs (*Andromeda polifolia, Betula nana*), and cloudberry (*Rubus chamaemorus*). The previous drainage ditches at MT were dammed in 2013.

Sampling and Laboratory Analyses

At the restored sites, peat cores were collected ~ 5–10 m away from the remnants of the previous drainage ditch. Peat cores are never extracted closer than five metres to the drainage ditch to avoid disturbance from restoration activities on the peat profiles. Sampling at distances greater than 10 m from the former drainage ditch increases the risk of capturing areas with a minimal restoration effect (Bring and others 2022).

The natural reference peatlands were located within the same peatland complex and sampled at distances ranging from 150 to 1500 m from the restored location, depending on site-specific conditions. These natural reference sites were selected to represent undisturbed conditions, including aspects such as microtopography and plant community composition.

At each site (n = 16), we sampled three 50 cm peat cores (Ø16 cm) using a circular stainless-steel corer (modified from Clymo 1988). Site AN was an exception, where six natural and restored peat cores were collected. In total, 54 cores, 27 from restored sites and 27 from natural sites, were sampled. After sampling, the cores were frozen to − 18 °C within 4 h and stored frozen until further processing. The frozen peat cores were sliced into 25 discs of two cm thickness using a bandsaw (Metabo Bas 318) with a stainless-steel blade. Slicing was done in a cold room (4 °C) to minimise melting of the frozen peat.

The discs were stored at − 18 °C before drying at 70 °C until constant weight (~ 72 h), after which bulk density (BD) was determined. The dry samples were then homogenised in a zip-lock bag to ensure a representative sample for further sample preparation. Approximately 1 g of dried and homogenised sample was milled to a fine powder using an IKA Tube Mill Control and placed in 15 ml Falcon Tubes.

The milled sample was used for determining loss on ignition (LOI) and analysis of total C, total N, δ^{13}C, and δ^{15}N. The LOI was used to calculate the organic matter content. LOI was measured by drying the milled sample overnight to ensure dry conditions while weighing the sample prior to determining LOI (550 °C for 4 h). The total amount of C and N (% m/m) was determined using a Flash EA 2000 Element Analyzer (Thermo Fisher Scientific, Bremen, Germany) and the δ^{13}C and δ^{15}N isotopic signatures a DeltaV Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Bremen, Germany). C and N contents for statistical analysis ($\%_{weight}$) were expressed as fractions of organic matter content derived from LOI.

The superficial peatland pH was measured in pore water collected from the pit resulting from the extraction of peat cores. A handheld Greisinger

GMH 5550 pH measurement device was used for these measurements conducted in the field.

Statistical Analysis

The samples were collected with the peatland surface as the reference level (depth zero). To minimise the effect of the vegetation, we separated the top 4 cm in the peat core from the remaining 4–50 cm of the peat core. The superficial 0–4 cm layer with living vegetation was characterised and statistically compared separately.

The site SM was excluded from statistical analysis due to the potential influence of previous peat extraction on the top 50 cm peat. The overall results with and without SM included in the data set were similar although inclusion led to larger differences between the treatments. As a precaution, the site SM was excluded from statistical analysis as a conservative measure. The data from SM, along with the other individual sites, are displayed in SI.

To minimise confounders related to environmental differences among the sites, the restoration effect was evaluated using extracted standard scores (z-scores) for every 2 cm layer from each peatland pair (Eq. 1).

$$z = \frac{x - \mu}{\sigma} \qquad (1)$$

In Eq. 1, x is the observed value, μ is the average value of the six peat cores at each site; three from the natural and restored site, respectively. σ is the standard deviation for each peatland pair.

A linear mixed-effects model was fitted for each parameter: BD, OM, C, N, C:N ratio, δ^{13}C, and δ^{15}N, respectively. Depth below peatland surface and peatland class (natural or restored) were chosen as predictor variables to account for differences in depth while also testing for differences between the two treatments (Eq. 2):

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + C_k + e_{ijk} \qquad (2)$$

where Y_{ijk} is a variable at a given depth (i) in peatland class (j; restored or natural) at a site (k). μ is the general mean, and α_i and β_j are the fixed effects of depth and peatland class. The interaction effect between depth and peatland class is denoted $\alpha\beta_{ij}$ and the C_k represents the random effect of a site (k). Finally, the random error is accounted for by e_{ijk}. The observations over depth throughout the peat cores were treated as dependent measurements, as a given peat layer can be assumed to be influenced by adjacent peat layers. The R function corCAR1 was therefore included in the code (Pinheiro and Bates 2000).

