



Impacts of forestry drainage on surface peat stoichiometry and physical properties in boreal peatlands in Finland

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Abstract Management of drained peatlands may pose a risk or a solution on the way towards climate change mitigation, which creates a need to evaluate the current state of forestry-drained peatlands, the magnitude of degradation processes and indicators for carbon (C) loss. Using a large dataset (778 profiles, 891 peat samples, collected between 1977 and 2017) from peatlands having different fertility classes across Finland, we investigate whether the surface peat profiles of undrained and forestry-drained peatlands differ in C:N, von Post and dry bulk density. The utility of element ratios (C:N:H stoichiometry) as site

indicators for degradation were further analyzed from a subsample of 16 undrained and 30 drained peat profiles. This subsample of drained sites had carbon dioxide (CO₂) and methane (CH₄) fluxes measured allowing us to link peat element ratios to annual C gas effluxes. Element ratios H:C, O:C and C:N and degree of unsaturation (combining C, N, H changes) were found widely valid: they captured both differences in the botanical origin of peat as well as its potential decomposition pathway (C lost via a combination of dissolved organic C and C gas loss and/or the gaseous loss predominantly as CO₂). Of the stoichiometric indexes, peat H:C ratio seemed to be the best proxy for degradation following drainage, it indicated not only long-term degradation but also explained 48% of the variation in annual CO₂ emission. The O:C ratio positively correlated with annual CH₄ flux, presumably because high O:C in peat reflected the availability of easily degradable substrate for methanogenesis. The differences in C:N ratio indicated notable decomposition processes for *Sphagnum*-dominated peatlands but not in *Carex*-dominated peatlands. Degree of unsaturation showed potential for an integrative proxy for drainage-induced lowering water table and post-drainage changes in peat substrate quality.

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Introduction

Northern peatlands have acted as continuous sinks of atmospheric carbon dioxide (CO₂) during the Holocene, leading to a large carbon (C) store of 400–500 Pg stored as peat (Loisel et al. 2014). Globally, peatlands constitute approximately one third of the total soil C pool, which is comparable to about 50% of the 863 Pg C currently held in the atmosphere as CO₂ (Loisel et al. 2014; Le Quéré et al. 2018).

Based on C dynamics and C storage, a peatland ecosystem can be in a state of progression, steady state, or regression. In a pristine state, peatlands typically accumulate C as the rate of biomass production is greater than the rate of decomposition. Functional peatlands with C accumulation are characterized by a high-water table where decomposition is inhibited by seasonal or permanent anoxia related to water chemical variables such as low pH found especially in ombrotrophic bogs (pH < 4) and oligotrophic fens (pH ~ 4). Overall, most of the organic matter is decomposed in the upper, seasonally water-saturated peat layer, i.e., the acrotelm, and approximately only 10% of the litter mass reaches the deeper, permanently water-saturated anoxic catotelm (Clymo et al. 1998; Frohling et al. 2002). The C sequestration rates of natural peatlands depend on the peatland type and its fertility level (nutrient content) with a long-term average rate of C accumulation approximately 20 g m⁻² yr⁻¹ (Gorham 1991; Turunen et al. 2002; Loisel et al. 2014).

The land use, such as forestry-drainage, will shift the peatland state towards regression by lowering the water table, increasing the thickness of aerated surface layer, increasing the microbiological activity, resulting in progressive loss of peat forming mire species and thus deteriorating the peat-forming conditions. In forestry-drained peatlands, the dry bulk density of the surface peat increases through subsidence and decomposition. Changes in peat physical properties decrease the pore volume and hydraulic conductivity and increase the water retention capacity due to higher degree of smaller pores (Menberu et al. 2021; Word et al. 2022). Additionally, the drying and possible shrinkage of the surface peat layers may change the moisture holding capacity and peat becomes more hydrophobic (Bechtold et al. 2018). Overall, the changes in surface peat moisture dynamics reduces or hinders the peat C accumulation, increasing the

CO₂ emissions and dissolved organic carbon (DOC) export, reduces the methane (CH₄) emissions (Alm et al. 2007; Nykänen et al. 1998), and can increase the occurrence of wildfires and smouldering fires in drier surface conditions (Zaccone et al. 2014). However, the magnitude of the drainage impact depends on the drainage intensity and nutrient status of the peatlands. After drainage, peatlands and especially the fertile, meso-eutrophic sites undergo large vegetation changes towards forest communities (Laine and Vanha-Majamaa 1992; Punttila et al. 2016; Laine et al. 2018) and become significant sources of CO₂ to the atmosphere, whereas the peat soil of the nutrient poor bog sites can continue to be a small net CO₂ sink even after drainage, because of an increased root and litter production, which compensate the increased heterotrophic respiration from the aerated peat (e.g., Ojanen et al. 2013, Minkkinen et al. 2018). In countries like Finland, where forestry drainage has been the most extensive land use applied to peatlands since 1950 with more than half of the original peatland area being drained for forestry (Finnish Statistical Yearbook of Forestry 2014), peatlands pose a potential threat or a solution on the way towards climate change mitigation. To steer the peatland management and restoration, there is an urgent need to evaluate the current state of the forestry-drained peatlands, the magnitude of degradation processes and C loss indicators behind the peat C balance.

The elemental ratios of soil organic matter such as C:N, C:P, H:C, O:C, C oxidation state (C_{ox}) and the oxidative ratio (OR) have been used as a measure of peat decomposition rates, the C losses and oxidation state of soils (Malmer and Holm 1984; Kuhry and Vitt 1996; Masiello et al. 2008; Leifeld et al. 2012; Clay and Worrall 2015; Worrall et al. 2016; Moore et al. 2018; Zaccone et al. 2018). C_{ox} can be calculated from the relative molar concentrations of C, H, O, N and S. OR represents the ratio of moles of oxygen (O₂) produced per mole CO₂ sequestered by the ecosystem. OR in soil organic matter is calculated as a derivative of C_{ox} and C and N concentrations (Masiello et al. 2008). The results from undrained and drained peatlands suggest that most of the changes seem to occur in the surface 0.5 m and ratios such as C:N, O:C and stoichiometry of decomposition may be used to estimate the total C loss (Moore et al. 2018; Leifeld et al. 2020). The studies show that the characteristics of the peat result from the

effect of decomposition processes based on the original peat forming vegetation and released C, H and O. Comparable patterns have also been found with peat decomposition rates and C_{ox} and OR. Moore et al. (2018) found that the C_{ox} and OR values were significantly correlated with the von Post humification index (H_{1-10} , von Post 1922) with most changes occurring in weakly decomposed surface peat layers with H-index values 1–4. In addition to C_{ox} and OR, degree of unsaturation (DU, the number of rings and p bonds within a molecule) has been presented as a potential quantity of interest (Worrall et al. 2016).

Data on stoichiometry in forestry-drained peatlands is very sparse. The C:N ratio has been found to be sensitive to land use and a good indicator for peatland degradation both in agricultural topsoils and in forestry-drained sites (Leifeld et al. 2020). Data from drained and decomposed peat reveals low C:N ratios, suggesting increased peat decomposition. Surface peat C:N ratio also significantly predicted heterotrophic CO_2 efflux (Ojanen et al. 2010) and N_2O flux (Liu et al. 2019), from drained peatlands, although these two studies noted that peat dry bulk density is a superior predictor over C:N ratio.

On a dry mass basis about 90% of peat is comprised of carbon, oxygen, and hydrogen (e.g., Moore et al. 2018). During microbial transformation of peat, production of CO_2 , CH_4 and inorganic compounds will determine the stoichiometry ratios of C:H:N:O:S and oxidation state of the drained surface layers. The relative proportion of decomposition processes (aerobic respiration, methanogenesis and loss as DOC) affect the H:C and O:C characteristics of the peat (e.g., Moore et al. 2018). Our focus was to assess whether stoichiometry changes of surface peat layers can be used as measurable site indicators of degradation, comparing undrained and forestry-drained peatlands. In this context, a further aspect was to examine whether stoichiometry provides a useful prediction for annual carbon gas emissions from decomposition in forestry-drained sites. Water table depth has been recognized as the overriding controlling factor for greenhouse gas emissions from managed peatlands (Evans et al. 2021), but direct water table data are laborious to obtain and therefore often unavailable in extensive peatland inventories (e.g., Alm et al. 2023) and thus simpler proxies for post-drainage peat degradation and for estimating greenhouse gas emissions are needed. More detailed data on the physical

properties and peat characteristics of different types of forestry-drained peatlands are needed especially in countries like Finland.

The aim of this study was to investigate whether the surface peat profiles of undrained (UDP) and forestry-drained peatlands (FDP) are associated with different peat stoichiometry. The specific objectives of the study were (1) to compare the physical properties and peat characteristics of UDP and FDP, (2) study if peat stoichiometry differs significantly between UDP and FDP in different fertility classes of peatlands, (3) can stoichiometry changes of surface peat layers be used as measurable site indicators of degradation, and thus the state of soil C balance in forestry-drained peatlands.

We hypothesise (1) that H:C and O:C are good indicators of drainage status of the peatlands, with FDP's that have more decomposed surface peat having lower values of H:C and O:C. This is based on findings by Moore et al. (2018) with values decreasing along with decomposition. The boreal FDP sites in our study may be expected to have distinctively lower H:C and O:C than Canadian undrained peatlands, due to the decadal drainage induced decomposition of the surface peat layers.

