Loss of the soil carbon storage function of drained forested peatlands

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SUMMARY

Peatlands form a large but unstable C store. Drainage of peatlands converts them into C sources, which is undesirable if increases in atmospheric CO_2 levels are to be minimised. Therefore, quantification of C stocks and an understanding of which ecosystems or management regimes are capturing or emitting C is needed. Such information is scarce for temperate European forests. We studied the soil properties of sixteen peatlands in Switzerland, representing three forest types, to test whether peatlands that are more strongly affected by drainage (according to vegetation) have lost their function as C sinks or stores. Bulk density and ash enrichment, as well as H/C, O/C and C/N quotients, indicated that the soils of the two forest types that appeared to be more strongly affected by drainage were more degraded and had lost their functions as C stores. Long-term net rates of C loss estimated using the ash residue method were similar across all three forest types, for sites where this could be estimated.

KEY WORDS: carbon stocks, drainage, greenhouse gas, peat quality, temperate zone

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INTRODUCTION

Peatlands cover only around 3 % of the world's land surface (Parish *et al.* 2008). Their high carbon (C) density means they are nonetheless important C stores, containing 20–50 % of the world's soil C (Bussell *et al.* 2010). However, this store is not stable and can be altered, for example by perturbation of the water table (Parish *et al.* 2008).

Peat forms under water-saturated anoxic conditions, where the rate of organic matter input to the system exceeds its rate of degradation (Clymo 1984). The drying of peat, for example through drainage, allows oxygen to enter the system. The oxygen enables oxidisation of organic C and its emission to the atmosphere as CO_2. Thus, the C store becomes a C source. It is estimated that drained and burned Histosols were responsible for around 13 % of greenhouse gas (GHG) emissions from the agriculture, forestry and land-use sector between 2000 and 2009 (Smith *et al.* 2014). Given that the increase in atmospheric CO_2 concentration should be minimised, this degradation of the C storage function of peatlands must be avoided. For this purpose, it is necessary to assess whether or not managed peatlands function as C stores, and one method involves comparing the characteristics of peat from sites with different levels of disturbance.

There has recently been a surge in research on the C storage and sink functions of organic soils under grassland and cropland in Europe (e.g. Petersen *et al.* 2012, Leiber-Sauheitl *et al.* 2014), as well as beneath boreal (e.g. Simola *et al.* 2012) and tropical (e.g. Couwenberg & Hooijer 2013) forests. However, little work has been carried out on organic soils occurring under temperate forest in Europe, which means the extent to which drained forested peatlands in this region are losing their C storage function is unclear. Forests cover 26 % of temperate Europe (Spiecker 2003) and it is estimated that more than 99 % of this area is managed (Parviainen 2005), so management impacts could be considerable.

Forest covers approximately 31 % of Switzerland (Anon. 2010) and 13 % of the country's peatlands; which, in turn, cover about 1 % of the country (Wüst-Galley *et al.* 2015). Swiss forests are classified by habitat type, based on a combination of vegetation (mostly following the forest community classification of Ellenberg & Klötzli (1972)), soil, and external factors such as the occurrence of avalanches and rock-falls (Stocker *et al.* 2002, von Wyl *et al.* 2003, Frey & Bichsel 2005). In this study we used peat cores from the three forest types that can grow on peat. The purpose was to determine whether the soil characteristics of these peatlands, including chemical composition, reflect their drainage intensity as inferred from what is seen above ground. We also test whether drained forested peatlands have lost their functions as C sinks and C stores and compare C stocks between the three forest types.

METHODS

Sites

The three forest habitat types sampled were "*Sphagnum* - mountain pine forest" (S-mp forest, Sphagno-Pinetum montanae), "*Sphagnum* - spruce forest" (S-s forest, Sphagno-Picetum typicum) and "birch - pine forest" (b-p forest, Pino-Betulum pubescentis). Latin names and classification of plant associations follow Ellenberg & Klötzli (1972).

Many S-mp forests form parts of raised bogs. The growth of trees indicates that this bog habitat type is drier than open raised bog (Grosvernier *et al.* 1994, Grünig 1994), suggesting the possibility of natural or artificial drainage. The forests are, nonetheless, sufficiently wet for *Sphagnum* (*S. capillifolium* and to a lesser extent *S. magellanicum*) to dominate the moss layer (Ellenberg & Klötzli 1972), and many of them are still considered to be raised bogs (calculated from Grünig *et al.* 1986).

S-s forest often occurs adjacent to raised bog, forming a concentric circle around S-mp forest and apparently reflecting more intense natural or artificial drainage (Grosvernier *et al.* 1994). The soil of S-s forest is correspondingly drier than that of S-mp forest (Ellenberg & Klötzli 1972), and this is reflected by the more vigorous growth of trees on these sites. Many S-s forests are not considered to be raised bogs (calculated from Grünig *et al.* 1986).

The third forest type, b-p forest, has *as wooded bog* become extremely rare in Switzerland (Ellenberg & Klötzli 1972). Occurring in the pre-alps or lowlands, the vast majority of b-p sites - including all sampled in this study - are artificially drained (Stocker *et al.* 2002, von Wyl *et al.* 2003). Very few (none in this study) are regarded as raised bog vegetation (Grünig *et al.* 1986) and, amongst the three forest types investigated, we consider b-p forest to be the most affected by drainage. Using this qualitative assessment of drainage intensity, we consider S-mp to be the least affected by drainage, p-b to be the most affected, and S-s to be intermediately affected.

Sampling

Seventeen sites, representing the geographical and altitude ranges of the three forest types from the central plateau to the pre-Alps, were sampled in March–May 2013 (Figure 1). Sites for which peat extraction had been documented were excluded. Table 1 gives the location, forest type, peat thickness, mean annual precipitation (MAP) and temperature

Figure 1. Map showing the location of the 17 sites sampled in Switzerland. Symbols representing some adjacent sites are superposed at this scale. Where separate symbols cannot be distinguished or overlap closely, the number of sites represented is indicated in brackets.

Table 1. List of sites sampled, including information on the forest type, location (to the nearest 100 m), peat thickness (a range refers to the different depths reached by the three or four cores), drainage history, mean annual precipitation (MAP) and mean annual temperature (MAT) of each site. The two-letter canton abbreviations are as follows: FR = Fribourg, LU = Luzern, SG = St. Gallen, ZH = Zürich.

Site name (canton)	Forest type	Co-ordinates (WGS 1984)	Peat thickness (cm)	Drainage	MAP (mm)[1]	MAT (°C)[2]
Bannwald (LU)	pine - birch forest (p-b)	8.191, 47.011	>100	drained 50–80 years ago[3]	1541.7	6.5
Chiemiwald (FR)		7.171, 46.846	>100	bordered by a peat-cutting face which was established by 1844–1851[4]	1034.0	9.0
Maas (ZH)		8.455, 47.359	80 to >100	drainage date unknown; drain seen during fieldwork	1118.6	9.1
Meiestossmoos A (LU)		8.211, 47.007	>100		1718.6	6.7
Sigigerwald (LU)		8.148, 47.053	45–60	drainage date unknown; drain seen during fieldwork	1317.2	8.7
Weidli (FR)		7.282, 46.768	30–60	drainage date unknown; drain seen during fieldwork	1295.2	7.7
nr. Aux Pâquier de dessus (FR)	*Sphagnum* - spruce forest (S-s)	7.159, 46.667	85–100	drained by 1942[5]	1682.6	6.0
Dévin des Dailles A (FR)		6.961, 46.523	60–90	unclear; road passing the bog was present in 1942[5]	1537.8	5.8
Foremoos (LU)		8.214, 47.009	65 to >100	adjacent site drained between 1901 and 1906[6]	1697.8	6.7
Joux Derrière (FR)		6.996, 46.577	60–100	forest drained by 1903[5]	1431.9	6.0
Meiestossmoos B (LU)		8.210, 47.007	60 to >100	peat extraction on adjacent site by 1890[7]	1719.2	6.7
Summerigchopf A (SG)		9.401, 47.213	>100	unclear; open land uphill from forest was drained by 1935[5]	1868.6	7.6
Dévin des Dailles B (FR)	*Sphagnum* - mountain-pine forest (S-mp)	6.963, 46.522	>100	possibly intact[8]	1537.0	5.8
Rüchiwald (LU)		8.039, 46.882	60 to >100	possibly intact[9]	1939.3	5.6
Summerigchopf B (SG)		9.402, 47.213	>100	drain established between 1935 and 1960[5]	1856.	7. 7
Vorderwengi (SG)		9.098, 47.198	95 to >100	unclear; open land uphill from forest was drained by 1935[5]	2149.0	4.6
Les Pueys (FR)		6.969, 46.524	0–30 cm	drain seen during fieldwork; drainage date unknown	1531.6	5.7

[1] MAP is the average for the years 1961–2009; [2] MAT is the average for the years 1981–2010; MAP and MAT derived from original data from MeteoSchweiz; [3] from local information; [4] survey dates for the Stryenski map of Canton Fribourg (Stryienski 1855); [5] information from aerial photographs; [6] Siegfried topographical maps (1870–1949), map sheet 204, 1901 and 1906; [7] Siegfried topographical map (1870–1949), map sheet 204, 1890; [8] Grünig *et al.* (1986) and Lüdi (1973); [9] Grünig *et al.* (1986).

(MAT), and information about the drainage history of each site. The dominant or common tree and shrub species present at every site except Les Pueys matched the list of characteristic species for the relevant forest type (Ellenberg & Klötzli 1972).

Cores were extracted using a Russian peat corer (Eijkelkamp, Giesbeek, The Netherlands), which extracts cores 50 cm long (diameter 5.2 cm). At all except two sites, a 1 m core was extracted at each of three locations. At Weidli and Braunwald, cores were extracted at four locations. At each location the 1 m core was obtained by sampling twice from the same hole. Possible disturbance was reduced by exactly aligning the corer with the blade facing in the same direction every time it was inserted. The one-borehole (rather than the two-borehole) technique was chosen in order to obtain a continuous peat core.