An ANOVA was used to test for a difference between natural and restored peatlands. If there was a significant difference ($p < 0.05$) in the effect of the peatland class (natural or restored), a least-squares mean post hoc test was used to identify the specific depths with significant differences (*emmeans* package; Searle and others 1980). P-values were adjusted using Bonferroni correction to account for the multiple comparisons problem (Dunn 1961). All statistical analyses were done using R version 4.2.3, and the package *nlme* and function *lme* were used for the linear mixed-effects model (Pinheiro and others 2024).

A principal component analysis (PCA) was performed in SIMCA multivariate data analysis software (Version 17, Umetrics Umeå, Sweden). Data were transformed to z-scores (see above) before extracting PCA scores.

Results

Peat Dry Bulk Density

The average BD of the natural peatland sites ranged from 0.025 to 0.087 g cm^{-3}, and from 0.024 to 0.12 g cm^{-3} at the restored peatland sites. (Fig. 3a, Table S2). The natural and restored sites had similar depth patterns of BD above $\sim$ 30 cm but increasingly deviated with depth. The z-scores normalised to each paired site showed significant differences at depths 36–40 cm and 42–50 cm, with a higher BD at the restored sites (Table S3). The total peat mass in the upper 50 cm was also higher in the restored (42.3 kg m^{-2} ± 3.05 SE) than in the natural peatlands (36.4 kg m^{-2} ± 3.52 SE; p = 0.037).

Peat Organic Matter Content

The depth-average organic matter content ranged from 97.7% to 98.6% in natural peatlands and from 96.6% to 98.1% in restored peatlands (Fig. 2b, Table S2). The restored peatland sites showed a distinct minimum in organic matter content between depths 18–26 cm. The natural peatlands had a similar depth pattern but did not show an organic matter minimum to the same extent as in the restored peatlands. Significant differences between the two peatland treatments were found at the depth intervals 22–26 cm, 34–36 cm, and 38–48 cm, where less organic matter of the total peat mass was found in the restored peatlands (Table S3).