We hypothesise (2) that C:N is a better descriptor of fertility gradient in both UDP's and FDP's, as H:C and O:C are not known to vary between bogs, fens and swamps (Moore et al. 2018), but C:N is (Watmough et al. 2022). C:N increases along with decreasing fertility.

Materials and methods

Selection and classification of the study sites

To compare the more widely measured peat characteristics (von Post humification index, dry bulk density, C, N, C:N) of undrained and forestry-drained surface peat profiles we selected study sites from the national peatland inventory of the Geological Survey of Finland (GTK). In GTK classification, the study sites are defined to four categories based on their drainage stage at the research moment: (1) undrained, (2) ditched with little changes in plant communities, (3) ditched, where the original mire vegetation has partially (<75%) been replaced by forest plant communities, and (4) drained peatland forest stage, where

over 75% of the original plant communities have been replaced by forest plant communities. The focus of the GTK inventory has been on peatlands most suitable for peat excavation. Thus, the peatlands sampled for laboratory analysis represent large areas with relatively deep peat layers. Also, during the 21st century, the focus has been on drained peatlands, which were considered most suitable for peat extraction. For these reasons, the data has more observations from nutrient poor, forestry drained peatlands. Due to drainage, pristine, nutrient rich peatlands with relatively shallow peat layers are rare in GTK dataset. Since the post-drainage successional plant communities develop usually towards the drained peatland forest stage, we selected the forestry-drained peatlands in categories 3 and 4 with clear changes in vegetation and tree stand. Also, undrained peatlands were selected for comparison. Thus, the selected GTK sites represent both undrained and drained peatlands classified as bogs and fens with different fertility classes (Fig. 1; Table 1). The ecological classification of peatlands based on their nutrient level is shown in Table 1 for comparison (e.g., Minkkinen 1999, Turunen et al. 2002). Also, a short description of drained peatland forest types used in this study is given in Appendix 1.

GTK peat sampling and laboratory analyses

All peat profiles were collected between 1977 and 2017, with a total of 225 UDP and 593 FDP profiles and 891 peat samples. The volumetric peat profiles were collected with a piston corer (80×200 mm), a box sampler (70×70×1000 mm) or with a Russian pattern side-cutting peat sampler (50×500 mm). All samplers were made of stainless steel. In the field, the mire types were determined based on the vegetation cover and surface topography (Laine et al. 2018). The peat type of each sample was determined based on the botanical composition (Lappalainen et al. 1984), where the composition of the sample is determined in 6-grade scale as *Sphagnum*, *Carex* or *Bryales* peat according to the most abundant plant remains. On the field, the degree of decomposition was estimated with von Post's (1922) 10-grade scale, (H_{1-10}). Von Post index is commonly used on the field to evaluate the degree of decomposition based on the recognizable plant structure and the amount of peat and the color of water squeezed from the peat. Completely undecomposed fibrous, light-coloured peat releasing

almost clear water is defined as H1, whereas the completely decomposed, dark-coloured material with no discernible plant structure is indicated as H10. For a more detailed description of the von Post scale, see also Stanek and Silc (1977) and Zaccone et al. (2018). pH values of the samples were not determined. The 20-cm peat samples were collected in plastic bags and stored in dark and cool conditions (+4 °C) before analysis. Peat samples were analyzed by GTK Laboratory or since 2006 in the Eurofins Labtium Laboratory in Kuopio, Finland, where samples were dried to a constant mass at 105 °C and weighed. The water content was determined using the gravimetric method, measured by weighing the wet soil sample, drying it in an oven, reweighing and calculating the mass of water lost as a percentage of the mass of the dried soil. The dry bulk density of the samples was calculated by dividing the dry mass by the sample fresh volume. The peat samples were milled, and the ash content analysis made as loss-on-ignition (LOI) at 815 °C. The C and N concentrations were analyzed with LECO 628 CHN analyzer. Samples were heated in oxygen atmosphere at 900° C, oxidizing C to CO₂ and N to N₂. The amounts of C and N were detected with infra-red detector (NDIR) and thermal conductivity cell (TC), respectively. Total sulphur (S) was analyzed with ELTRA CS-2000 CS-analyzer. Sample was heated in oxygen atmosphere at 1400° C and S was detected as SO₂ with infra-red detector (IR). H and O concentrations of the large GTK dataset were not determined. In this part of the study analyzing the large GTK dataset we used only peat sample collected from the peat layers 0 to 40 cm from the surface.

Data for elemental stoichiometry analyses

To study further the stoichiometry of UDP and FDP's we reanalyzed a set of peat samples collected from sites National Forest Inventory of Finland (NFI) and GTK national peatland inventory.

A subsample of 30 drained peatland forests in Finland was selected from the permanent sample plots of the 8th National Forest Inventory (systematic sample of 657 plots on drained peatland forests, e.g., Hotanen et al. 2006). The subsample included equally different site types of forestry-drained peatlands of those parts of Finland where drainage for forestry is economically viable (Latitude 60–66 °N, annual temperature sum 1450–750 dd, Fig. S1). All the selected

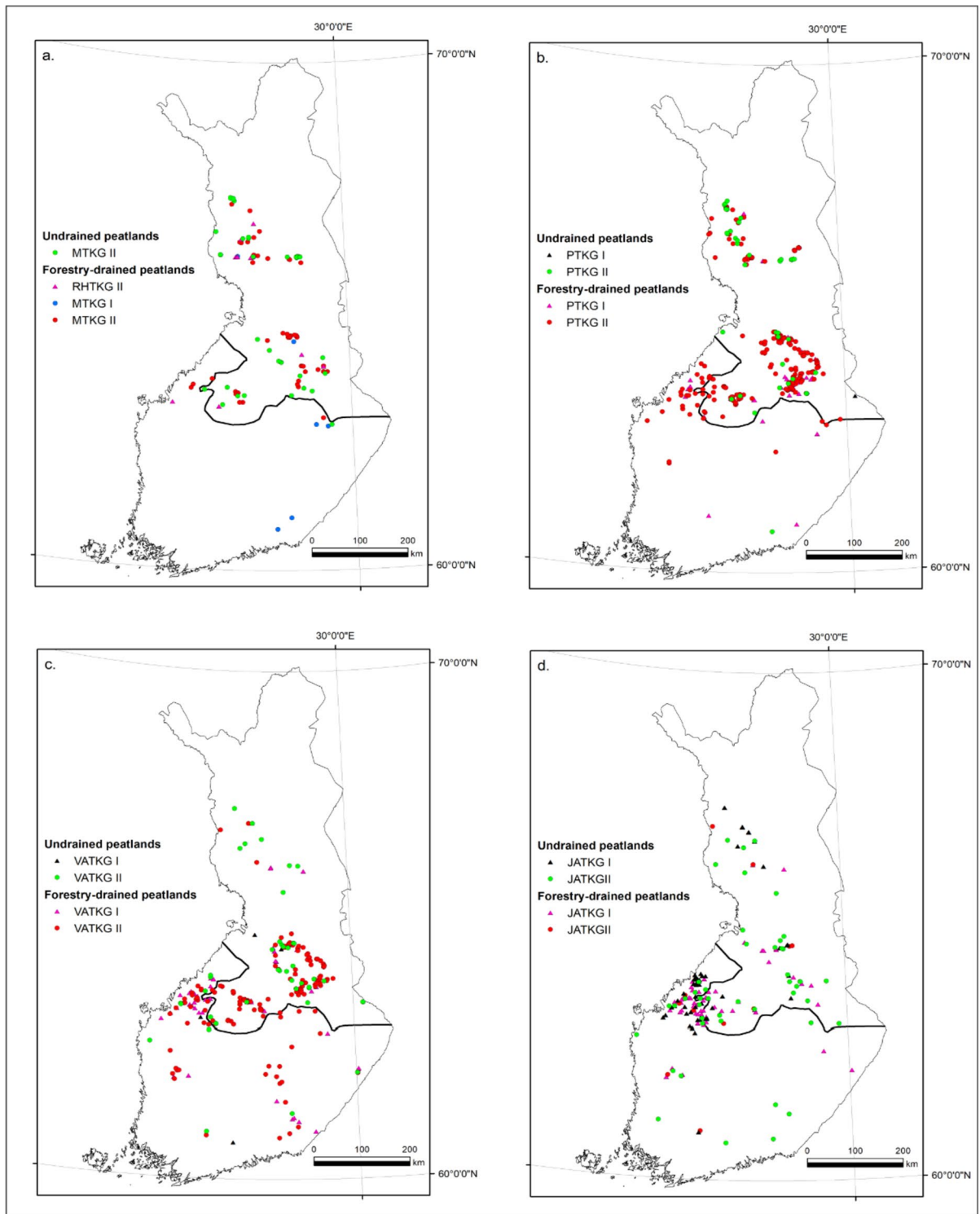


Fig. 1 GTK study sites, a total of 225 undrained peatlands (UDP) and 593 forestry-drained peatlands (FDP). **a** Eutrophic and meso-oligotrophic UDP and FDP (Rhtkg II-Mtkg II).

b Oligotrophic UDP and FDP (Ptkg I-Ptkg II). **c** Ombro-oligotrophic UDP and FDP (Vatkg I-Vatkg II). **d** Ombrotrophic UDP and FDP

Table 1 Characteristics of the peatland groups (mean \pm SE). Stars indicate differences between undrained (UDP) and forestry-drained (FDP) types (* $p < 0.05$). Ash max 20%