If the mineral layer was reached before 1 m, coring was discontinued. To ensure that sufficient material for element analysis would be collected from the surface layer, an additional peat sample was taken at each location, adjacent to the main core, using a sharpened metal cylinder (diameter 5.5 cm, length 10 cm). Samples were stored in airtight containers at 4 °C for a maximum period of four months before drying.

Preparation and analysis of samples

Samples were cut into 5 cm (10–30 cm depth) and 10 cm (0–10 cm and 30–100 cm depth) segments. Each segment (sample) was analysed separately. Samples were initially dried at 105 °C for approximately 20 hours then ground using a ball mill (RETSCH, Hann, Germany). Residual moisture was quantified and removed by heating the samples to 130 °C using a prepAsh®129 machine (Precisa Instruments AG, Dietikon, Switzerland). The resulting dry matter was used to calculate bulk density (g cm^{-3}), and ash and elemental concentrations. Loss of mass upon ignition (600 °C) was used to infer the proportion of ash in each sample, using the PrepAsh machine. C, H, N and O were measured using a CHNS–O element analyser EuroEA3000 (HEKAtech, Germany). All samples were free of carbonate, so we assume total C is equal to organic C. Any segments containing mineral soil, together with adjacent segments, were omitted from all analyses unless stated. pH was measured for one core (occasionally two) from each site (238 segments from 23 cores in total) using an ExStik® pH100 pH meter (ExTech Instruments, Nashua, New Hampshire, USA), calibrated at pH 7 and pH 4.01. For this, an aliquot of fresh peat (equivalent to 10 g dry matter) was diluted in distilled water (2.5 parts water to 1 part material by mass), shaken, left for approximately 20 hours and re-shaken before measurement.

With the exception of one site, all cores from all sites were long enough and contained sufficient organic C for the soil to be classified as organic (IPCC 2006). At “Les Pueys” (S-mp forest), the peat layer met the thickness criterion (> 10 cm) only at the coring location in the centre of the site; this site was excluded from all further analyses.

Data analysis

Bulk density, ash concentration, C/N quotient and pH
The soil properties bulk density, ash concentration, C/N quotient and pH were analysed using mixed models, in order to test whether these properties differed significantly between the wetter (S-mp) and drier (S-s and p-b) forest types as well as between the two drier (S-s and p-b) forest types. Segment depth was treated as a covariate and forest type was treated as an unordered factor. The four soil properties listed above were treated as dependent variables, and were $\log_{10}$ transformed to remove heteroscedasticity from the residuals of the statistical models.

In a first step, ANOVAs were carried out to test whether the factor ‘forest type’ was a significantly important factor in explaining variation in the each of the four soil properties ($\alpha = 0.05$). To do this, the following two mixed models, [1] and [2], were run for each dependent variable and compared using an ANOVA.

$$variable \sim depth + forest\ type + random\ effects \qquad [1]$$

$$variable \sim depth + \ random\ effects \qquad [2]$$

where the *random effects* ‘core’ and ‘site’ (‘core’ nested in ‘site’) were included to account for multiple segments from each core and multiple cores from each site, respectively. A linear mixed model was used to model pH. Because bulk density, ash concentration and C/N quotient varied non-linearly with depth, additive mixed models were run for these variables, with a cubic smoothing spline applied to the variable ‘depth’ and the optimal amount of smoothing determined by generalised cross-validation (Wood 2006, Zuur *et al.* 2009).

In a second step, for all soil properties except pH (for which forest type was not significantly important), mixed models were run using orthogonal Helmert contrasts (from the "Stats" core package; R Core Team (2014)). Contrasts generally allow the user to specify between which factor levels comparisons are made, and we used Helmert contrasts to test specifically: (i) whether the two drier forest types (S-s and p-b) differed from S-mp forest, which we expected to be less affected by drainage; and (ii) whether the two drier forest types differed from one another. These models were also used to obtain parameter estimates for the different forest types. For bulk density and ash concentration, additive mixed models (Equation 1) were run. For C/N quotient, inspection of the raw data suggested that a linear mixed model incorporating a term for interaction between habitat type and depth was necessary (the model described by Equation 3, with random effects as described above).

$$variable \sim depth \times forest\ type + random\ effects \qquad [3]$$

The functions lme from the package nlme (Pinheiro *et al.* 2014) and gamm (Wood 2011) from the package mgcv (Wood 2014) were implemented using R (R Core Team 2014) to run linear and additive mixed models, respectively. Graphs of the residuals of the final model showed no heteroscedasticity or departure from normality. To compare models with nested fixed effects, models were estimated with maximum likelihood; to obtain coefficient estimates, models were estimated with restricted maximum likelihood (Zuur *et al.* 2009).

H/C and O/C quotients

Molar O/C and H/C quotients of the upper 30 cm and the lower 70 cm of cores were displayed in van Krevelen plots (van Krevelen 1950), with values averaged across replicates and sites.

C stocks

C stocks, C_{tot} (t ha^{-1}), were calculated as:

$$C_{tot} = \sum_{i=1}^{n} C_{\%i} \times D_i \times \tau_i \qquad [4]$$

where n is the total number of segments, $C_{\%i}$ is the percentage C of the ith segment, D_i is its bulk density (g cm^{-3}) and τ_i its thickness (cm). C stocks were calculated for the upper 30 cm and upper 1 m of organic soil (including the segment adjacent to the mineral layer); where soil cores were shorter than 1 m, the latter calculation referred only to the thickness of peat layer sampled.

The C stock, average bulk density and average C concentration (%) of each core (i.e. across all depths) were modelled to test whether C stocks differed significantly between forest types and whether they were affected by differences in bulk density or C concentration. For each of these three dependent variables the following two mixed models (models described by Equations 5 and 6) were compared using an ANOVA:

$$variable \sim forest\ type + random\ effect \qquad [5]$$

$$variable \sim random\ effect \qquad [6]$$

where the *random effect* ‘site’ was included to account for multiple cores from each site. Where a model including the factor ‘forest type’ was significantly better than a model without this factor ($\alpha = 0.05$), the model described by Equation [5] was run including the factor ‘forest type’, using orthogonal Helmert contrasts (as described above) to test the differences (i) between the two drier forest types (S-s and p-b) and the S-mp forest type, and (ii) between the two drier forest types. The functions and likelihood methods used were the same as those described for the analysis of bulk density, ash concentration, C/N and pH.

C loss

C loss was calculated for each peat core using the ash residue method of Leifeld *et al.* (2011a). This method assumes a constant ratio of organic C to ash throughout the period of peat accumulation (Leifeld *et al.* 2011a) and requires identification of conditions assumed to represent those of the core in an undisturbed state. As adjacent pristine or near-natural sites were not available for most of the sites investigated, we relied upon identification of a reference layer in the deeper part of each core, as follows. For each core, each segment was assigned to one of the categories ‘disturbed’ and ‘undisturbed’, according to whether it occurred above or below a given ‘break point’. To find the optimal break point, the quotient of ash content (%) of ‘disturbed’ / ‘undisturbed’ segments was calculated for each site and these two groups were compared using a Welch’s t-test assuming non-equal variance (Welch 1947) considering, in turn, all depths (15 cm to 90 cm) as the potential ‘break point’. The break point that resulted in the greatest disturbed / undisturbed segments quotient was identified as that which best represented the onset of disturbance for the site, as long as: (i) the quotient exceeded unity, ensuring higher ash content in the disturbed layer; and (ii) the P-value of the Welch’s t-test was greater than 0.05, ensuring that only cases in which a stable reference horizon with low ash content were identified. Segments occurring below the identified break point were classified as undisturbed, i.e. within the ‘reference layer’.

The C loss, C_d, for the whole peat core (t ha^{-1}) was calculated as:

$$C_d = \sum_{i=1}^{n} \frac{C_i}{ash_r} \times ash_i - C_i \qquad [7]$$

where n is the number of segments occurring above the pre-defined reference horizon and thus assumed to be disturbed, C_i and ash_i are the amounts of C (t ha^{-1}) and ash (t ha^{-1}) in the ith segment, and ash_r is the amount of ash in the reference layer. The amount of C (t ha^{-1}), C, in each segment is calculated as:

$$C = C_{rel} \times D \times 100 \qquad [8]$$

where C_{rel} is the fraction of C in that segment and D is the bulk density (g cm^{-3}) of that segment. Similarly, ash amount (t ha^{-1}), ash, in each segment is calculated as:

$$ash = ash_{rel} \times D \times 100 \qquad [9]$$

where ash_{rel} is the fraction of ash in that segment.

Long-term net rates of C loss (LTRCL) were calculated by dividing the C loss for the whole peat core by the number of years since drainage. Where only a range of years since drainage was known, rather than the exact date, the minimum and maximum LTRCLs were calculated by using the oldest and most recent possible drainage dates for this calculation, respectively.

RESULTS

Bulk density, ash, C/N and pH

The values of bulk density, ash concentration and C/N differ significantly between the different forest types (α = 0.05, Table 2). The peat of S-mp forests has significantly lower bulk density and ash concentration than that of S-s and p-b forests, whereas bulk density and ash concentration do not differ significantly between the latter two forest types (Table 2, Figure 2). The C/N quotient of peat from S-mp forest decreases with increasing depth (by 0.18 % cm^{-1}), whereas it increases with increasing depth for S-s and p-b forests (by 0.07 % cm^{-1} for S-s forest and by 0.16 % cm^{-1} for p-b forest; Figure 2). The three rates of change of C/N with depth are significantly different from one another (α = 0.05, Table 2).

pH is similar across all forest types (Table 2, Figure 2). The total variation across all except two of the cores is 3.26–5.50. Two cores, one from S-mp forest and one from p-b forest, contain a total of five segments with pH > 5.5 (maximum pH 6.47).

H/C and O/C

The H/C and O/C quotients of the upper and lower segments of the cores from the 16 sites lie between the typical signature values for carbohydrates and lignin (Figure 3). The values for deeper segments of the cores tend to be smaller than those for shallower segments (Figure 3). For deeper segments, the three forest types cannot be differentiated on the basis of H/C and O/C (Figure 3b); whereas for shallower segments, the O/C quotients of peat from S-mp forests tend to be larger than those of peat from the other two forest types, which are indistinct from one another (Figure 3a).