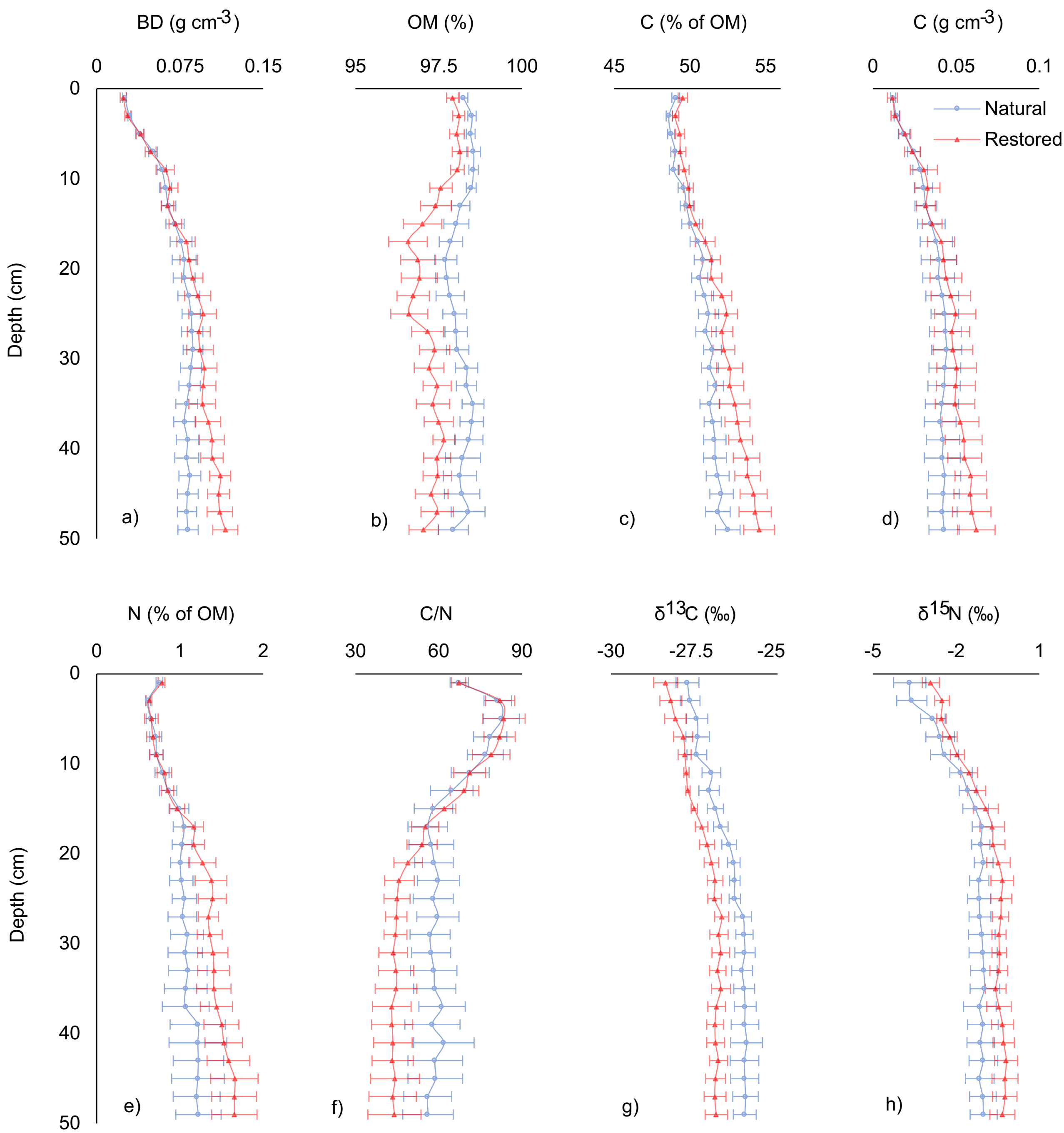

Figure 2. Average (± SE n = 7) of **a** dry bulk density (BD), **b** organic matter content (OM), **c** carbon (C) content, **d** volumetric C content (N), **e** nitrogen content (N), **f** C:N ratio (C/N), and **g** δ^{13}C, and **h** δ^{15}N. The C- and N- content are normalised to the OM content.

Carbon Content in Organic Matter and Total C Content

The depth-average C content of organic matter ranged from 48.6% to 52.5% for natural peatlands and from 49.0% to 54.6% for the restored peatlands (Fig. 2c, Table S2). Both treatments displayed a pattern of increasing C content with depth, and maximum C content was found at the bottom of the 50 cm peat profiles for both natural and restored peatlands. The C content in organic matter was significantly higher at the restored peatlands at the depth intervals 22–24 cm and 36–42 cm (Table S3). Using C% by weight to calculate the total C mass in the superficial 50 cm peat also rendered significantly higher C content in the restored peatlands ($p = 0.042$). The C storage in the top 50 cm was 21.0 kg m^{-2} ± 1.54 SE in the restored peatlands and 18.1 kg m^{-2} ± 1.84 SE at the natural peatlands.

Nitrogen Content in Organic Matter and Total N Content

The depth-average N content in organic matter ranged from 0.62% to 1.22% in the natural and 0.63% to 1.66% in the restored peatlands (Fig. 2e, Table S2). The N content in organic matter was similar between the two treatments from the surface to ~ 20 cm. Below this depth, the N content in the natural peatlands stabilised, whereas it increased at the restored peatlands. The restored peatlands showed a significantly higher N content in organic matter at depths 20–28 cm, 36–38 cm, and 44–46 cm (Table S3).

C:N Ratio

The depth-average C:N ratio ranged from 56.1 to 82.7 in natural and 43.1 to 83.5 in the restored peatlands (Fig. 2f; Table S2). Following an increase in the top six centimetres, the C:N ratio decreased to approximately 20 cm depth. Above this depth, the C:N ratio was nearly identical for both peatland treatments. In the bottom half of the 50 cm peat profiles, the C:N ratio approached lower values at the restored peatland sites with significant differences at depths 22–28 cm, 36–38 cm, and 44–46 cm (Table S3).