Peatland type	Water content %	Dry BD g dm ⁻³	Ash %	Humification von Post index H ₁₋₁₀	C %	N %	C:N	S %	n
<i>Eutrophic mires (Rhtkg II)</i>									
UDP	–	–	–	–	–	–	–	–	–
FDP	85.2 (0.5)	128.5 (4.8)	6.4 (0.6)	3.8 (0.1)	49.5 (0.6)	3.01 (0.09)	16.7 (0.5)	0.28 (0.03)	14–19
<i>Meso - oligotrophic forested mires (Mtkg I)</i>									
UDP	–	–	–	–	–	–	–	–	–
FDP	83.8 (1.6)	114.2 (12.9)	7.8 (1.6)	3.4 (0.5)	47.7 (0.9)	2.03 (0.14)	24.3 (1.8)	0.26 (0.03)	5–7
<i>Meso – eutrophic open-sparsely treed mires (Mtkg II)</i>									
UDP	92.0 (0.4)	64.6 (6.8)	7.1 (0.8)	3.2 (0.2)	47.8 (0.7)	2.13 (0.13)	25.5 (1.5)	0.24 (0.01)	16–38
FDP	87.7 (0.4)*	93.2 (4.7)*	7.2 (0.9)	3.7 (0.1)*	49.1 (0.6)	2.40 (0.10)	22.8 (1.3)	0.25 (0.01)	35–51
<i>Oligotrophic forested mires (Ptkg I)</i>									
UDP	87.9	45.1	2.3	4.0	50.5	1.04	48.6	0.12	1
FDP	86.8 (0.4)	100.2 (6.8)	3.1 (0.3)	3.1 (0.2)	50.2 (0.4)	1.55 (0.08)	35.6 (1.5)	0.41 (0.18)	24–45
<i>Oligotrophic open-sparsely treed fens (Ptkg II)</i>									
UDP	91.4 (0.4)	68.4 (5.8)	5.6 (0.6)	3.0 (0.1)	48.4 (0.6)	2.10 (0.11)	27.1 (1.8)	0.27 (0.03)	20–48
FDP	87.6 (0.2)*	96.9 (2.7)*	4.6 (0.2)*	3.6 (0.1)*	50.1 (0.2)*	2.08 (0.05)	27.1 (0.7)	0.24 (0.01)	146–219
<i>Ombro – oligotrophic open bogs (Vatkg I)</i>									
UDP	87.8 (1.5)	93.5 (12.6)	2.3 (0.6)	3.5 (0.5)	51.6 (0.9)	1.38 (0.30)	45.6 (7.8)	0.19 (0.03)	2–6
FDP	87.3 (0.5)	98.0 (6.3)	2.9 (0.2)	3.7 (0.2)	50.5 (0.4)	1.48 (0.06)	37.6 (1.5)	0.18 (0.01)	41–61
<i>Ombro – oligotrophic forested bogs (Vatkg II)</i>									
UDP	92.6 (0.4)	44.9 (5.9)	3.0 (0.2)	2.7 (0.2)	47.6 (0.4)	1.21 (0.07)	43.8 (1.9)	0.17 (0.01)	26–49
FDP	89.9 (0.2)*	71.4 (3.0)*	3.2 (0.2)	3.2 (0.1)*	48.9 (0.2)*	1.39 (0.04)*	39.3 (0.9)*	0.17 (0.01)	105–164
<i>Ombrotrophic forested bogs (Jätkg I)</i>									
UDP	92.3 (0.3)	49.6 (5.5)	1.8 (0.1)	2.5 (0.1)	47.5 (0.3)	0.91 (0.04)	55.0 (1.5)	0.14 (0.01)	13–53
FDP	90.4 (0.4)*	70.4 (7.1)*	2.3 (0.1)*	3.0 (0.1)*	48.2 (0.3)	1.12 (0.05)*	46.4 (1.4)*	0.16 (0.01)	21–63
<i>Ombrotrophic open-sparsely treed bogs (Jätkg II)</i>									
UDP	94.0 (0.3)	45.8 (6.0)	2.0 (0.1)	2.1 (0.1)	47.2 (0.3)	1.02 (0.06)	51.6 (1.9)	0.14 (0.01)	21–51
FDP	91.7 (0.6)*	47.1 (6.0)	1.7 (0.2)	2.2 (0.2)	47.7 (0.5)	1.08 (0.13)	49.5 (3.99)	0.13 (0.01)	7–13

sites had heterotrophic carbon gas fluxes (CO₂, CH₄) measured in 2007–2008, average peat layer thickness of over 20 cm, no clear-cut areas, and ditching had detectably altered hydrology or vegetation. The exact drainage year of the sites is not known, but all sites were drained before 1995 (For original data on heterotrophic CO₂ efflux, CH₄ efflux, water table depth and the measurement methods, see Ojanen et al. 2010). In addition to these criteria, Ojanen et al. (2010) had taken into account vicinity of research units of the Finnish Forest Research Institute to facilitate field work in five regions across the country. Our subsample consisted of all those gas flux sites that had peat samples collected in 2002 still available (N=30, consisting of 6 \pm 2 sites from each of the five region).

Here we analyzed the remaining samples at depths 20–30, 30–40 cm to calculate stoichiometric indexes.

In addition, a subset of 16 undrained peatland sites (32 peat samples) was selected from GTK peat sample archives. These 16 sites represented two pine-*Sphagnum*-dominated site types (IR, KR) and two treeless sedge fen types (VSN, RhSN) all in 4 replicates and sampled in 2 depths 20–40, 40–60 cm). These sites were sampled between 2002 and 2017. No gas flux data were available from these undrained sites.

The peat samples were analyzed for C:H:N:S and ash concentration with Leco 628 CHNS analyzer following standard SFS EN13039 with FINAS accredited adjustments JOK3023. The dry matter content

was analyzed after drying the sample at 105 °C and ash content based on loss on ignition at 550 °C. The O concentration was determined by difference: %O = 100 - % (ash + total C + N + H + S).

We chose to compare the peat characteristics of a set depth of 20–40 cm in drained and undrained sites. Owing to the peat subsidence typically following drainage, the drained peat sampled at 20–40 cm may represent peat originating from a deeper peat layer under pristine conditions. On the other hand, growing tree stand produces more litter accumulating on the drained site than on undrained site (e.g., Laiho and Pearson 2016). The extent of either of these two phenomena was not available from our individual sites and is likely to vary. Therefore, we also analyzed the impact of sampling depth on selected peat properties (see below 2.4).

Calculation and statistical analyses of indicators

Atomic ratios of C:N, H:C and O:C were calculated based on the individual sample mass values. Further, the C oxidation state (C_{ox}), which is based on the relative molar concentrations of C, H, O, N, and S, and the oxidative ratio (OR), which is a derivative of C_{ox} and C and N concentrations, and the degree of unsaturation (DU) were applied to surface peat samples (Masiello et al. 2008).

The C oxidation state can be calculated simply as:

$$C_{ox} = \frac{2[O] - [H] + 3[N] + 4[S]}{[C]} \quad (1)$$

by assuming oxidation states H=1, O=-2, S=-4, N=-3. The oxidation state -3 for nitrogen follows the assumption that the majority of organic nitrogen is in amine groups (Masiello et al. 2008).

The oxidative ratio is formulated differently for various sources of nitrogen in the ecosystem. Assuming nitrate as the source (Masiello et al. 2008):

$$OR = 1 - \frac{C_{ox}}{4} + \frac{2[N]}{[C]} \quad (2)$$

The degree of unsaturation is calculated as:

$$DU = [C] - [H]/2 - [N]/2 + 1 \quad (3)$$

Degree of unsaturation indicates the number of rings and p bonds within a molecule (Worrall et al. 2016). We studied correlations between six quantities

of interest (Cox, OR, DU, H:C, O:C, C:N) using principal components analysis (PCA) on the samples. PCA was performed using correlation matrix. We analysed the impact of sampling depth (20–40 cm vs. 40–60 cm) on OR, DU, H:C, O:C, and C:N in undrained peats first for all 16 undrained sites across four peatland site types in a paired-samples test for each indicator. The test utilized t statistic compared against the distribution obtained from permutations of the pairs. Secondly, we examined the difference distributions of each indicator by peatland site type to inspect within which peatland site type those differences lie. This approach was chosen owing to the small number observations within each peatland site type (n=4).

SPSS Statistics 29 and R 4.3.1 software were used to analyze the relationships between different variables. The tests of normal distribution and the homogeneity of variances of GTK dataset and the subsample for elemental stoichiometry were tested using the Kolmogorov-Smirnov and Levene statistical tests ($p < 0.05$). In GTK dataset, samples with ash content larger than 20% were removed as outliers (n=5). Since the normality of the residuals was not equal among all UDP and FDP groups, the Mann-Whitney U test was used to test the equality of physical properties between different UDP and FDP groups. The statistical significance ($p < 0.05$) between UDP and FDP pairs is reported in results and in accompanied tables. Pearson's correlation coefficient was used for correlation analysis. To compare differences between the elemental stoichiometry of the subsets, analysis of variance (ANOVA) was conducted. In case of small sample sizes ($n < 20$), permutation tests were used instead of the regular F-test, provided by the R package ImPerm (Wheeler and Torchiano 2022). The relationship between these variables and the site types was studied by ordinal analysis of variance, treating the site type as an ordinal variable with the order defined by nutrient levels. The method used here follows Gertheiss (2014) and is implemented in the R package ordPens.