All soil characteristics measured at individual sites (mean and standard deviation across replicates) are given in Table A1 (Appendix); and mean bulk density, ash concentration and soil pH (across all depths) for the three forest types are shown in Table 3.

Table 2. Results of statistical modelling of bulk density, ash concentration, C/N quotient and soil pH of cores. P values generated by ANOVA are listed for the comparison of models [1] and [2] ([1] *vs*. [2]) and the two contrasts between forest types.

Attributes	Models	Forest types	
	[1] *vs*. [2]	S-mp *vs*. S-s and p-b	S-s *vs*. p-b
Bulk density	0.0183	0.005	0.895
Ash (%)	0.0303	0.008	0.855
C/N	0.0346	< 0.001[1]	0.031[1]
Soil pH	0.8253	n/a[2]	n/a[2]

[1] P values of the interaction terms forest type × depth.

[2] comparison not carried out because the difference between forest types was not significant.

C stocks

C stocks differ significantly between forest types in the upper 30 cm but not in the upper 1 m (Figure 4 and Table 4). In the upper 30 cm, the C stocks of peat from S-mp forest are significantly lower than those of peat from the other two forest types (Figure 4a and Table 4), between which C stocks do not differ significantly (at both depths, P > 0.3). The overall mean C stock in the upper 30 cm is 145.6 ± 24.1 t C ha^{-1}. Organic C concentration does not differ between the forest types (Table 4). The bulk density of peat from S-mp forests is significantly lower within both depth ranges (Table 4).

C loss

Reference horizons were identified for three sites from each of the p-b forest and S-s forest types

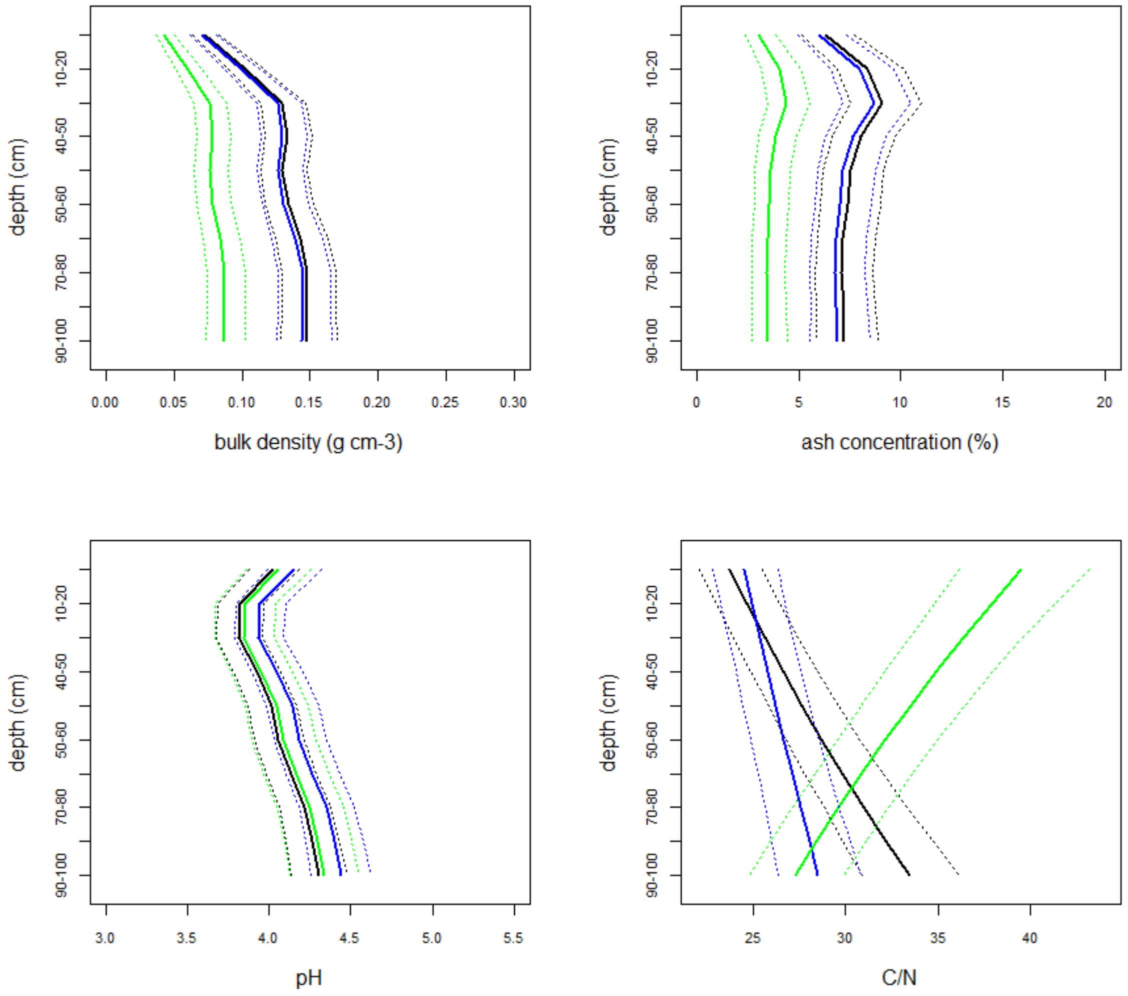

Figure 2. Predicted values of the final models of bulk density, ash content, soil pH and C/N, for the three forest types (black = p-b forests, blue = S-s forests, green = S-mp forests); solid lines are predicted values based on mean coefficient values, dotted lines indicate predicted ranges based on the standard errors of the mean coefficient values.

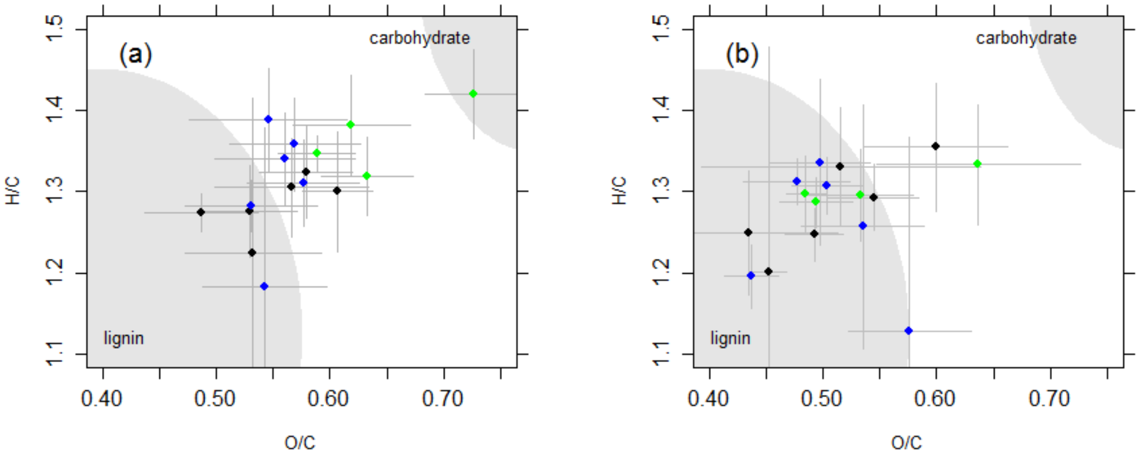

Figure 3. Van Krevelen plots for (a) the upper 30 cm and (b) the lower 70 cm of the 16 sites. Points represent averages for relevant core segments from each site; grey bars represent one standard deviation; grey surfaces represent the range of O/C and H/C for lignin and carbohydrates, adapted from Preston & Schmidt (2006).

Table 3. Mean and standard deviation (in brackets) of the bulk density, ash concentration and soil pH of the three forest types, across all segments of all cores.

Forest type	Bulk density ($g\ cm^{-3}$)		Ash (%)		Soil pH	
	mean	SD	mean	SD	mean	SD
S-mp	0.089	0.051	4.37	2.44	4.07	0.48
S-s	0.127	0.040	9.84	7.82	4.07	0.45
p-b	0.127	0.057	9.81	9.23	3.90	0.56

(Table 5). At other sites belonging to these two forest types, ash concentration is higher than at sites where a reference horizon could be identified and (more importantly) is variable throughout the core, including the deepest layers (Table A1) where an undisturbed layer might be expected to occur. A reference horizon was identified for one S-mp forest site (Table 5). For the other S-mp sites, ash concentration either increases slightly and continually with increasing depth, or shows enrichment only in the deeper parts of the profiles (70 cm and below at Dévin des Dailles B, 30 cm and below at Sommerichopf B; see Table A1).

LTRCL values range from 0 to 8.8 t C $ha^{-1}a^{-1}$. The ranges of values at S-s and p-b sites for which rates could be calculated overlap (Table 5).