δ^{13}C Isotopic Signature

The depth-average δ^{13}C spanned from − 27.6‰ to − 25.8‰ in natural and from − 28.3‰ to − 26.5‰ in restored peatlands (Fig. 2g; Table S2). The δ^{13}C values of natural and restored peatlands were slightly offset already at the peatland surface with a 0.5‰ difference. The δ^{13}C isotopic signature was then lower throughout the peat profile at the restored peatlands, with significant differences at the depth intervals 4–18 cm, 20–42 cm, and 44–48 cm (Table S3).

δ^{15}N Isotopic Signature

The depth-average δ^{15}N ranged from -3.67‰ to − 0.97‰ in the natural peatlands, while the restored peatlands showed δ^{15}N values ranging from − 2.92‰ to − 0.20‰ (Fig. 2g; Table S2). Like the δ^{13}C isotopic signature, there was thus a slight offset between the two peatland treatments. However, there were no statistical differences throughout the 50 cm depth profile regarding δ^{15}N (Table S3). Both natural and restored peatland sites showed a slight δ^{15}N increase to approximately 20 cm depth but stabilised in the depth interval 20–50 cm.

Principal Component Analysis

The results of the linear mixed-effects model and ANOVA are reflected in the PCA ($R^2X = 0.67$; $Q^2 = 0.33$; Fig. 3). Parameters characterising restored peatlands predominantly vary along the first component in the scores and loading plots, respectively. The first component explained 54% of the variance, while the second component explained 13%.

Discussion

At depths of 20–50 cm restored and natural peatlands showed significant differences in all variables measured (except for δ^{15}N), suggesting that effects of drainage mainly persisted below 20 cm peat depth. Few differences were found when only comparing a single restored peatland to a corresponding natural adjacent peatland (Figs. S1–S7). However, while incorporating seven pairwise sampled peatlands into our statistical evaluation, systematic differences between natural and restored peatlands were found.

Another interesting result is the lack of differences between natural and restored peatlands in the top 20 cm layer for several variables. It has been shown that Sphagnum growth can be quite vigorous following rewetting (Laatikainen and others 2025) and such response may have sustained post-restoration peat formation in the top 20 cm at the restored sites. However, considering that the vertical growth rate of peat per se at the surface (top 10 cm) in more nutrient-poor boreal peatlands has been estimated to approximately 1 cm y^{-1} (Eriksson and others 2010; Olid and others 2014) it is unlikely that all this peat represents formation after restoration. Thus, it is possible that peat accumulated in the restored sites even before rewetting. Given that the drainage was conducted about a century ago, the ditches can be expected to have lost much of their hydrological function even before they were restored. Clogging of ditches occurs naturally if a peatland drainage system is not maintained (Päivänen and Hånell 2012). Thus, conditions for natural peat accumulation could have been established even before the