For the subset of 30 drained peatland forests that had existing data on CH₄ and heterotrophic CO₂ fluxes (Ojanen et al. 2010), we also examined how the fluxes were linked to peat properties (dry bulk density, DU, H:C, O:C, C_{ox}), water table depth, and location (Latitude N) using Spearman rank correlation and ordinary least squares regression analyses. We used Spearman rank correlation because of the small

number of observations ($N=30$). We used simple or stepwise multiple linear regression models to predict heterotrophic CO_2 efflux, CH_4 flux and the combined heterotrophic flux of CO_2 and CH_4 . Simple regression analysis for each of the gas fluxes was applied for the following independent variables: WT, H:C, DU, O:C, Latitude N. These variables were selected based on Spearman rank correlation results (See Results). Here we built on analyses by Ojanen et al. (2010) who examined which factors (such as water table, mean annual temperature, volume of tree stand, bulk density, C:N ratio) explain gas fluxes, but did not analyze other peat properties. Ojanen et al. (2010) reported positive correlations of mean annual summer temperature with the volume of tree stand and with water table depth, the last being the strongest driver of CO_2 efflux.

Therefore, using a subset of Ojanen et al. (2010) gas flux data we did not rerun all of those but focused on peat properties as either a single independent variable or in combination with WT. Two independent variable models were run applying stepwise forwards method for the combinations of WT and the above peat variables H:C, DU, O:C or Latitude N if the one independent variable model with peat property in question or latitude was significant. This stepwise method was chosen to explore if including the selected peat property explained any variation unrelated to WT. The selection criteria were based on p-value (<0.05). The regression equations and uncertainties in annual Rhet values (based on Ojanen et al. 2010) are presented in Table S1.

In all CH_4 models, excluding two outliers (data points above 3rd Quartile + 1.5 Interquartile Range), which were cases with high annual fluxes of 12.5 g m^{-2} (WT 1 cm) and 3.89 g m^{-2} (WT 17 cm), improved the models R^2 , e.g., for the CH_4 model with WT and O:C as independent variables the R^2 was improved from 0.20 to 0.52. In Rhet or Combined C gas models, no cases were excluded.

Results

Peat characteristics of undrained and forestry-drained surface peat profiles

Most of the surface peat profiles of different UDP and FDP peatland groups were weakly decomposed as

determined by von Post humification index (H_{1-10}), and *Sphagnum* dominated (Table 1; Fig. 2a). However, the amount of *Carex* was high in three peatland groups (RhtkgII, Mtkg I and Ptkg II) characterised by equally weakly decomposed peat layers (Table 1). The visual 6-grade determination of abundant plants remains of the peat samples seemed to be relatively reliable and was reflected in decreased C:N ratios

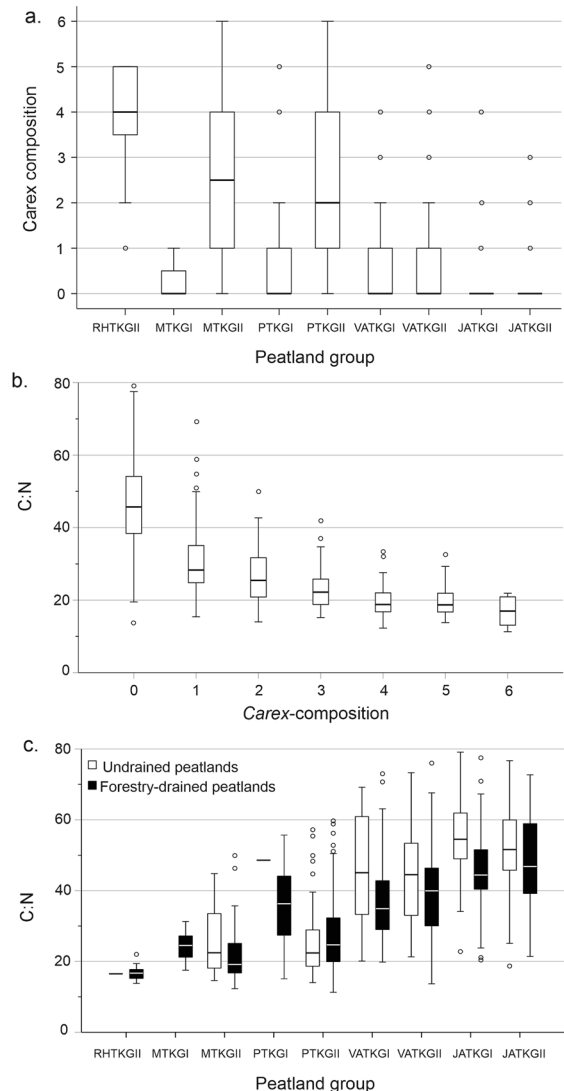


Fig. 2 Box plots showing **a** the *Carex* composition of the different peatland groups determined on the field in 6-grade scale, **b** C:N ratio and the *Carex* content of the peat samples. **c** C:N ratio of undrained (UDP) and forestry-drained (FDP) peatland groups. Whiskers and box bands denote minimum, first quartile, median, third quartile and maximum

with increased *Carex* content (Fig. 2b). Overall, the mean von Post humification index was H2.7 and H3.6 (H_{1-10}), dry bulk density 0.55 and 0.90 g cm⁻³ and C:N ratio 41 and 32 for UDP and FDP, respectively. The difference between the mean C:N ratio, von Post humification index, dry bulk density and ash content of the samples were found significant between UDP and FDP groups ($p < 0.05$).

In most of the peatland groups, the physical properties and peat characteristics differed between UDP and FDP sites. FDP sites had larger dry bulk density, ash content, von Post humification index and N concentration in all peatland groups with a decreased water content of the surface peat samples (Table 1). However, differences in mean C concentrations between FDP and UDP sites of the nine different peatland groups were marginal except within two groups (Ptkg II and Vatk II) with a significantly larger C concentration at FDP sites (Table 1). Also, the mean N concentrations were slightly larger in FDP sites compared to UDP. Differences in C and N concentrations were reflected in lower C:N ratios in FDP peatland groups (Table 1; Fig. 2c). However, the differences in C:N ratio were statistically significant only in two nutrient poor peatland groups (Vatk II and Jätkg I). The detailed results of the peat characteristics and the statistical differences between UDP and FDP peatland groups are shown in Table 1.

The high amount of *Carex* in three peatland groups (Fig. 2a: Rhtkg II, Mtkg I and Ptkg II) was reflected in their lower C:N ratios (25.7 ± 0.5) compared to *Sphagnum* dominated group (41.7 ± 0.6). In FDP sites, the changes in decreased water content and increased dry bulk density, von Post humification index and C concentration were statistically significant (Table 2). However, within *Carex*-dominated

peatland group, the difference between the mean C:N ratio for UDP (25.8 ± 1.5) and FDP (25.7 ± 0.6) was not significant ($p = 0.89$). In *Sphagnum*-dominated peatland group, the difference between UDP (44.8 ± 1.1) and FDP (39.9 ± 0.7) was significant ($p < 0.05$). The results of the peat characteristics and the statistical differences between *Carex* and *Sphagnum* dominated UDP and FDP groups are shown in Table 2.

Stoichiometry patterns

Elemental analyses and derived chemical indicators

The correlations (Fig. 3) between the quantities of interest: C_{ox} , OR, DU, H:C, O:C, C:N revealed that the degree of unsaturation DU and the H:C ratio were strongly negatively correlated ($r = -0.87$) indicating that the increase in hydrogen with respect to C provides less aromatic peat matter. These two quantities also clearly changed depending on the drainage status (Table 3), with the drained sites having smaller H:C-ratios (means: 1.474 (undrained) vs. 1.317 (drained), permutation ANOVA $p = 2.5e-9$), and respectively higher DU (means: 1.011 (undrained) vs. 1.015 (drained), permutation ANOVA $p = 2.62e-8$). In addition, Cox and OR were strongly negatively correlated ($r = -0.89$), which is also understandable because OR is proportional to $1 - Cox$. The clearest relationship with the site type was found with the O:C ratio (ordinal ANOVA $p = 0.0002$), but C:N ratio (ordinal ANOVA $p = 0.0006$) and H:C ratio (ordinal ANOVA $p = 0.0017$) were also related. The correlation structure among the sites was also revealed in Principal components analysis (Fig. 4).