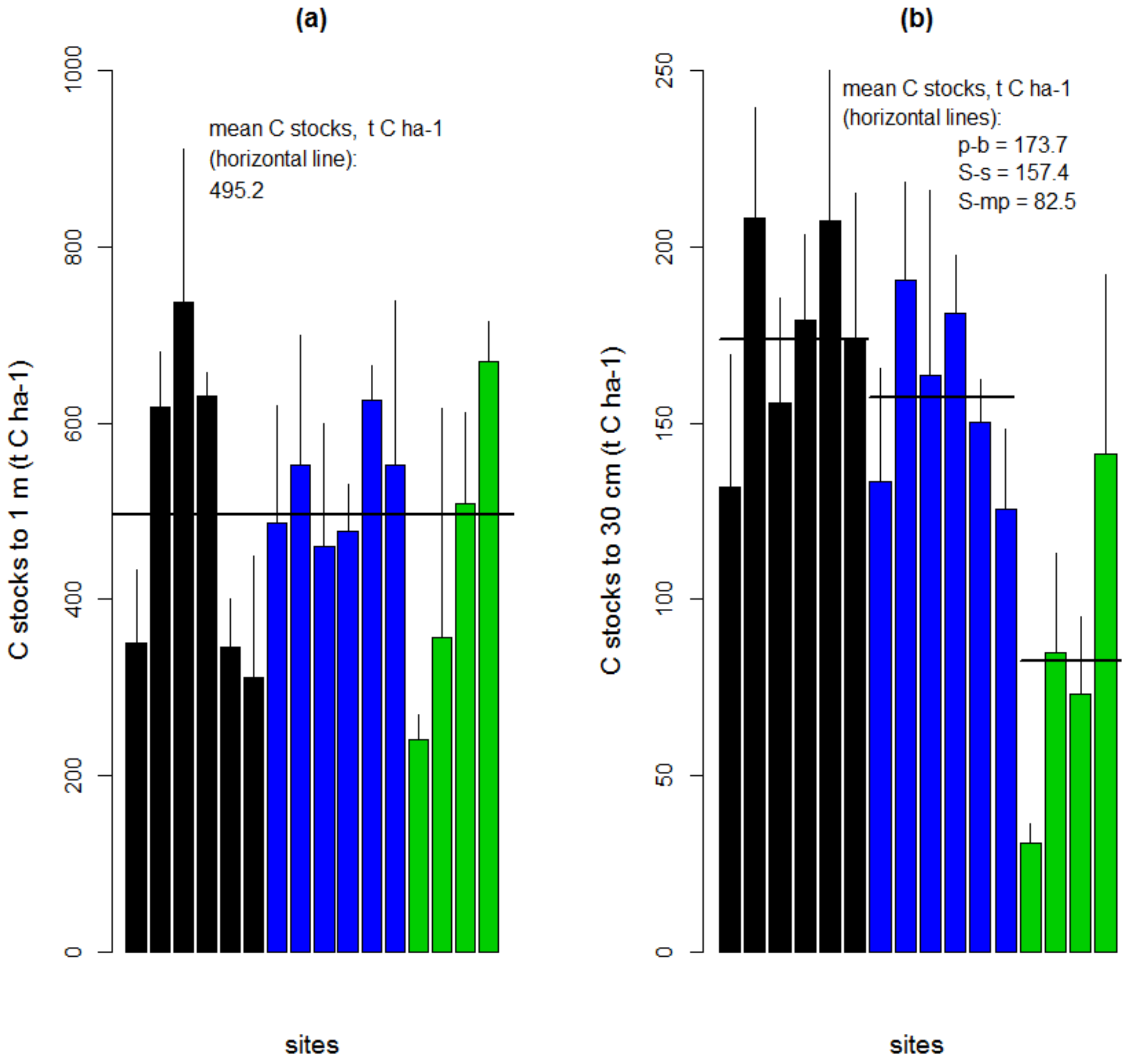

Figure 4. C stocks in (a) the uppermost metre and (b) the uppermost 30 cm of soil at the 16 sites; black = p-b forests, blue = S-s forests, green = S-mp forests; horizontal lines indicate mean C stocks, vertical lines indicate standard deviation of C stocks within each site; note that y-axis scales differ between the two plots.

Table 4. Results of analysis of organic C concentration, bulk density and C stocks, of the upper 1 m or 30 cm of cores.

Attribute	Importance of 'forest type', P value[1]	Intercept[2]	P value[2]	Importance of 'forest type', P value[1]	Intercept[2]	P value[2]
	to 1 m			upper 30 cm		
C org (%)	0.7477	-	-	0.8186	-	-
Bulk density (g cm^{-3})	0.0325	-0.03	0.0226	0.0004	-0.03	0.0006
C stocks (t C ha^{-1})	0.6564	-	-	0.0005	-41.9	0.0007

[1] P value of ANOVA comparing linear mixed models with and without the factor 'forest type'.
[2] P value of factor 'forest type' in the contrast S-mp *versus* S-s and p-b; intercept estimate for forest type S-mp.

Table 5. Results of the identification of reference horizons and calculation of LTRCL for the 16 sites. SD = standard deviation.

Site name	Forest type	Depth of start of ref. horizon (cm)	Mean C loss (t C ha^{-1}) (and SD)	Ash concentration (%) of ref. horizon[1] or of deepest 20 cm of core[2]	LTRCL (t C ha^{-1} a^{-1})	
					Minimum	Maximum
Bannwald	Pine-birch (p-b)	40	47.3 (52.3)	2.7[1]	0.20	1.80
Chiemiwald		30	77.8 (77.4)	5.7[1]	0.02	1.06
Meiestossmoos A		60	471.2 (125.2)	3.2[1]	¤	8.83
Maas		*		22.9[2]		
Sigigerwald		*		12.7[2]		
Weidli		*		9.6[2]		
nr. Au Pâquier de des.	*Sphagnum*-spruce (S-s)	30	39.2 (9.7)	2.7[1]	¤	0.77
Dévin des Dailles A		25	38.9 (11.4)	5.9[1]	¤	0.87
Meiestossmoos B		25	191.5 (75.1)	2.5[1]	¤	2.23
Joux Derrière		*		13.0[2]		
Foremoos		*		10.0[2]		
Sommerigchopf A		*		20.9[2]		
Rüchiwald	*Sphagnum*-mountain pine (S-mp)	60	41.3 (14.5)	1.44[1]	¤	¥
Dévin des Dailles B		*		6.1[2]		
Sommerigchopf B		*		5.3[2]		
Vorderwengi		*		6.1[2]		

* = reference horizon not identified. Minimum and maximum LTRCLs incorporate error from drainage dates (a minimum and maximum number of years since drainage), and error associated with the estimate of C loss (the minimum and maximum rates obtained from the 3 or 4 replicates per site); minimum LTRCL = minimum rate / maximum number of years since drainage; maximum LTRCL = maximum rate / minimum number of years since drainage); maximum (¤) or minimum (¥) number of years since drainage unknown.

DISCUSSION

pH, bulk density and ash concentration

Strong- to medium-acidic soil pH values, as found in all forests investigated here, are typical for raised bog ecosystems (Gobat *et al.* 2013).

Comparison of the peat bulk density values found in this study with values found in the scientific literature suggests that the bulk density of peat from S-mp forest lies towards the upper end of the range of bulk density values reported from other undrained wooded and non-wooded peatlands (Table 6). Bulk density values for undisturbed forested peatlands overlap with those for drained forested peatlands, although the latter are generally higher (Table 6). Values obtained for S-s and p-b forests in this study lie within the same total range. Upon drainage, bulk density increases due to a combination of three factors relating to hydrological disturbance, namely: loss of supporting pore water pressure; shrinkage due to evaporation; and oxidation of low-density organic matter (Kasimir-Klemedtsson *et al.* 1997). The significantly higher bulk density of peat from S-s and p-b forests, as compared to peat from S-mp forests, supports the hypothesis that the former two forest types have been more strongly affected by hydrological disturbance and/or compaction than the latter.

Hydrological disturbance can also be inferred by using information on ash concentration, as ash remains in the soil following the removal of organic matter through oxidative decomposition. Thus, we would expect to see more ash enrichment in the upper layers of peat from S-s and p-b forests than in the corresponding layers at S-mp forests. However, caution must be exercised in using ash enrichment to infer increased peat decomposition through oxidation because ash enrichment can also result from an increase in atmospheric ash deposition or a reduction in peat accumulation rate (Steinmann & Shotyk 1997, Zaccone *et al.* 2012). Although the rate of atmospheric ash deposition may change through time, given the spatial proximity of our sites we assume that any such changes were similar at all of them, meaning that changes in deposition rate should not have affected the layer-by-layer comparisons of ash content. Indeed, for the two localities (Dévin des Dailles and Sommerigchopf) where adjacent S-mp and S-s forests were sampled, the ash content of S-s forest peat is consistently higher than that of S-mp forest peat (Table A1). It is more difficult to assign the cause of increased ash concentration between reduced peat accumulation and increased decomposition, but this may be unnecessary because both processes can be caused by the same agents (e.g. lowered water table due to artificial drainage, or trampling by cattle which mixes peat and changes hydrological conditions at the surface) and, importantly, both reduce the ecosystem’s ability to sequester C.

Ash enrichment was commonly identified in cores from S-s and p-b forests. Almost all of these sites showed considerable ash enrichment, either in the upper peat layers (five sites) or throughout the core (the six sites for which no reference horizon could be identified, suggesting that the entire peat profile is disturbed). The exception (Bannwald) has only very low ash enrichment near the surface; this is also the one p-b site where *Sphagnum* dominates the forest floor. In contrast, ash enrichment was identified in the upper peat layer at only one of the four S-mp sites (Rüchiwald). At two other S-mp sites (Sommerig-

Table 6. Peat bulk density values from other undrained forested and open peatlands, and drained forested peatlands, from published studies.

Situation of peatland	Peat bulk density (g cm^{-3})	Reference
undrained wooded	0.02-0.19	Grigal *et al.* (1989)
	~0.05-0.11	Minkkinen & Laine (1998)
undrained, non-wooded	~0.04-0.13	Clymo (1983)
	~0.05-0.13, 0.03-0.08, 0.05-0.1	Anderson (2002)
	0.01-0.1	Leifeld *et al.* (2011a)
drained, wooded	~0.10-0.16	Minkkinen & Laine (1998)
	0.4-0.14	Leifeld *et al.* (2011a)
	0.125-0.26, 0.087-0.248	Lienert (2013)

chopf and Dévin des dailles) the upper peat layers have lower ash levels than the deeper layers, providing (importantly) no evidence of present-day net C loss due to oxidative decomposition. For another S-mp site (Vorderwengi) we did not identify a distinct reference layer but, rather, a slow and steady downward increase in ash concentration consistent with the ongoing catotelm decomposition that may occur even in undisturbed mires (Clymo 1984). Overall, the ash enrichment data suggest that drainage is less important in the present-day dynamics of S-mp forests than in those of p-b and S-s forests, and support the hypothesis that the C sequestering function of peat from the latter two forest types is impaired.