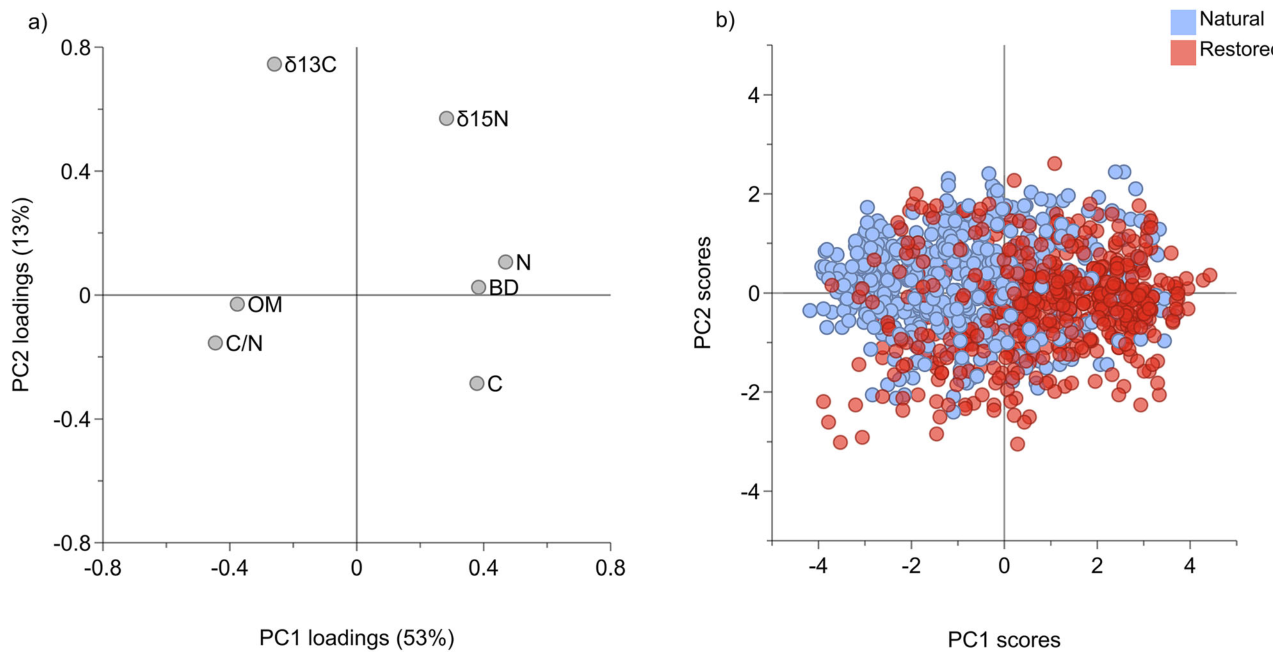

Figure 3. PCA loadings **a** and scores **b** of physical and chemical peat properties of natural and restored peatlands.

restoration measures were taken. However, more detailed investigations are needed to distinguish between, and quantify, peat formation that have occurred before and after restoration, respectively.

Physical Changes in the Peat Column

The denser peat layers below 36 cm depth at the restored peatlands likely stem from the previously drained conditions (Minkkinen and Laine 1998; Hoijer and others 2012). Peat above ~ 20 cm depth does not show any differences between restored and natural peatlands and is likely formed after the initial drainage effect. During and after drainage, the peat can subside as the water-filled pore space decreases and layers become compressed, causing an increase in BD (Minkkinen and Laine 1998). Peat decomposition and enrichment of mineral content in the peat likely also contributed to the BD increase (Clymo 1984; Krüger and others 2015). A potential reason for increased BD below 30 cm depth could be that the soil profile might have been compacted from above, thus compressing deeper peat layers (Laiho 2006; Liu and Lennartz 2019).

C and N in Organic Matter

The chemical peat properties differed between natural and restored peatlands at varying depths below 20 cm. The restored peatlands had higher C and N content and a decrease in the C:N ratios, as well as the total organic matter content.

Even though C is lost during decomposition, the concentration of C in the organic matter increases due to preferential microbial degradation of less C-rich polymers, for example carbohydrate-based polymers, over more resistant structures such as aromatic and aliphatic polymers (Reddy and others 2022; Serk and others 2022). Carbohydrate polymers generally contain less C than the more recalcitrant organic matter, for example, aromatic and aliphatic polymer forms (Nilsson and Öquist 2013; Reddy and others 2022; Serk and others 2022). Mineralisation of carbohydrates ($C_x(H_20)_y$) leads to concurrent loss of O and H along with C (Voet and others 2016). Thus, the initial stages of decomposition lead to a loss of, for example, carbohydrates due to the relatively quick metabolisation by microbes (Berg and McClaugherty 2020; Nilsson and Öquist 2013; Serk and others 2022). For example, glucose ($C_6H_{12}O_6$) contains 40% C (Berg and others 2015; Reddy and others 2022). This can be compared to other organic polymers such as lignin and lipids, which contain 60–65% C and 75–80% C, respectively (Sjöström 1993; Reddy and DeLaune 2008). Accumulation of recalcitrant C-compounds following decomposition will, therefore, lead to a relative C increase in the remaining organic matter.