Table 2 Characteristics of the *Carex* and *Sphagnum* dominated peatland groups (mean \pm SE). Stars indicate differences between undrained (UDP) and forestry-drained (FDP) types (* $p < 0.05$). Ash max 20%

Peatland type	Water content %	Dry BD g dm ⁻³	Ash %	Humification von Post index H_{1-10}	C %	N %	C:N	S %	n
<i>Carex</i> dominated group									
UDP	92.1 (0.4)	61.6 (6.5)	6.7 (0.7)	3.1 (0.2)	48.0 (0.6)	2.11 (0.13)	25.8 (1.5)	0.24 (0.01)	15–37
FDP	87.5 (0.2)*	98.1 (2.3)*	5.0 (0.2)*	3.6 (0.1)*	50.0 (0.2)*	2.20 (0.04)	25.7 (0.6)	0.24 (0.01)	196–286
<i>Sphagnum</i> dominated group									
UDP	92.5 (0.2)	52.7 (3.1)	3.0 (0.2)	2.6 (0.1)	47.8 (0.2)	1.30 (0.05)	44.8 (1.1)	0.17 (0.01)	83–209
FDP	89.1 (0.2)*	80.8 (2.5)*	3.0 (0.1)	3.2 (0.1)*	49.1 (0.1)**	1.38 (0.03)*	39.9 (0.7)*	0.19 (0.02)	211–354

Table 3 Characteristics of the peatland groups (mean \pm SE). Stars indicate differences between undrained (UDP) and forestry-drained (FDP) types (* $p < 0.05$) calculated from two-sided permutation tests on the difference between sam-

ple means. ^ denotes fewer samples in the Dry BD column, and the number of samples available for Dry BD analyses is marked inside parentheses in the n column

Peatland type	Dry BD g dm ⁻³	Oxidative Ratio (OR) mol mol ⁻¹	Degree of Unsaturation (DU) mol	H:C mol mol ⁻¹	C:N g g ⁻¹	O:C mol mol ⁻¹	n
<i>Eutrophic mires (Rhtkg)</i>							
UDP	–	–	–	–	–	–	–
FDP	186 (2.48)	1.125 (0.0178)	1.0149 (0.00276)	1.17 (0.0159)	24.2 (1.87)	0.440 (0.0374)	2
<i>Meso - oligotrophic forested mires (Mtkg I)</i>							
UDP	–	–	–	–	–	–	–
FDP	160 (24.5)	1.152 (0.0122)	1.0159 (0.00111)	1.28 (0.0350)	34.0 (3.72)	0.409 (0.0268)	3
<i>Meso – eutrophic open-sparsely treed mires (Mtkg II)</i>							
UDP	92.7 (12.8)^	1.226 (0.00685)	1.0107 (0.000658)	1.49 (0.0228)	21.7 (1.34)	0.411 (0.00752)	4 (3)
FDP	151 (16.5)^	1.164 (0.0123)*	1.0156 (0.000556)*	1.30 (0.0168)*	30.4 (3.35)	0.411 (0.0177)	8 (7)
<i>Oligotrophic forested mires (Ptkg I)</i>							
UDP	105 (10.7)	1.161 (0.0112)	1.0124 (0.000741)	1.43 (0.0286)	37.6 (4.83)	0.462 (0.0205)	4
FDP	160 (6.15)*	1.171 (0.00434)	1.0155 (0.000815)*	1.33 (0.0233)*	37.6 (4.42)	0.394 (0.0173)*	5
<i>Oligotrophic open-sparsely treed fens (Ptkg II)</i>							
UDP	92.8^	1.197 (0.00624)	1.0106 (0.000540)	1.49 (0.0232)	24.3 (0.444)	0.454 (0.0109)	4 (2)
FDP	145	1.194	1.0166	1.30	32.3	0.338	1
<i>Ombro – oligotrophic open bogs (Vatkg I)</i>							
UDP	94.6 (5.74)^	1.145 (0.0254)	1.0108 (0.000565)	1.49 (0.0247)	49.7 (12.1)	0.514 (0.0385)	4 (3)
FDP	137 (24.8)	1.160 (0.00762)	1.0136 (0.000809)*	1.39 (0.0325)*	36.9 (2.82)	0.442 (0.0244)	4
<i>Ombro – oligotrophic forested bogs (Vatkg II)</i>							
UDP	–	–	–	–	–	–	–
FDP	63.7 (4.34)	1.074 (0.00945)	1.0129 (0.000185)	1.38 (0.00991)	52.7 (5.03)	0.588 (0.0148)	4

In undrained peats, some of the differences between depths (20–40 cm vs. 40–60 cm, $n=16$) were significant under a 0.05 level based on a paired-samples test: These were DU difference -0.0008 ($p=0.0197$), H:C difference 0.0213 ($p=0.0468$), C:N difference -4.25 ($p=0.0218$). OR and O:C did not show a significant difference ($p=0.499$ and $p=0.235$, respectively). Differences were most reflected in fen site types (RhSN, VSN) for DU and H:C and for bog site type (IR) in C:N (See Supplement for more details).

In FDP sites, the annual heterotrophic CO₂ efflux from soil correlated significantly with properties DU ($r=0.67$), H:C (-0.64) and bulk density (0.37) as well as with WT (0.71) and latitude (-0.38). The H:C ratio was the best single proxy for annual heterotrophic CO₂ efflux from soil ($R_{\text{het}} = -3943(\pm 755)$ H:C + $6358(\pm 1007)$ coefficient's SE in parentheses, $R^2=0.48$, $df_{\text{reg}} 1$, $df_{\text{res}} 28$ Fig. 5a, followed by DU

($R^2=0.44$), and WT ($R^2=0.41$, Table 4, S1). The properties H:C and DU were strongly negatively correlated (for gas flux sites, Spearman rho -0.85 , $N=30$). Instead, after H:C the stepwise regression selected WT, which additionally explained 21% of the variation in annual heterotrophic CO₂ efflux. That is, the combination of two factors raised the variation in heterotrophic CO₂ efflux explained to 69% ($R_{\text{het}} = -3099 (\pm 615)$ H:C + $12 (\pm 3)$ WT + $4848 (\pm 851)$ coefficient's SE in parentheses, $R^2=0.69$, $df_{\text{reg}} 2$, $df_{\text{res}} 27$ Table 4, S1, Fig. 5b). Latitude, a surrogate to annual temperature sum ranging from 1450 dd in the south to 750 dd in the north, was moderately correlated to WT (0.40), Regressing heterotrophic CO₂ efflux as a function of latitude only resulted in a model with $R^2=0.19$, but latitude did not explain any variation unrelated to WT (Table 4). Latitude was not correlated to any of the properties DU, O:C or H:C. Heterotrophic CO₂ efflux contributed more than 99%