Inference about decomposition - element quotients

During the processes of peat formation and decomposition, the preferential loss of easily decomposable polysaccharides, proteins or phenols and the co-occurring enrichment of aromatic molecules lower the O/C and H/C quotients (Klavins *et al.* 2008, Biester *et al.* 2014). If the p-b and S-s forests are more affected by drainage than the S-mp forests, then we would expect the values of H/C and O/C to reflect this, given that drainage in these forests has been happening for decades or centuries. Firstly, we would expect H/C and O/C in peat from S-mp sites to decrease with increasing depth, reflecting the long-term ‘background’ decomposition of peat that occurs even in intact peatlands (Clymo 1984). Although the process occurs in all peatlands, we would expect to see this pattern only in sites that are less affected by oxidative decomposition due to disturbance, because the pattern would be masked in sites where oxidative decomposition had altered H/C and O/C, especially in the upper peat layers. Indeed, we observed a decrease in these quotients with increasing depth in the S-mp sites only (Table A1). Secondly, and more importantly, we would expect the H/C and O/C quotients of upper-layer peat from p-b and S-s sites to be lower than those of upper-layer peat from S-mp sites, and more similar to those of lower-layer peat from S-mp sites. This expectation follows from the hypothesis that some of the peat originally present in the upper layers at sites affected by decomposition (S-s and p-b forests) will have been oxidised. In the long term, this decomposition (which generally begins in the upper layer) leads to the exposure of older and more recalcitrant peat (Leifeld *et al.* 2012) which is then sampled, for example during this study, as present-day upper-layer peat. This effect was reported by Leifeld *et al.* (2011b) from a peatland that was drained in 1864 and subsequently used as cropland or grassland, whose upper peat layer was aged at almost 4,000 years. Krüger *et al.* (2015) similarly identified much older upper-layer peat in intensively-used grassland than in extensively-used grassland. The qualitative assessment of H/C and O/C in this study indicates that the upper peat layers of the two supposedly drier forest types (p-b and S-s), which have lower O/C quotients, are more decomposed than those in the S-mp forest and similar to the (relatively decomposed) lower peat layer in S-mp forests. We suggest that the upper layers of peat at the two drier forest types have lost organic C through oxidative decomposition.

A second approach to comparing peat decomposition at these sites uses C/N quotients, which are related to humification indices (Anderson 2002, Biester *et al.* 2014) and have been interpreted by several authors as indicating degree of decomposition (e.g. Malmer & Holm 1984, Kurhy & Vitt 1996) by reflecting preferential loss of C over N during the decomposition process. However, C/N varies between different mire plant species (Hornibrook *et al.* 2000), with the result that the C/N quotient of peat can be additionally affected by changes in mire vegetation (Anderson 2002, Biester *et al.* 2014). Nonetheless, for *Sphagnum*-dominated peat, lowered C/N quotients predominantly indicate mass loss due to peat decomposition rather than vegetation change (Kurhy & Vitt 1996, Biester *et al.* 2014). The higher C/N values near the peat surface at S-mp sites indicate that litter and less-decomposed peat are more abundant here than deeper in the profile. These results are consistent with the evidence provided by the H/C and O/C data. The lower C/N values for p-b and S-s sites might be due to the greater abundance of vascular plants (especially trees) at these sites, or to more-decomposed peat, or to a combination of both. Likewise, the decline of C/N with decreasing depth at these sites is consistent with an increase in the abundance of vascular plants over time, an increase in peat decomposition towards the peat surface, or both. As both would signify drying of the site, we can conclude that the pattern shown by the C/N data is consistent with these sites being drier than S-mp sites and having become drier over time, even though the mechanism by which the C/N patterns have arisen remains unclear.

C stocks

C stocks are affected by three factors, namely: C concentration, bulk density and - if calculating C stock for the whole peat layer - the thickness of the peat layer. In this study, the differences in C stocks across the three forest types are determined by differences in soil bulk density rather than C concentration. One consequence for comparisons of C stocks between different land cover types *to a given depth* (as in the GHG inventory, where C stocks in the upper 30 cm are reported (Anon. 2014)) is that apparent differences between C stocks associated with different land uses may be artefacts of land use intensity; through compaction and oxidation, previously deeper layers of peat become, in effect, incorporated into the upper layers of peat. This is important for the GHG inventory because, for example, a change from less to more intensive use of a peatland could lead to an apparent gain of C stock. This artefact can only be circumvented by calculating C stocks for the full thickness of the soil layer.

C loss

We present LTRCL values for about half of the sites investigated. These are similar for the S-s and p-b forests. Although LTRCL could not be calculated for the S-mp forests, their mean C loss falls within the range of mean C loss from the S-s and p-b forests. This suggests that, once disturbed, the peat of S-mp forests is no more resilient than that of the other forest types; if drained, these peatlands may lose C just as rapidly. Indeed, at one of the drained S-mp sites (Les Pueys), there was only a very thin layer of peat and bare tree roots were observed, indicating a substantially lowered soil surface.

The LTRCL values are average rates of C loss through time. They are unlikely to indicate the current rate of C loss through peat oxidation, which can be expected to vary through time with changes in water table and temperature (Byrne *et al.* 2004, Holden 2005, Laiho 2006), in the quality of the peat, and in the quality of organic material available for decomposition which in turn varies with vegetation type or plant growth form (e.g. Dorrepaal *et al.* 2005, Laiho 2006, Moore *et al.* 2007). Studies have shown that the concentrations of molecules related to organic matter decomposability change with depth within the peat layer (e.g. Cocozza *et al.* 2003, Zaccone *et al.* 2007, Klavins *et al.* 2008, Leifeld *et al.* 2012), supporting the hypothesis that more recalcitrant peat occurs at greater depths. Therefore, decomposition rates should be highest immediately following drainage or disturbance of the site and decrease through time as the less recalcitrant peat is decomposed (Laiho 2006).

Implications for forest management

The lack of data regarding peat characteristics is seen as the greatest source of uncertainty in quantifying C stocks in northern peatlands (Yu 2012). This study represents one step towards increasing this knowledge for peatland under forests in temperate Europe. Our findings suggest that peat is less affected by drainage in S-mp forests than in S-s and p-b forests, and are consistent with what is known about the drainage of the study sites. Our results also suggest that quite similar peats are associated with the two supposedly drier forest types, despite differences in their general appearance and plant species composition (Ellenberg & Klötzli 1972). We suggest that the soils of S-s and p-b forests have lost their functions as net C sinks, unlike those of S-mp forests.

It is recognised that forests play an important role in supporting biodiversity and in protecting the land against soil erosion (Frehner *et al.* 2005, Arnold *et al.* 2011); and that in mountainous areas (such as large parts of Switzerland) the value of their protective role, including protection from avalanches, exceeds their value as sources of timber (Grünig 1994). Forests growing on peatland provide an additional ecosystem service, namely the storage of organic C. Some 3,670 ha (or 13 %, calculated from Wüst-Galley *et al.* 2015) of Switzerland's organic soils occur under forest, which means that approximately 1.8 million tonnes of C is stored in the upper metre of the country's forested organic soils. On the other hand, the stunted growth of trees on raised bogs suggests that wetter sites offer poor timber productivity, although this can sometimes be improved by drainage. In spite of this, given their small area (< 1 % of forests on organic soil) and the high C density of their soils, we propose that peatland forests should be managed for C storage, enhanced water retention and biodiversity, rather than for timber production.

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Appendix

Table A1. Mean (averaging across replicate sites) and standard deviation (SD) of bulk density (BD), ash concentration, soil pH, organic C concentration, C/N, O/C and H/C. Where there was only one measurement (i.e. no replicates), no standard deviation is given (“-“).

Site name	Forest type	Depth (cm)	BD (g cm^{-3})		ash (%)		pH		Organic C (%)		C/N		O/C		H/C	
			mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Bannwald	p-b	0–10	0.094	0.031	3.120	0.865	3.66	0.27	49.72	1.94	26.85	3.55	0.58	0.01	1.25	0.01
Bannwald	p-b	10–15	0.094	0.036	5.218	1.008	3.57	0.08	49.64	1.81	25.03	3.11	0.59	0.02	1.24	0.06
Bannwald	p-b	15–20	0.100	0.023	5.790	2.051	3.63	0.01	48.52	1.29	25.89	4.58	0.61	0.03	1.30	0.08
Bannwald	p-b	20–25	0.085	0.026	4.971	0.720	3.61	0.08	48.26	1.18	26.62	2.32	0.62	0.03	1.33	0.08
Bannwald	p-b	25–30	0.067	0.016	3.801	0.895	3.65	0.04	47.97	1.30	30.01	5.66	0.63	0.03	1.37	0.05
Bannwald	p-b	30–40	0.069	0.022	3.496	1.857	3.70	0.04	49.02	1.45	31.12	7.50	0.60	0.06	1.35	0.09
Bannwald	p-b	40–50	0.060	0.014	2.733	1.253	3.60	0.27	49.49	2.18	31.95	6.90	0.59	0.06	1.34	0.07
Bannwald	p-b	50–60	0.049	0.013	2.253	0.958	3.72	0.30	48.90	2.52	39.64	11.92	0.61	0.07	1.37	0.09
Bannwald	p-b	60–70	0.051	0.017	1.958	1.118	3.88	0.19	48.72	2.63	46.08	12.81	0.64	0.08	1.39	0.11
Bannwald	p-b	70–80	0.058	0.019	3.155	1.189	4.05	0.02	49.49	2.17	35.90	12.35	0.59	0.05	1.34	0.08
Bannwald	p-b	80–90	0.072	0.028	3.144	1.228	4.08	0.02	50.13	2.41	32.18	12.47	0.58	0.08	1.34	0.10
Bannwald	p-b	90–100	0.068	0.009	3.258	0.720	4.24	0.23	49.88	2.41	29.94	5.86	0.58	0.08	1.36	0.06
Chiemiwald	p-b	0–10	0.132	0.007	8.709	1.830	3.91	0.04	48.06	1.40	20.20	1.19	0.56	0.01	1.29	0.02
Chiemiwald	p-b	10–15	0.152	0.040	10.846	1.164	3.56	0.21	49.38	2.12	24.49	0.03	0.49	0.06	1.29	0.00
Chiemiwald	p-b	15–20	0.163	0.021	12.010	6.370	3.45	0.08	50.30	4.01	25.39	2.88	0.47	0.03	1.28	0.00
Chiemiwald	p-b	20–25	0.168	0.055	14.084	14.890	3.52	0.01	49.52	8.65	29.71	4.83	0.46	0.02	1.26	0.02
Chiemiwald	p-b	25–30	0.149	0.036	10.195	7.176	3.44	0.04	52.55	3.17	32.60	1.81	0.45	0.03	1.25	0.03
Chiemiwald	p-b	30–40	0.141	0.020	7.157	4.243	3.54	0.11	53.39	2.40	36.10	4.36	0.49	0.01	1.23	0.03
Chiemiwald	p-b	40–50	0.104	0.025	4.063	0.943	3.59	0.10	54.42	1.31	37.00	1.57	0.50	0.02	1.23	0.01
Chiemiwald	p-b	50–60	0.101	0.024	6.387	1.907	3.57	0.08	52.19	2.10	29.67	5.30	0.50	0.00	1.26	0.02
Chiemiwald	p-b	60–70	0.104	0.043	7.202	1.752	3.54	0.02	52.15	2.08	27.29	2.25	0.49	0.02	1.27	0.03
Chiemiwald	p-b	70–80	0.116	0.048	3.209	1.128	3.67	0.16	53.34	0.76	23.67	1.15	0.51	0.01	1.27	0.01
Chiemiwald	p-b	80–90	0.121	0.031	5.458	3.013	3.60	0.26	53.12	3.82	24.00	1.51	0.49	0.04	1.22	0.02