The decomposition of high-quality organic matter during the initial stages of drainage might also be reflected in the C:N ratio and N% in the residual organic matter (Malmer and Holm 1984; Krüger and others 2015; Leifeld and others 2020). The N released following peat decomposition is often immobilised by microorganisms and/or peat-forming vegetation, particularly at oligotrophic boreal peatlands (Malmer and Holm 1984; Kuhry and Vitt 1996; Granberg and others 2001; Chen and others 2024). Thus, the cause of the reduction in the C:N ratio is often dominated by the C release following peat decomposition.

Interpretation of δ^{13}C *and* δ^{15}N *Isotopic Signatures*

The isotopic signature of δ^{13}C and δ^{15}N can offer insights into C and N dynamics (Nadelhoffer and Fry 1988; Högberg 1997). Peat from the restored sites was systematically depleted in ^{13}C, but there were no significant statistical differences in δ^{15}N. However, throughout the entire depth profile the ^{15}N values of the restored peatlands were less negative, that is, enriched relative to the samples from the natural peatlands. The cause for the observed δ^{13}C depletion can stem from several different responses and processes. Depletion in peat δ^{13}C has been suggested to reflect changes in for example both vegetation shifts (Drollinger and others 2020), but can also be caused by decomposition of peat per se. A shift in vegetation resulting in an increased occurrence of roots, tree remains, and below-ground litter from vascular plants may have altered the δ^{13}C signature in the restored peatlands (Broder and others 2012). However, similar shifts can also occur as recalcitrant, for example, lignin-derived, aromatic, and aliphatic compounds, accumulate in the peat while more readily oxidised polymeric structures are decomposed (Benner and others 1987; Serk and others 2022). When more readily oxidised organic compounds, such as polysaccharides, are synthesised, they become slightly δ^{13}C enriched compared to more recalcitrant organic matter (Rice and Giles 1996; Serk and others 2022; Möckel and others 2024). The preferential initial loss of carbohydrate polymers during the drained phase may thus have contributed to the δ^{13}C depletion in the remaining peat.

In addition to soil in situ processes, the δ^{13}C signature can also be influenced by external factors (Krüger and others 2024). The atmospheric ^{13}C abundance has decreased since the onset of the industrial revolution due to the combustion of ^{13}C-depleted fossil fuels (Keeling and others 2005; Graven and others 2017). It is, thus, expected that recently accumulated peat is slightly ^{13}C depleted in the superficial soil. Recycling of ^{13}C-depleted CO_2 following microbial respiration might also alter the δ^{13}C input signature, further emphasising the contrast between depth and superficial soil layers if the decomposition rate is high (Clymo and Bryant 2008; Nykänen and others 2018).

There were very small but constant differences in δ^{15}N between natural and restored peatlands. Loss of N from bulk soil samples depends on leaching, plant uptake, and emission of N gases (Drollinger and others 2020; Högberg 1997; Nadelhoffer and Fry 1988). However, in oligotrophic and mesotrophic peatlands, the occurrence of inorganic N in the peat might be limited (Luan and others 2019), especially due to N-limited plant growth. The C:N ratio of the peatlands sampled in this study ranges from 43 to 84, and N is less likely to be converted in inorganic forms at C:N ratios above ~ 21 (Klemedtsson and others 2005), but instead incorporated in microbial- or plant biomass. This could be a factor for the limited δ^{15}N fractionation in the peat bulk samples. The slight difference in δ^{15}N was similar at the superficial as in the deeper peat (50 cm depth), and vegetation shift could be a key influence for the δ^{15}N signatures (Jones and others 2010; Broder and others 2012).

Total C Amount in the Superficial Peat

The total amount of C in the top 50 cm peat was significantly higher in the restored peatlands compared to the natural reference peatlands. This is likely influenced by peat subsidence and BD increase during the drained phase (Minkkinen and Laine 1998; Liu and Lennartz 2019). The top 50 cm of restored peatlands may represent a longer time scale, which could explain the increased total C content at the restored peatlands. The differences in physical and chemical peat properties indicate peat degradation and subsequent C loss from the peat. However, increased soil oxygen availability and plant nutrient acquisition might also have promoted simultaneous C input (Minkkinen and others 2018). Increased biomass production and increased root biomass can increase the below-ground C content (Rydin and Jeglum 2013), as well as physical factors such as BD (Minkkinen and Laine 1998). Thus, drained peatlands can remain a C sink, both in the peat column (Turetsky and others 2011; Minkkinen and others 2018) and on an ecosystem scale (Meyer and others 2013; Ojanen and others 2013; Ratcliffe and others 2019;

Tong and others 2024). But it must be pointed out that firm conclusions on changes in peat accumulation rates must contain a detailed recollection of the time intervals involved and the age of the peat, which is a topic that warrants further research.