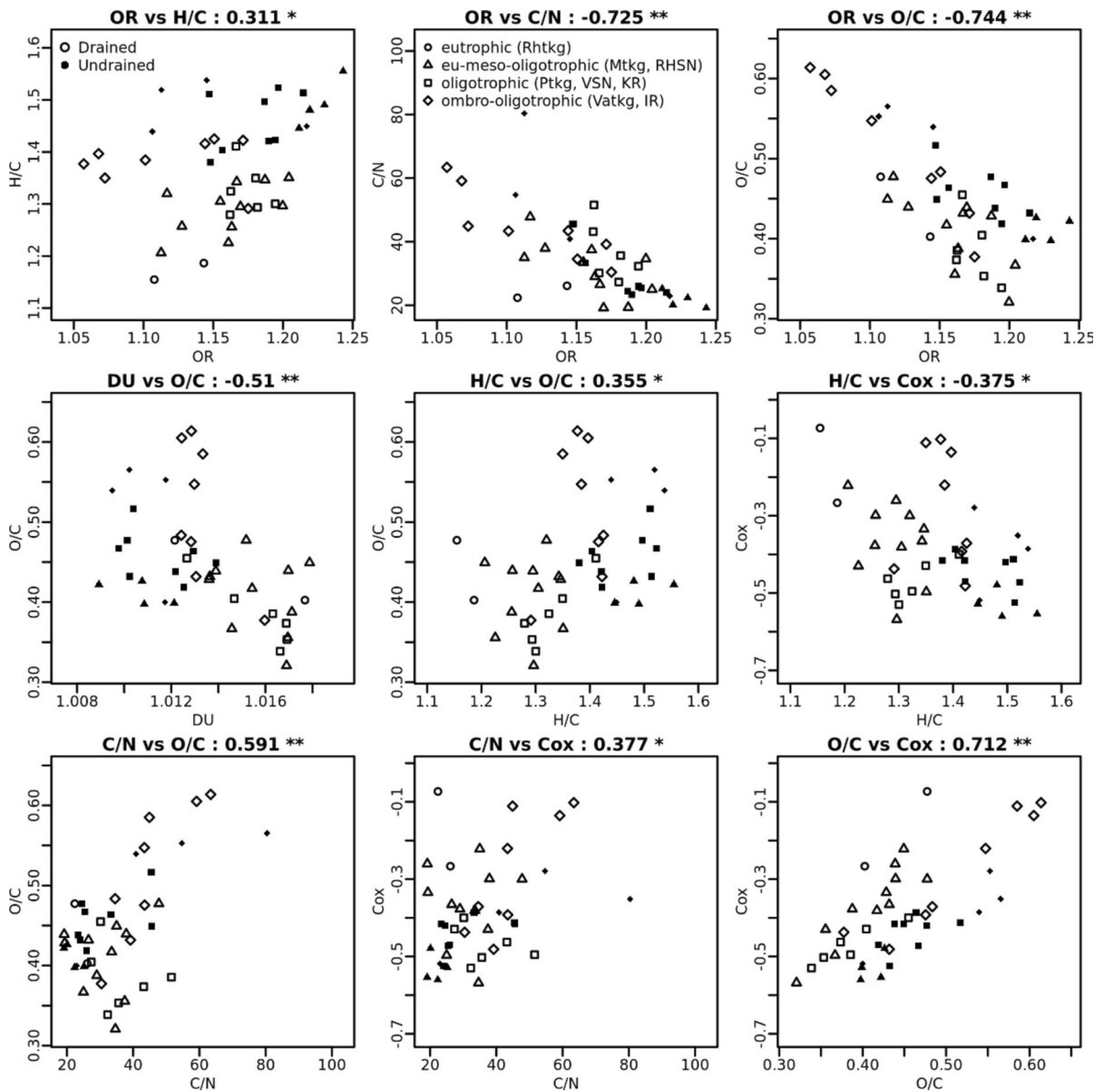


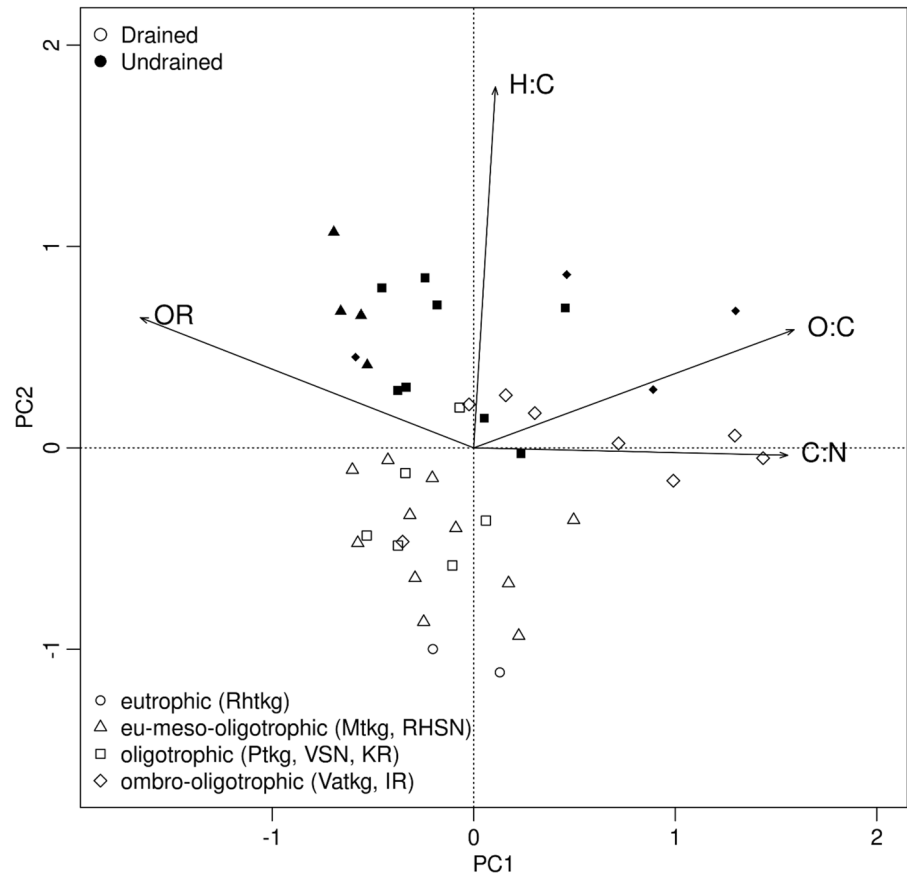
Fig. 3 Correlations among selected peat properties. Markers show the individual samples from undrained sites (filled) and foresty-drained (open) sites

to the net combined flux of heterotrophic CO_2 and CH_4 (as moles of C, net C gas flux = $3230 (\pm 658)$ DU – $3256 (\pm 668)$) $R^2=0.44$, $df_{\text{reg}} 1$, $df_{\text{res}} 28$ Fig. 5c; Table 3,S1).

Annual CH_4 flux from soil correlated significantly ($p < 0.05$) with a set of peat properties DU ($r = -0.62$), O:C (0.52), H:C (0.40) and Cox (0.36) as well as with WT (-0.83). Single peat properties DU

and O:C at the depth of 30–40 cm explained 36% and 29% of the variation in CH_4 flux, respectively. The water table level was the best single proxy for CH_4 flux ($R^2=0.40$, $df_{\text{reg}} 1$, $df_{\text{res}} 26$) as found earlier (Ojanen et al. 2010), a combination of WT and O:C raised the variation explained to 52% (Fig. 6a–c). Latitude, a surrogate to annual temperature sum was not correlated to CH_4 efflux (Table 4). See Table S1 for

Fig. 4 Principal components analysis. Markers show the individual samples from undrained sites (filled) and drained sites (open). The axes explain 59.4% (PC1) and 30.7% (PC2) of the variance



more details on regression equations, coefficients, R^2 , degrees of freedom).

Discussion

Peat C:N ratio is a good degradation indicator for *Sphagnum*-dominated forestry-drained peatlands but not for *Carex*-dominated peatlands.

Our large dataset from peatlands of different fertility classes across Finland revealed a clear overall trend in peat properties between UDP and FDP. The difference between the mean C:N ratio for UDP and FDP was significant, suggesting increased peat decomposition in drained topsoil profiles. In peat decomposition studies, the C:N ratio is used to describe the humification pattern and mass loss (Malmer and Holm 1984; Kuhry and Vitt 1996; Biester et al. 2014; Zaccone et al. 2018; Leifeld et al. 2020; Watmough et al. 2022). The C:N ratio has also been found to be sensitive to land use and a

good indicator for peatland degradation both in agricultural topsoils and in forestry-drained sites (Leifeld et al. 2020). The C:N ratio approach is based on the observation that during organic matter decay, an enrichment of N relative to C generally occurs, resulting in a decrease in the C:N ratio (Malmer and Holm 1984; Kuhry and Vitt 1996). In this study, also, the correlations between C:N ratio and von Post humification index, the dry bulk density values and the ash content of the samples were found to be significant, reflecting changes in peat properties due to peat degradation processes. In FDP, changes in hydrology and in water chemical variables such as pH is an overall factor affecting the peat chemistry. Forestry drainage of boreal peatlands typically lowers the pH of the surface peat solution owing to decomposition processes producing dissolved organic acids (Laine et al. 1995; Minkinen et al. 1999; Laiho et al. 1999). In this study, the pH values were not measured.

While an overall significant difference was found between UDP and FDP, there was also a major

Fig. 5 a Estimated annual rates of heterotrophic respiration, CO₂ release to the atmosphere (R_{het} CO₂ g m⁻² y⁻¹) in relation to peat H:C ratio from drained peatland forest sites (n=29). The predicted rate is also plotted ($R_{\text{het}} = -3943 (\pm 755) \text{ H:C} + 6358 (\pm 1007)$ coefficient's SE in parentheses). **b** The residuals of regression model R_{het} with H:C ratio as the independent factor plotted against WT, **c** Annual rates of heterotrophic carbon gas release to the atmosphere in relation to degree of unsaturation. A net value of the combined flux of heterotrophic CO₂ and CH₄ from sites is plotted (net C gas flux = 3230 (± 658) DU - 3256 (± 668))

difference in C:N ratios when comparing peatlands groups. As was observed in a global study of undrained peatlands (Watmough et al. 2022), the C:N ratio of drained peatlands in our study also followed the fertility gradient, so that the more fertile drained fens had lower C:N than bogs. In here we were able to investigate the peatland group differences based on the botanical composition of the peat, namely whether the peat was mainly composed of *Carex* or *Sphagnum* residues. *Sphagnum* mosses are known to be more recalcitrant than other mire plants and it could be expected that *Sphagnum* peat has chemical properties to resist decomposition and induce C accumulation (Hájek et al. 2011; Del Giudice and Lindo 2017). In our study, in the *Carex*-dominated peatland groups (RhtkgII, Mtkg I and Ptkg II), the difference between the mean C:N ratio for UDP and FDP was not significant whereas in the *Sphagnum*-dominated peatland group (Ptkg I, Vatkg, Jätkg), the difference between UDP and FDP was significant. The C:N ratio seems to be a good indicator of aerobic decomposition processes for the less fertile forestry-drained peatlands with *Sphagnum* dominated peat but not for the *Carex*-dominated peatlands. After the drainage, the relative enrichment in C and N concentrations was reflected in lower C:N ratios (Table 1). The results indicate that the overall increase in mean C concentrations (1%) is significantly less compared to the increased N concentrations (14%), thus the C:N ratio is mainly controlled by N concentrations. Since bogs are nitrogen-deficient ecosystems, a relatively small enrichment in N concentration as a results of aerobic peat mineralization is clearly shown in decreased C:N ratio. In fertile peatlands, the original total N concentration is much higher and a larger change in N or C is needed to produce an equal decrease in C:N ratio. Parallel to decomposition, the results of Biester et al. (2014) indicate that N recycling can be controlled