Site name	Forest type	Depth (cm)	BD (g cm^{-3})		ash (%)		pH		Organic C (%)		C/N		O/C		H/C	
			mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Chiemiwald	p-b	90–100	0.122	0.014	5.927	0.560	3.70	0.48	53.80	3.39	25.50	3.04	0.48	0.06	1.21	0.02
Maas	p-b	0–10	0.086	0.019	5.395	1.190	3.84	-	48.50	1.14	27.64	8.20	0.57	0.01	1.32	0.03
Maas	p-b	10–15	0.072	0.036	7.313	3.988	4.59	-	49.26	0.75	27.10	8.96	0.51	0.07	1.31	0.05
Maas	p-b	15–20	0.133	0.047	8.473	4.187	4.23	-	49.66	1.17	24.19	3.84	0.53	0.04	1.29	0.04
Maas	p-b	20–25	0.129	0.028	7.039	1.837	3.84	-	50.54	0.65	24.47	2.14	0.51	0.03	1.26	0.05
Maas	p-b	25–30	0.118	0.047	9.776	1.476	3.84	-	50.55	2.77	23.28	5.09	0.52	0.03	1.21	0.05
Maas	p-b	30–40	0.137	0.020	10.494	2.266	3.79	-	51.07	3.58	38.88	20.78	0.50	0.06	1.21	0.09
Maas	p-b	40–50	0.149	0.021	11.618	1.533	3.89	-	52.91	1.29	25.42	0.23	0.45	0.06	1.16	0.01
Maas	p-b	50–60	0.185	0.044	28.506	12.793	3.86	-	41.34	8.71	21.52	6.92	0.48	0.06	1.27	0.11
Maas	p-b	60–70	0.288	0.041	24.640	5.500	4.05	-	47.99	6.33	38.04	20.60	0.34	0.05	1.32	0.04
Maas	p-b	70–80	0.223	0.066	22.029	2.234	0.00	-	49.40	1.39	37.99	6.00	0.35	0.07	1.27	0.02
Maas	p-b	80–90	0.174	0.007	23.459	8.989	0.00	-	44.02	7.81	29.12	2.35	0.46	0.07	1.28	0.00
Maas	p-b	90–100	0.237	-	21.363	-	0.00	-	44.49	-	22.85	-	0.46	-	1.27	-
Meiestossmoos A	p-b	0–10	0.097	0.032	10.187	0.928	4.63	-	46.13	1.56	21.57	2.32	0.59	0.02	1.34	0.04
Meiestossmoos A	p-b	10–15	0.126	0.044	19.565	13.917	3.80	-	40.45	7.34	21.50	4.00	0.61	0.01	1.31	0.05
Meiestossmoos A	p-b	15–20	0.127	0.021	10.522	3.564	3.91	-	45.19	1.87	23.79	3.16	0.60	0.01	1.29	0.04
Meiestossmoos A	p-b	20–25	0.186	0.080	19.222	13.237	3.81	-	42.48	4.40	21.90	4.65	0.55	0.05	1.34	0.11
Meiestossmoos A	p-b	25–30	0.186	0.011	13.892	4.384	3.83	-	45.97	1.23	21.33	3.00	0.54	0.05	1.33	0.03
Meiestossmoos A	p-b	30–40	0.178	0.032	10.348	4.340	3.82	-	48.92	3.46	25.27	8.59	0.53	0.01	1.31	0.03
Meiestossmoos A	p-b	40–50	0.128	0.008	6.010	0.646	3.69	-	51.28	1.71	29.89	7.81	0.53	0.02	1.27	0.01
Meiestossmoos A	p-b	50–60	0.145	0.009	6.644	0.812	3.47	-	50.29	1.58	29.07	6.53	0.53	0.03	1.28	0.02
Meiestossmoos A	p-b	60–70	0.126	0.017	3.259	1.511	3.87	-	50.75	1.16	40.21	8.86	0.54	0.03	1.30	0.03
Meiestossmoos A	p-b	70–80	0.121	0.019	3.136	1.655	3.94	-	52.21	0.77	39.18	9.91	0.53	0.02	1.26	0.09
Meiestossmoos A	p-b	80–90	0.104	0.015	3.360	1.904	4.33	-	51.75	0.38	42.32	14.40	0.54	0.01	1.29	0.03
Meiestossmoos A	p-b	90–100	0.093	0.019	3.127	1.578	4.51	-	49.59	2.11	45.27	5.73	0.61	0.07	1.34	0.00
Sigigerwald	p-b	0–10	0.084	0.020	7.928	2.646	4.15	0.30	55.21	14.93	21.47	1.82	0.56	0.12	1.24	0.10
Sigigerwald	p-b	10–15	0.181	0.034	17.409	6.291	4.05	0.18	43.46	3.57	19.93	2.52	0.59	0.07	1.34	0.04
Sigigerwald	p-b	15–20	0.199	0.012	20.680	4.976	4.62	0.64	43.98	5.22	20.89	4.34	0.54	0.08	1.36	0.00

Site name	Forest type	Depth (cm)	BD (g cm^{-3})		ash (%)		pH		Organic C (%)		C/N		O/C		H/C	
			mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Sigigerwald	p-b	20–25	0.168	0.018	13.883	2.839	4.98	0.82	47.42	3.72	21.17	0.92	0.57	0.07	1.30	0.01
Sigigerwald	p-b	25–30	0.154	0.016	10.869	1.832	5.26	0.76	47.81	1.23	20.60	1.60	0.57	0.03	1.29	0.05
Sigigerwald	p-b	30–40	0.160	0.027	19.296	14.648	5.66	0.71	43.62	8.71	19.77	1.65	0.50	0.15	1.32	0.09
Sigigerwald	p-b	40–50	0.187	-	23.137	-	6.47	-	43.07	-	20.88	-	0.55	-	1.36	-
Weidli	p-b	0–10	0.093	0.024	11.851	4.303	4.46	0.59	44.90	1.54	24.55	1.59	0.58	0.01	1.24	0.20
Weidli	p-b	10–15	0.094	0.040	7.321	1.940	3.71	0.32	47.75	1.04	25.58	2.33	0.57	0.01	1.17	0.22
Weidli	p-b	15–20	0.130	0.049	11.214	12.113	3.68	0.17	46.85	4.38	27.60	2.77	0.55	0.05	1.19	0.23
Weidli	p-b	20–25	0.175	0.041	22.701	16.362	3.61	0.21	43.04	9.45	30.19	6.15	0.49	0.06	1.25	0.19
Weidli	p-b	25–30	0.219	0.086	22.468	29.735	3.70	0.25	43.57	16.12	32.72	4.34	0.46	0.02	1.24	0.27
Weidli	p-b	30–40	0.173	0.049	12.678	15.293	3.46	-	49.39	8.39	29.18	7.80	0.46	0.01	1.16	0.32
Weidli	p-b	40–50	0.200	0.047	9.107	4.254	3.61	-	51.76	1.38	30.22	3.48	0.45	0.02	1.32	0.02
Weidli	p-b	50–60	0.245	-	34.569	-	3.51	-	38.83	-	33.44	-	0.43	-	1.33	-
Dévin des Dailles A	S-s	0–10	0.044	0.023	5.118	2.282	3.94	-	46.13	0.51	28.45	6.96	0.64	0.05	1.39	0.06
Dévin des Dailles A	S-s	10–15	0.093	0.046	11.327	6.649	3.60	-	45.34	1.88	22.05	4.59	0.59	0.05	1.37	0.04
Dévin des Dailles A	S-s	15–20	0.129	0.021	16.185	1.849	3.92	-	44.66	0.37	20.59	0.63	0.55	0.01	1.36	0.00
Dévin des Dailles A	S-s	20–25	0.174	0.031	19.887	18.024	3.67	-	43.64	9.98	25.99	7.37	0.51	0.01	1.31	0.00
Dévin des Dailles A	S-s	25–30	0.140	0.009	5.903	2.818	4.05	-	51.16	2.74	30.93	6.68	0.51	0.04	1.27	0.04
Dévin des Dailles A	S-s	30–40	0.139	0.003	4.238	0.590	4.26	-	52.37	1.86	28.56	4.92	0.49	0.03	1.32	0.04
Dévin des Dailles A	S-s	40–50	0.124	0.007	5.390	0.440	4.81	-	50.98	0.77	29.84	1.75	0.52	0.01	1.31	0.05
Dévin des Dailles A	S-s	50–60	0.107	0.024	5.590	0.437	5.07	-	50.71	0.93	30.72	0.28	0.52	0.01	1.33	0.01
Dévin des Dailles A	S-s	60–70	0.133	0.029	7.123	0.340	5.22	-	50.91	0.12	27.52	1.96	0.51	0.00	1.30	0.01
Dévin des Dailles A	S-s	70–80	0.145	0.030	7.376	0.298	5.29	-	52.26	0.28	29.92	5.64	0.47	0.01	1.26	0.02
Dévin des Dailles A	S-s	80–90	0.163	-	7.245	-	-	-	53.09	-	27.62	-	0.46	-	1.30	-
Dévin des Dailles A	S-s	90–100	0.116	-	5.678	-	-	-	49.45	-	37.57	-	0.56	-	1.37	-
Foremoos	S-s	0–10	0.092	0.021	4.618	1.380	4.03	-	48.33	0.54	23.02	1.74	0.58	0.01	1.29	0.03
Foremoos	S-s	10–15	0.123	0.023	7.218	4.966	3.76	-	47.61	2.08	22.31	2.21	0.58	0.02	1.25	0.00
Foremoos	S-s	15–20	0.166	0.059	11.548	8.715	3.48	-	46.54	3.68	22.78	2.25	0.53	0.04	1.31	0.04
Foremoos	S-s	20–25	0.156	0.026	11.171	1.001	3.59	-	48.66	0.87	22.37	1.01	0.50	0.05	1.30	0.03