Implications for Biogeochemical Processes

The impact of restoration on biogeochemical processes might be challenging to predict since the drained conditions have altered properties in the upper 50 cm of the peat, especially at the depth of 20–50 cm below the surface. This must be considered when predicting the overall effects of drainage and ensuing restoration on greenhouse gas-related processes. Based on the observations in this paper, several features of this influence can be discerned.

Restoration will promote anaerobic biogeochemical processes such as CH_4 production and Hg methylation (Tjerngren and others 2012; Turetsky and others 2014; Darusman and others 2023). However, the availability of high-quality organic substrate exerts a master control on microbially mediated processes (Bergman and others 1999, 2000; Nilsson and Öquist 2013). Therefore, despite reintroduced anoxic conditions by rewetting, rates of CH_4 production and Hg methylation may be restrained due to the lack of readily degradable organic matter (Urbanová and Bárta 2020). Our results indicate that the main effects of organic matter decomposition were observed at peat depths of 20–50 cm in the restored peatlands. This is where the redox conditions in the restored soil profiles would be favourable for methanogenesis and Hg methylation. A significant source of substrate for anaerobic processes is supplied by vascular plant root exudation (Öquist and Svensson 2002; Ström and others 2003), which will be released in the root zone. The establishment of, for example, sedges may thus promote CH_4 production and Hg methylation when anoxic conditions are reintroduced (Joabsson and others 1999; Bergman and others 2000; Granberg and others 2001). Vascular plants can also mediate CH_4 emission by acting as conduits transporting CH4 from deeper layers through aerenchyma bypassing superficial zones of CH4 oxidation (Öquist and Svensson 2002). The hydrological connectivity of fens to downstream ecosystems could also facilitate methylmercury export if methylation increases following restoration. The altered physical and chemical peat properties have changed the conditions for biogeochemical processes following restoration. Our findings contribute to linking the drainage-induced changes in peat properties to the biogeochemical effects of restoration.

Conclusion

Up to a century of drained conditions and subsequent restoration measures have drastically changed surface peat properties. Almost a decade after restoration efforts, most of the soil properties between 20 and 50 cm depth and some aspects of the chemical composition of the entire soil profile to 50 cm remain different from that of pristine peat soil. Thus, these recently restored peatlands will -not provide the same biogeochemical conditions and ecosystem services as natural peatlands.

Our study emphasises that long-term peat drainage has a strong effect on the surface peat characteristics in the peat profile. Several effects caused by long-term drainage are strongly manifested in the peat profiles after a decade after restoration, especially below 20 cm depth. These differences were difficult to discern when comparing natural and rewetted conditions in the peat profile at a single site. However, by integrating the eight pairs of natural and restored sites, 16 peatlands in total, in a mixed-effects model, the variables BD, organic matter content, C, N, C:N ratio, $\delta^{13}C$ all showed significant differences between natural and restored peatlands. This highlights the importance of a broad and representative sampling effort to robustly evaluate how peat drainage and subsequent rewetting influence peatland soil properties in the surface peat.

Most importantly, the largest differences were found below 20 cm depth. The potential accumulation of peat before restoration measures are in place has implications for the C balance of drained boreal peatlands where ditches have not been maintained. We hypothesise that the ditches might have lost their drainage effect even before restoration, enabling the accumulation of more recent peat in the upper $\sim$ 20 cm zone, which is more similar to pristine peat. If true, the action of rewetting the kind of systems represented in this investigation for increased climate benefit may be questioned. However, to allow generalisation, detailed information on the hydrologically linked redox conditions at specific sites must be taken into account and evaluated.

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DATA AVAILABILITY

Data and scripts can be found at https://doi.org/https://doi.org/10.6073/pasta/239a69aefcd355a4d4610fbfb66eb6ed.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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