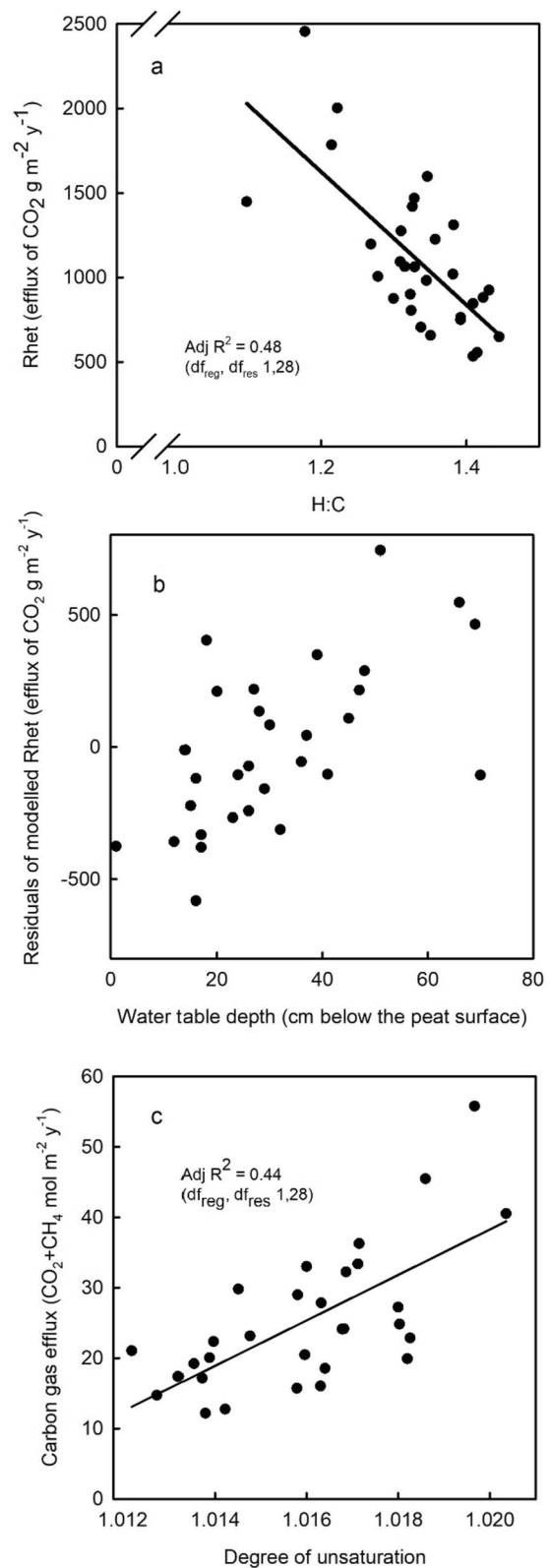


Table 4 Regression models predicting gas fluxes as a function on water table depth, latitude and selected peat stoichiometric properties either as a single independent variable or in combination with WT. For single factor Rhet and C gas models df_{reg} , df_{res} 1,28 and for single factor CH_4 models df_{reg} , df_{res} 1,26. NS=not significant, NA not available, the nonsignificant variables were not included in two factor models for respective gas. Regression equations are in Table S1

Variable	Model R ²		
	Rhet	CH ₄ flux	C Gases
WT	0.41	0.40	0.41
H:C	0.48	-0.01NS	0.48
DU	0.44	0.36	0.44
O:C	0.05NS	0.29	0.05
Latitude N	0.19	-0.03NS	0.18
H:C + WT	0.69	NA	0.68
DU + WT	0.57	0.43	0.57
O:C + WT	NA	0.55	NA
Lat. + WT	NA	NA	NA

by the shifts in vegetation and plant uptake in the acrotelm in peat bogs. Thus, shifts in peatland vegetation after the drainage can also affect C:N ratios with aerobic decomposition.

Peat H:C ratio and degree of unsaturation strongly connected with drainage status of peatlands

In our set of undrained and forestry-drained peatlands, the best indicators for peat degradation following drainage were a significant decrease in peat H:C ratio and concomitant increase in degree of unsaturation. Furthermore, within drained sites, peat H:C was the best single proxy for heterotrophic CO₂ respiration with almost half of the variation explained. A high CO₂ efflux was associated with low peat H:C ratios.

Both these indicators: peat H:C ratio and degree of unsaturation were moderately ($r=0.44$ – 0.57) associated with O:C ratio, but only weakly associated with most of the other decomposition indicators measured, such as C:N ratio, OR or C_{ox}. None of these conventional indicators could be used to distinguish the drainage status equally well.

Peats from undrained oligotrophic forested sites tended to have lower H:C ratios than fen peats, but both peat types showed a high variation. Low H:C in treed sites agreed with the findings by Teickner et al.

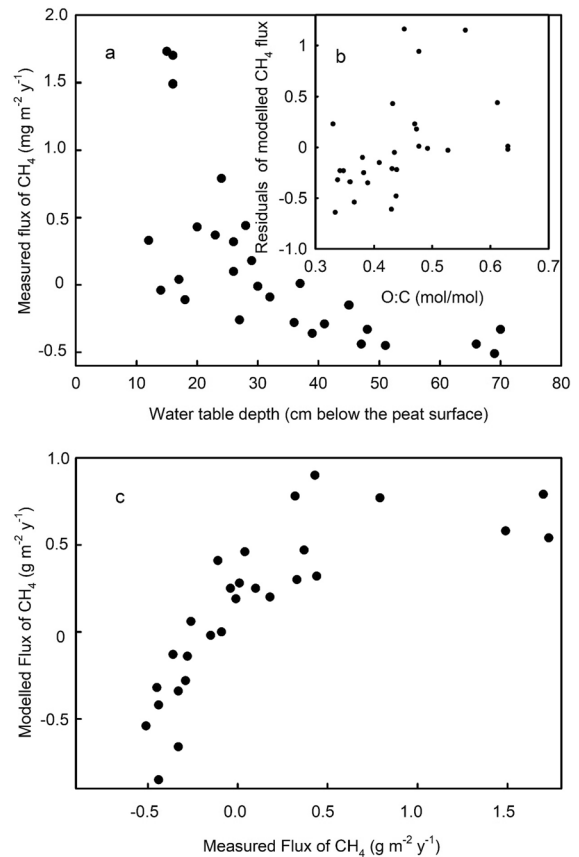


Fig. 6 **a** Measured annual flux of CH₄ (negative values represent net CH₄ uptake from the atmosphere to soil) in relation to water table depth (cm below the peat surface). **b** The residuals of regression model with water table as the independent factor (model CH₄ flux = $0.94 (\pm 0.20) - 0.02 (\pm 0.006) WT$) plotted against peat O:C ratio. **c** Predicted CH₄ flux from a regression model with WT and O:C as independent variables (CH₄ flux = $-0.34 (\pm 0.52) - 0.02 (\pm 0.005) WT + 2.63 (\pm 0.99) O:C$, R² 0.52, df_{reg} , df_{res} 2,25) plotted against measured CH₄ flux. Two cases with annual CH₄ fluxes of 12.5 g m⁻² (WT 1 cm) and 3.89 g m⁻² (WT 17 cm) were omitted from the analyses

(2022) that the peats with the smallest H:C ratio contain more polymeric quinones and phenols and were, inferred from their sampling site, likely to contain larger amounts of wood and root remains from trees and shrubs. In our data, H:C ratios were significantly lower in drained peats than in undrained ones (the peatland groups with the number of observations allowing statistical testing, Table 3). The decrease was proportionally largest in fen peats (PtkgII, Mtkg II), even after taking into account that the drained peat sampled at 20–40 cm may represent under undrained

conditions peat originating from a deeper peat layer (40–60 rather than 20–40 cm), with a lower H:C than the undrained peat at 20–40 cm (Fig. S3). In our undrained peats, the mean H:C difference between depths 20–40 cm vs. 40–60 cm was 0.0213, which was about 0.14 fold the mean H:C difference (0.157) between undrained and drained peat at 20–40 cm depth. However, we cannot rule out that some small part of this difference found between undrained and drained peats was due to compaction on drained peatlands. The extent of compaction was not available from our individual sites or from peatland groups in general and is likely to vary depending, e.g., on intensity of and time since drainage (e.g., Laiho and Pearson 2016).

The highest H:C ratios were determined in undrained moderately nutrient rich fen samples, often in combination with the lowest C:N ratios. The lowest H:C ratios were found in drained moderately nutrient rich fen samples with low C:N ratios. Overall, the H:C difference of 0.10–0.19 between our drained and undrained peats within peatland groups (Table 4) was quite a large one, up to 80% of the difference in mean H:C between hemiboreal bogs in Latvia and tropical swamps in Indonesia (Moore et al. 2018).

A large H:C ratio in decomposed peat indicates richness in lipids, but depletion in phenols and quinones, and peat formed by sedges and minerotrophic *Sphagnum* mosses (Teickner et al. 2022). These differences in forested vs. fen peats may be partly explained by patterns suggested by Leifeld et al. (2012) that intense aerobic decomposition of peat under drainage results in a larger H:C ratio, whereas less oxic conditions result in a decrease of the H:C ratio during decomposition. Our findings of H:C ratios are also consistent with Zaccone et al. (2018), where the H:C ratio was proposed as a good humification proxy for *Sphagnum* dominated peat deposits despite the different climatic conditions, botanical composition, depth and age of peat formation.

It is also noteworthy that in comparison to the regression model explaining CO₂ efflux with only water table depth, including also peat H:C ratio improved the model significantly. This points to the role of both substrate quality and water table depth in determining CO₂ release from peat. To our knowledge, this is the first study to show that H:C ratio is a useful predictor for annual heterotrophic CO₂ efflux on a plot scale. It seems to capture the change in peat properties associated in long-term lowering of water

table depth after forestry drainage. Our discovery finds support from laboratory incubations carried out under controlled conditions (e.g. adjusted water potential) that reported relationship between the specific measured respiration rate and H:C (model R²=0.43, Leifeld et al. 2012: Fig. S1).

In our data set WT was able explain additionally the residual variation in CO₂ release from peat unrelated to H:C ratio. At annual and intra-annual time scales, the water table determines the depth of the aerobic peat layer and thus influences not only CO₂ production but also its rate of diffusion to through surface peat.