Site name	Forest type	Depth (cm)	BD (g cm^{-3})		ash (%)		pH		Organic C (%)		C/N		O/C		H/C	
			mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Foremoos	S-s	25–30	0.168	0.051	13.988	6.513	4.11	-	48.87	3.58	23.94	1.46	0.46	0.02	1.27	0.02
Foremoos	S-s	30–40	0.144	0.036	9.319	1.064	4.16	-	53.38	1.18	28.21	3.27	0.44	0.02	1.24	0.04
Foremoos	S-s	40–50	0.134	0.022	9.166	2.797	4.70	-	53.10	2.91	29.76	6.99	0.45	0.02	1.20	0.04
Foremoos	S-s	50–60	0.147	0.018	8.585	1.654	-	-	54.66	0.12	26.72	6.69	0.43	0.01	1.19	0.01
Foremoos	S-s	60–70	0.139	0.021	7.032	4.099	-	-	53.47	2.74	27.21	4.73	0.45	0.02	1.17	0.02
Foremoos	S-s	70–80	0.121	0.026	8.632	2.288	-	-	54.69	1.54	23.47	4.41	0.43	0.03	1.16	0.04
Foremoos	S-s	80–90	0.119	0.015	9.672	5.389	-	-	57.17	-	26.11	-	0.39	-	1.18	-
Foremoos	S-s	90–100	0.119	-	9.615	-	-	-	53.56	-	19.78	-	0.44	-	1.21	-
Joux derrière	S-s	0–10	0.046	0.009	4.456	1.858	4.15	-	46.04	0.79	31.03	3.63	0.66	0.01	1.42	0.01
Joux derrière	S-s	10–15	0.118	0.083	11.344	9.460	3.78	-	45.37	3.80	23.48	0.81	0.59	0.03	1.34	0.08
Joux derrière	S-s	15–20	0.155	0.063	10.073	2.878	3.71	-	49.35	0.25	23.87	3.72	0.55	0.04	1.33	0.07
Joux derrière	S-s	20–25	0.160	0.026	10.100	2.826	3.74	-	50.24	3.39	22.83	4.67	0.52	0.03	1.36	0.03
Joux derrière	S-s	25–30	0.149	0.033	8.486	3.381	3.71	-	51.10	2.63	25.50	7.73	0.53	0.01	1.34	0.04
Joux derrière	S-s	30–40	0.119	0.010	6.604	1.865	3.97	-	51.58	1.35	25.74	6.70	0.51	0.03	1.33	0.03
Joux derrière	S-s	40–50	0.123	0.008	7.988	1.677	4.12	-	53.60	1.81	23.91	4.92	0.44	0.09	1.30	0.04
Joux derrière	S-s	50–60	0.131	0.003	8.289	1.725	4.35	-	53.04	0.32	24.17	3.56	0.46	0.01	1.31	0.03
Joux derrière	S-s	60–70	0.137	0.025	8.074	5.590	4.49	-	52.15	4.13	24.52	3.90	0.49	0.01	1.29	0.03
Joux derrière	S-s	70–80	0.126	0.019	14.223	3.474	5.01	-	48.39	2.63	25.06	2.94	0.49	0.02	1.32	0.03
Joux derrière	S-s	80–90	0.102	-	17.958	-	-	-	46.75	-	23.22	-	0.49	-	1.33	-
Meiestossmoos B	S-s	0–10	0.113	0.038	10.681	8.795	4.40	-	45.72	3.67	17.97	0.26	0.57	0.03	1.15	0.28
Meiestossmoos B	S-s	10–15	0.149	0.035	14.512	11.129	3.74	-	44.39	7.02	20.99	3.05	0.51	0.10	1.35	0.03
Meiestossmoos B	S-s	15–20	0.151	0.011	10.192	3.761	3.64	-	47.48	2.97	23.51	4.46	0.55	0.03	1.18	0.22
Meiestossmoos B	S-s	20–25	0.132	0.029	7.022	0.289	3.74	-	50.56	3.46	26.01	2.62	0.54	0.04	1.12	0.17
Meiestossmoos B	S-s	25–30	0.115	0.009	5.295	2.854	3.62	-	51.21	3.35	28.93	2.39	0.55	0.07	1.11	0.24
Meiestossmoos B	S-s	30–40	0.125	0.026	8.934	10.380	3.72	-	49.59	2.98	31.47	6.27	0.54	0.04	1.07	0.30
Meiestossmoos B	S-s	40–50	0.103	0.042	11.035	15.010	3.67	-	45.40	4.03	44.59	17.23	0.60	0.07	1.32	0.06
Meiestossmoos B	S-s	50–60	0.128	0.062	8.045	9.680	3.86	-	47.93	2.79	34.22	8.43	0.56	0.05	1.28	0.03
Meiestossmoos B	S-s	60–70	0.093	0.006	2.177	0.559	3.93	-	50.86	2.14	36.62	8.48	0.59	0.05	1.01	0.36

Site name	Forest type	Depth (cm)	BD (g cm^{-3})		ash (%)		pH		Organic C (%)		C/N		O/C		H/C	
			mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Meiestossmoos B	S-s	70–80	0.094	0.002	2.077	0.059	3.97	-	48.25	4.50	58.22	20.12	0.62	0.06	1.08	0.32
Meiestossmoos B	S-s	80–90	0.088	0.004	2.136	0.336	3.98	-	50.64	2.50	41.51	7.81	0.59	0.06	1.03	0.31
Meiestossmoos B	S-s	90–100	0.103	0.010	2.185	0.455	4.04	-	52.76	2.23	29.26	4.86	0.53	0.05	0.98	0.33
Summerigchopf A	S-s	0–10	0.069	0.024	8.173	5.117	4.56	-	46.83	0.80	49.00	40.02	0.62	0.02	1.31	0.03
Summerigchopf A	S-s	10–15	0.113	0.025	18.160	8.993	4.44	-	40.57	3.79	24.85	11.66	0.60	0.07	1.44	0.07
Summerigchopf A	S-s	15–20	0.145	0.015	22.327	5.805	4.47	-	41.73	2.93	18.60	2.39	0.54	0.05	1.42	0.06
Summerigchopf A	S-s	20–25	0.133	0.020	19.015	7.800	4.43	-	45.24	4.88	19.54	3.62	0.49	0.05	1.38	0.06
Summerigchopf A	S-s	25–30	0.159	0.030	17.607	4.813	4.58	-	45.23	3.17	19.00	2.32	0.49	0.03	1.39	0.04
Summerigchopf A	S-s	30–40	0.141	0.033	12.674	6.178	4.69	-	48.44	3.17	20.40	3.83	0.47	0.02	1.39	0.09
Summerigchopf A	S-s	40–50	0.131	0.041	16.052	11.739	4.88	-	46.63	5.86	20.13	4.35	0.47	0.01	1.37	0.04
Summerigchopf A	S-s	50–60	0.132	0.044	20.508	16.813	4.56	-	43.83	8.81	20.12	2.20	0.50	0.04	1.36	0.08
Summerigchopf A	S-s	60–70	0.166	0.019	22.647	9.184	4.74	-	43.27	5.90	19.70	1.84	0.50	0.06	1.32	0.04
Summerigchopf A	S-s	70–80	0.175	0.023	23.543	11.301	4.99	-	41.19	6.41	22.29	1.33	0.52	0.05	1.26	0.24
Summerigchopf A	S-s	80–90	0.177	0.034	17.568	8.825	4.85	-	44.70	4.46	23.99	6.97	0.51	0.06	1.28	0.08
Summerigchopf A	S-s	90–100	0.173	0.070	24.158	4.663	5.03	-	41.06	1.91	21.32	5.80	0.52	0.05	1.35	0.04
nr. Au Pâq. de des.	S-s	0–10	0.043	0.010	3.042	0.154	3.94	0.49	48.20	1.42	33.46	4.99	0.62	0.03	1.34	0.00
nr. Au Pâq. de des.	S-s	10–15	0.076	0.020	4.576	1.435	3.71	0.14	47.86	1.29	23.74	9.61	0.59	0.04	1.62	0.66
nr. Au Pâq. de des.	S-s	15–20	0.103	0.038	8.008	1.782	3.80	0.09	47.35	0.88	26.61	3.21	0.58	0.03	1.34	0.01
nr. Au Pâq. de des.	S-s	20–25	0.136	0.018	10.656	5.470	3.77	0.09	47.60	2.79	26.10	3.59	0.53	0.02	1.29	0.01
nr. Au Pâq. de des.	S-s	25–30	0.121	0.036	8.280	8.820	3.77	0.02	47.79	4.91	30.98	7.65	0.55	0.04	1.30	0.04
nr. Au Pâq. de des.	S-s	30–40	0.112	0.024	2.616	0.573	3.57	0.16	48.74	4.13	34.20	9.47	0.57	0.07	1.29	0.04
nr. Au Pâq. de des.	S-s	40–50	0.104	0.030	2.987	0.678	3.76	0.12	50.78	2.58	37.06	11.07	0.54	0.05	1.09	0.39
nr. Au Pâq. de des.	S-s	50–60	0.122	0.027	2.771	0.764	3.88	0.15	50.22	3.15	32.70	5.08	0.53	0.07	1.29	0.02
nr. Au Pâq. de des.	S-s	60–70	0.151	0.043	2.277	0.552	3.94	0.09	51.83	3.04	33.42	10.27	0.52	0.07	1.29	0.02
nr. Au Pâq. de des.	S-s	70–80	0.138	0.044	2.519	0.162	3.95	0.13	50.97	2.69	36.06	8.43	0.54	0.05	1.29	0.04
nr. Au Pâq. de des.	S-s	80–90	0.156	0.025	2.788	0.063	4.13	0.07	52.08	2.75	28.84	6.53	0.51	0.04	1.28	0.07
nr. Au Pâq. de des.	S-s	90–100	0.146	0.025	3.210	1.202	4.14	0.13	52.92	3.38	27.91	9.08	0.49	0.04	1.27	0.07
Dévin des Dailles B	S-mp	0–10	0.017	0.008	2.446	0.469	4.02	-	46.73	1.45	54.93	2.53	0.70	0.04	1.46	0.05