Our results on undrained peat O:C ratios (Fig. 3; Table 4) were in the same range as those reviewed by Moore et al. (2018), whereas our undrained peat H:C ratios were higher than but the drained H:C ratios were similar to that global set of undrained peats. Based on the range of original O:C and H:C ratios in the litter input for peatlands, Moore et al. (2018) plotted the trajectories of ratios associated with increasing decomposition and two modes of decomposition: entirely with respiration and methanogenesis (a loss with ratios of H:C of 2 and O:C of 1) or a combination of 75% respiration and methanogenesis and 25% DOC (average fulvic and humic acid ratios of H:C~1.25 and O:C of ~0.7). For a more detailed description of the estimated ratios, see also Rice and McCarthy (1991) and Clay and Worrall (2015). A comparison with these estimated trajectories (Fig. S2) revealed that our drained peats had larger O:C and especially larger H:C than the trajectory for CO₂ to CH₄ loss in one-to-one ratio would suggest according to Moore et al. (2018). Assuming that the average atomic H:C and O:C ratios used in Moore et al. (2018) are applicable, the larger than estimated H:C in peat hints that our peats had likely lost C either or both via a combination of DOC, CO₂ and CH₄ loss or the gaseous loss was predominantly as CO₂, as it would be expected following drainage.

Similarly to earlier studies (e.g., Teickner et al. 2022), we found that O:C ratio was moderately or strongly correlated to conventional decomposition indicators, such as C:N ratio, OR and C_{OX}, but they all seemed to reflect the nutrient status (change along site type gradient) rather than drainage status. Furthermore, our drained peats' O:C ratio at the measured depth of 30–40 cm was not significantly associated with heterotrophic CO₂ efflux.

Overall, a high O:C ratio could indicate a higher concentration of polysaccharides. In a global sample set from undrained peatlands, CO₂ production increased with the proportion of *O*-alkyl C, an easily degradable carbohydrate, until levelling off around 50% *O*-alkyl C (Normand et al. 2021). The proportion of *O*-alkyl C, but not bulk O:C ratio, predicted CO₂ production rates in surface peat from a Swiss drained site (Leifeld et al. 2012). Supportingly, Serk et al. (2022) found that decomposition of specific hemicellulose structures mainly caused the loss of organic matter in surface peats whereas other types of polysaccharides were accumulating in drained sites. In all, the relationships between atomic ratios and specific molecular compounds may be compound specific and our findings of the indicative value of O:C and H:C ratio should be validated by further analysis of molecular compound composition.

Here, O:C ratio and degree of unsaturation (larger degree of unsaturation tend to have lower amounts of easily degradable substrates), were good proxies for CH₄ flux. In most of our sites, the measured peat O:C ratio at 30–40 cm originated from peat layers below the annual median water table, thus experiencing anoxia at least a part of the year and presumably being an active layer of methane production. Including peat O:C ratio improved the regression model explaining CH₄ flux in comparison to model with only water table depth.

The regulation of soil respiration has been linked to SOM characteristics on one hand to polysaccharide compounds with oxygenated functional groups (e.g., Leifeld et al. 2012) and on the other hand aromatic C (e.g., Freeman et al. 2004) that may reflect the persistence and resistance of lipid and lignin-like plant compounds, microbial transformations and accumulation of stable byproducts (e.g., Leifeld et al. 2017). Leifeld et al. (2012) suggested that drainage triggers the loss of younger topsoil C from peatlands, resulting in the exposure of older and more recalcitrant organic matter that will eventually control the decomposition rates. Increasing degree of unsaturation may imply accumulation of aromatic compounds (e.g., Worrall et al. 2016). These earlier results on drivers of soil respiration agree with our findings on the stronger correlation of degree of unsaturation ($r=0.67$), closely followed by H:C ratio (-0.64), than that of O:C (non-significant correlation) with CO₂ efflux in drained peats. In our forestry-drained peatlands, CO₂

efflux was also weakly but significantly correlated with peat dry bulk density, an indicator for both biochemical and physical transformation earlier demonstrated to be a sensitive proxy for CO₂ efflux (Ojanen et al. 2010), DOC release and N₂O efflux (Liu et al. 2019).

Degree of unsaturation not only showed the strongest positive correlation with CO₂ efflux, but also the strongest negative correlation with CH₄ flux. In all, these associations hint that degree of unsaturation can be a useful proxy for the lowering water table and integrate associated changes in peat quality after drainage.

Conclusions

Our analysis of extensive dataset on peat properties in undrained and forestry-drained peatlands with different fertility classes across Finland revealed that simple ratios of hydrocarbon constituents with oxygen and nitrogen H:C, O:C and C:N and their combination that indicate degree of unsaturation were widely valid degradation proxies. They captured both differences in the botanical origin of peat (fen, bog, treed swamps), its degree of degradation as well as potential decomposition pathways. These data indicated that peat H:C ratio is a useful proxy for peat degradation following drainage, as it indicated not only longevity of degradation but could also be directly linked to annual CO₂ emission from decomposition. Thus, Hypothesis 1 was partly supported, H:C ratio was significantly lower in drained peats than in undrained peats in most cases, but O:C ratio in drained peats did not significantly differ from undrained peats, except for oligotrophic forested mires.

In our dataset, the O:C ratio positively correlated with annual CH₄ flux from forestry-drained sites, presumably because high O:C in peat reflected the availability of easily degradable substrate for methanogenesis under anoxic conditions. The peat H:C ratio did not explain variation in annual CH₄ flux among drained sites, suggesting that peat H:C is not a good indicator for current annual CH₄ flux. Nevertheless, it does not exclude that H:C ratio may illustrate decomposition pathways and link to C loss as CH₄ during longer time scales as described above.

The C:N ratio seemed to be a good indicator of aerobic decomposition processes for *Sphagnum*

dominated forestry-drained peatlands but not for *Carex* dominated peatlands. The C:N ratio also reflected the nutrient status (change along site type gradient), as predicted by Hypothesis 2. Degree of unsaturation, calculated from changes in peat C, N and H, has potential for a robust integrative proxy for degradation, annual C gas losses and drainage-induced lowering water table. Applicability of these soil proxies should be tested for other land uses such as cropland and grassland on drained peat soils as well as rewetted and restored peatlands in boreal zone.

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Data Availability The data sets of the Geological Survey of Finland and Natural Resources Institute Finland analyzed in this study are deposited in Zenodo. The data of the Geological Survey of Finland is available in Zenodo: <https://doi.org/10.5281/zenodo.8434148>. Dataset on surface peat stoichiometry and physical properties in boreal undrained peatlands in Finland, Natural Resources Institute Finland <https://doi.org/10.5281/zenodo.10068486>. Dataset on surface peat stoichiometry and physical properties in boreal forestry-drained peatlands in

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Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

Appendix

In the Finnish classification of drained peatlands in practical forestry, the post-drainage successional plant communities of recently drained areas have been traditionally classified based on their original mire type. However, the older drainage areas have been classified into so called “drained peatland forest types”. The drained peatland types follow Laine (1989). A short description of drained peatland forest types used in this study is given below.

Rhtkg = drained peatland forest herb-rich type. Tree stand mainly composed of spruce (*Picea abies*) with a mixture of birch (*Betula pubescens*) and alder (*Alnus glutinosa*). Typical species include *Rubus idaeus*, *Sorbus aucuparia*, *Rhamnus frangula*, *Athyrium filix-femina*, *Dryopteris expansa*, *Matteuccia struthiopteris*, *Thelypteris connectilis*, *Filipendula ulmaria*, *Viola sp.*, *Pyrola sp.*, *Calamagrostis purpurea*, *Rhizomnium sp.*, *Plagiomnium sp.*, *Sphagnum squarrosum*, *S. warnstorffii*, *S. centrale*. Peat typically highly decomposed sedge-wood peat.

Mtkg I = drained peatland forest *Vaccinium myrtillus* type. Tree stand dominated by spruce (*Picea abies*) with a mixture of birch (*Betula pubescens*). Typical species include *Dryopteris carthusiana*, *Trientalis europaea*, *Equisetum sylvaticum*, *Linnaea borealis*, *Maianthemum bifolium*, *Orthilia secunda*, *Hylocomium splendens*, *Polytrichum commune*. Peat typically highly decomposed *Sphagnum*-wood-peat.

Mtkg II = drained peatland forest *Vaccinium myrtillus* type. Species similar to *Mtkg I* type. However, tree stand a mixture of spruce (*Picea abies*) and birch (*Betula pubescens*). Peat typically moderately decomposed *Sphagnum*-sedge-peat.

Ptkg I = drained peatland forest *Vaccinium vitis-idaea* type. Tree stand varies from spruce (*Picea abies*) to pine forest (*Pinus sylvestris*) with a mixture of birch (*Betula pubescens*, *B. pendula*). Typical species include *V. vitis-idaea*, *V. myrtillus*, *V. uliginosum*,

Ledum palustre. Peat typically moderately decomposed *Sphagnum*-wood-peat.

Ptkg II=drained peatland forest *Vaccinium vitis-idaea* type mainly with pine (*Pinus sylvestris*) with a mixture of birch (*Betula pubescens*). Species similar to *Ptkg I* type. Peat typically *Sphagnum*-sedge or sedge-*Sphagnum*-peat.

Vatkg=drained peatland forest dwarf-shrub type mainly with pine (*Pinus sylvestris*). Typical species include *Ledum palustre*, *Betula nana*, *Chamaedaphne calyculata*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *V. myrtillus*, *Pleurozium schreberi*, *Dicranum polysetum*. Peat typically weakly decomposed cotton grass (*Eriophorum*)-*Sphagnum*-peat.

Jätkg=drained peatland forest lichen type with pine (*Pinus sylvestris*). Typical species include *Cladonia arbuscula*, *Cladonia rangiferina*, *Caluna vulgaris*. Peat typically weakly decomposed *Sphagnum*-peat.

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