Site name	Forest type	Depth (cm)	BD (g cm^{-3})		ash (%)		pH		Organic C (%)		C/N		O/C		H/C	
			mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Dévin des Dailles B	S-mp	10–15	0.020	0.003	2.293	0.242	3.68	-	45.96	2.10	61.10	8.02	0.72	0.07	1.38	0.04
Dévin des Dailles B	S-mp	15–20	0.022	0.002	2.302	0.864	3.26	-	45.13	1.35	61.54	5.80	0.74	0.04	1.41	0.08
Dévin des Dailles B	S-mp	20–25	0.030	0.007	2.652	0.566	3.54	-	45.46	1.24	52.07	8.63	0.73	0.04	1.41	0.06
Dévin des Dailles B	S-mp	25–30	0.031	0.006	2.615	0.456	3.72	-	45.02	0.95	52.48	4.13	0.74	0.03	1.43	0.05
Dévin des Dailles B	S-mp	30–40	0.032	0.006	2.537	0.612	3.96	-	45.10	0.31	55.88	3.88	0.74	0.01	1.40	0.01
Dévin des Dailles B	S-mp	40–50	0.039	0.010	2.789	0.462	4.05	-	45.58	0.32	53.97	3.32	0.69	0.03	1.39	0.04
Dévin des Dailles B	S-mp	50–60	0.041	0.003	3.302	0.459	3.99	-	45.72	1.62	41.17	1.62	0.70	0.05	1.38	0.04
Dévin des Dailles B	S-mp	60–70	0.054	0.014	3.502	1.115	3.86	-	47.33	1.37	44.67	10.61	0.66	0.06	1.35	0.05
Dévin des Dailles B	S-mp	70–80	0.079	0.008	8.205	5.083	4.11	-	46.91	0.23	30.25	3.83	0.60	0.06	1.32	0.02
Dévin des Dailles B	S-mp	80–90	0.106	0.021	8.289	3.080	3.82	-	49.30	1.25	31.53	2.61	0.53	0.02	1.28	0.08
Dévin des Dailles B	S-mp	90–100	0.085	0.018	3.808	3.037	3.82	-	51.50	0.83	38.51	12.18	0.53	0.06	1.22	0.06
Rüchiwald	S-mp	0–10	0.043	0.015	2.324	0.383	4.13	-	47.71	3.14	40.69	12.57	0.64	0.07	1.41	0.07
Rüchiwald	S-mp	10–15	0.054	0.019	2.879	1.499	3.60	-	48.23	2.57	38.31	15.43	0.63	0.07	1.38	0.09
Rüchiwald	S-mp	15–20	0.068	0.010	3.592	0.847	3.73	-	47.73	0.64	31.92	8.88	0.61	0.01	1.36	0.04
Rüchiwald	S-mp	20–25	0.065	0.019	3.447	1.241	3.73	-	47.67	0.78	36.20	15.22	0.61	0.04	1.38	0.03
Rüchiwald	S-mp	25–30	0.079	0.046	4.059	1.844	3.76	-	47.93	1.13	33.96	9.92	0.60	0.07	1.39	0.08
Rüchiwald	S-mp	30–40	0.129	0.054	6.961	2.133	3.52	-	50.12	1.00	26.86	2.73	0.50	0.02	1.34	0.00
Rüchiwald	S-mp	40–50	0.148	0.004	5.109	2.917	3.81	-	52.33	1.29	31.81	5.16	0.46	0.00	1.30	0.05
Rüchiwald	S-mp	50–60	0.144	-	1.950	-	3.89	-	52.52	-	32.78	-	0.50	-	1.30	-
Rüchiwald	S-mp	60–70	0.142	-	1.660	-	3.83	-	53.43	-	33.29	-	0.49	-	1.21	-
Rüchiwald	S-mp	70–80	0.133	-	1.050	-	3.85	-	53.34	-	35.12	-	0.49	-	1.25	-
Rüchiwald	S-mp	80–90	0.122	-	1.349	-	4.08	-	53.25	-	33.28	-	0.50	-	1.28	-
Rüchiwald	S-mp	90–100	0.137	-	1.721	-	4.03	-	52.39	-	12.04	-	0.47	-	1.33	-
Summerigchopf B	S-mp	0–10	0.046	0.026	2.676	0.729	4.28	-	47.73	1.81	39.55	10.62	0.63	0.06	1.32	0.08
Summerigchopf B	S-mp	10–15	0.040	0.013	2.870	0.629	3.95	-	47.26	0.79	39.36	10.75	0.65	0.03	1.32	0.00
Summerigchopf B	S-mp	15–20	0.059	0.021	2.730	0.998	3.67	-	48.04	1.88	40.26	12.07	0.63	0.07	1.31	0.06
Summerigchopf B	S-mp	20–25	0.053	0.021	2.538	0.948	3.84	-	47.47	0.60	40.49	11.97	0.65	0.04	1.34	0.03
Summerigchopf B	S-mp	25–30	0.062	0.012	2.767	0.312	3.90	-	48.18	0.83	34.19	4.59	0.62	0.02	1.31	0.06

Site name	Forest type	Depth (cm)	BD (g cm^{-3})		ash (%)		pH		Organic C (%)		C/N		O/C		H/C	
			mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Summerigchopf B	S-mp	30–40	0.072	0.022	5.561	2.686	3.92	-	47.79	0.85	38.34	19.80	0.58	0.05	1.35	0.07
Summerigchopf B	S–mp	40–50	0.101	0.018	9.784	0.614	3.99	-	47.46	0.39	25.72	0.67	0.53	0.02	1.30	0.04
Summerigchopf B	S-mp	50–60	0.147	0.028	8.954	2.463	3.94	-	47.91	0.61	31.49	6.98	0.52	0.04	1.35	0.06
Summerigchopf B	S-mp	60–70	0.169	0.015	7.124	2.789	4.03	-	49.40	1.09	21.23	3.82	0.51	0.01	1.26	0.04
Summerigchopf B	S-mp	70–80	0.152	0.040	4.821	1.801	4.22	-	50.81	1.20	29.39	9.17	0.52	0.05	1.25	0.01
Summerigchopf B	S-mp	80–90	0.123	0.047	4.262	2.336	4.13	-	50.59	0.92	66.75	36.17	0.53	0.06	1.28	0.06
Summerigchopf B	S-mp	90–100	0.118	0.044	6.372	3.820	4.03	-	49.70	1.28	35.91	10.52	0.54	0.08	1.29	0.04
Vorderwengi	S-mp	0–10	0.047	0.021	4.069	0.695	4.09	-	48.38	1.32	30.92	3.82	0.63	0.03	1.36	0.02
Vorderwengi	S-mp	10–15	0.087	0.032	4.850	1.271	3.81	-	49.80	0.42	28.89	5.62	0.60	0.03	1.53	0.39
Vorderwengi	S-mp	15–20	0.112	0.036	4.740	1.501	4.02	-	50.39	0.51	28.67	6.02	0.58	0.01	1.35	0.01
Vorderwengi	S-mp	20–25	0.120	0.038	5.278	1.015	4.18	-	50.47	1.14	27.02	2.81	0.58	0.03	1.35	0.01
Vorderwengi	S-mp	25–30	0.149	0.056	5.559	0.643	4.18	-	50.35	1.96	21.67	1.03	0.56	0.04	1.35	0.02
Vorderwengi	S-mp	30–40	0.161	0.016	4.905	1.459	4.26	-	53.25	1.86	25.98	7.96	0.53	0.02	1.28	0.03
Vorderwengi	S-mp	40–50	0.133	0.019	5.727	1.155	4.66	-	52.82	1.31	22.84	1.18	0.50	0.01	1.29	0.04
Vorderwengi	S-mp	50–60	0.118	0.014	4.040	1.397	5.07	-	53.45	2.13	27.18	3.48	0.51	0.05	1.31	0.04
Vorderwengi	S-mp	60–70	0.145	0.023	4.552	1.766	5.12	-	55.10	0.99	23.38	3.78	0.49	0.04	1.30	0.03
Vorderwengi	S-mp	70–80	0.169	0.012	5.359	0.507	5.36	-	55.79	1.21	22.25	5.14	0.47	0.03	1.26	0.03
Vorderwengi	S-mp	80–90	0.142	0.007	5.338	2.334	5.39	-	54.93	0.19	18.79	2.59	0.48	0.02	1.28	0.03
Vorderwengi	S-mp	90–100	0.142	0.001	6.697	0.984	5.54	-	54.68	0.92	19.79	2.09	0.47	0.01	1.28	0.01