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Vulnerability of soil organic matter of anthropogenically disturbed organic soils

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Abstract

Drained peatlands are hotspots of carbon dioxide (CO_2) emissions from agriculture. As a consequence of both drainage-induced mineralisation and anthropogenic mixing with mineral soils, large areas of former peatlands under agricultural use now contain soil organic carbon (SOC) at the boundary between mineral and organic soils and/or underwent a secondary transformation of the peat (e.g. formation of aggregates). However, low carbon organic soils have rarely been studied since previous research has mainly focused on either mineral soils or true peat soils. The aim of the present study was to evaluate the soil organic matter (SOM) vulnerability of the whole range of organic soils including very carbon rich mineral soils (73 g kg^{-1} < SOC < 569 g kg^{-1}) and to identify indicators for mineralisation of such anthropogenically disturbed organic soils. Using a large sample pool from the German Agricultural Soil Inventory, 91 soil samples were selected covering a broad range of soil and site characteristics. Fen and bog samples were grouped into disturbance classes according to their pedogenetic features. Potential CO_2 production by aerobic incubation was then measured. Specific basal respiration rates (SBR) per unit SOC showed the highest potential emissions for heavily disturbed fen (12.1 ± 5.0 µg CO_2-C g SOC^{-1} h^{-1}) and moderately disturbed bog samples (10.3 ± 5.2 µg CO_2-C g SOC^{-1} h^{-1}). Surprisingly, SOM vulnerability increased with an increasing degree of disturbance and a decreasing SOC content, indicating positive feedback mechanisms as soon as peat soils are disturbed by drainage. Furthermore, with increasing degree of disturbance the variability of the SBR increased drastically, but correlations between soil properties and SBR could not be identified. Respiration rates increased more strongly with an increasing degree of disturbance in bog than in fen samples. Peat properties that positively influenced the turnover of SOM in less disturbed soil samples were mainly pH value and nitrogen content, while phosphorus was important for the mineralisation of increasingly disturbed samples and bog peat in general. Furthermore, a narrow carbon-to-nitrogen ratio correlated strongly with potential emissions. Given the high potential of CO_2 emissions from organic soils with a low SOC content, mixing with mineral soil does not seem to be a promising option for decreasing emissions.

1 Introduction

Organic soils worldwide cover approximately 330 million ha or 2.2 % of the global terrestrial surface. One third of this area is in Europe (Tubiello et al., 2016), corresponding to 3 % of the European landmass (Montanarella et al., 2006). Despite the small extent of this area, peatlands store more than one third of global soil organic carbon (SOC) (Gorham, 1991). Moreover, intact peatlands under waterlogged conditions are ongoing carbon (C) sinks in that their mineralisation rates are lower than their biomass production rates (Clymo et al., 1998). Large areas of peatland are drained for agriculture, forestry and peat mining for energy and horticulture. To date 25.5 million ha of peatlands worldwide have been drained for agriculture alone, of which around 60 % are in the boreal or temperate zone (Tubiello et al., 2016). The majority of the drained peatlands in Russia, Belarus, Ukraine, Poland, the Netherlands and Germany are used for agricultural purposes, primarily as grassland (Joosten and Clarke, 2002). These anthropogenic impacts lead to a disturbance of the peatlands' hydrological and biogeochemical cycles, e.g. to the destabilisation of the soil organic matter (SOM) (Holden et al., 2004). Thus drainage turns peatlands into net greenhouse gas (GHG) sources, which emit large amounts of carbon dioxide (CO_2) and nitrous oxide (N_2O) (Maljanen et al., 2010; Tiemeyer et al., 2016).

Furthermore, drainage alters physical and chemical peat properties considerably. The loss of buoyancy following drainage leads to compaction and thus to an increase in bulk density and decrease in total porosity (Rovdan et al., 2002). Compaction and mineralisation jointly cause subsidence of the soil surface. Mineralisation and transformation of SOM lead to the formation of aggregates, shrinkage cracks, earthification and finally to the formation of a dusty, fine-grained ("moorshy") horizon (e.g. Ilnicki and Zeitz, 2003). Consequently, the majority of topsoils of drained agricultural peatlands show a von Post decomposition degree of H10 (von Post, 1924).

Drainage favours carbon over nitrogen (N) mineralisation and microbial N immobilisation during decomposition. Thus, the concentrations of N increase, and both the C concentration and C:N-ratio decrease with increasing degrees of SOM decomposition, especially in the topsoil (Wells and Williams, 1996). Phosphorus (P) concentrations usually increase after drainage, while potassium (K), calcium (Ca) and iron (Fe) concentrations decrease (Sundström et al., 2000; Wells and Williams, 1996; Zak et al., 2010). As aerobic decomposers preferably use the lighter ^{12}C for respiration, the remaining peat is enriched in ^{13}C (Ågren et al., 1996). Similarly, drained peatlands are depleted in ^{14}N and show increases in $\delta^{15}N$ values (Krüger et al., 2015).

Besides drainage, the conversion from pristine peatlands to agricultural land can comprise the active enrichment of the mineral soil fraction in the top peat layer in order to enhance trafficability. This can be achieved by mixing with mineral soil layers underlying the peat (deep ploughing) or by surface application of mineral soil with or without subsequent ploughing (Göttlich, 1990; Okruszko, 1996). As a consequence of both drainage-induced mineralisation and anthropogenic mineral soil mixing, especially the topsoils of large areas of former peatlands under agricultural use contain SOC at concentrations between those of mineral and organic soils (Schulz and Waldeck, 2015).

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As previous investigations mainly have focused either on mineral (< 150 g SOM kg^{-1} according to the German definition, Ad-Hoc-AG Boden, 2005) or "true" peat soils (> 300 g SOM kg^{-1}), there are very few studies on soil properties or SOM dynamics of "low C organic soils" (between 150 and 300 g SOM kg^{-1}). However, measurements of GHG emissions in the field have shown that organic soils with a SOC content of around 100 g kg^{-1} still emit large amounts of CO_2 similar to the levels emitted by "true" peat soils (Leiber-Sauheitl et al., 2014; Tiemeyer et al., 2016). This is rather surprising as the remaining organic matter should not be readily available for mineralisation, given that the SOC content at this stage of decomposition is fairly low and CO_2 emissions and SOC content are closely related in mineral soils (Don et al., 2013; Wang et al., 2003). However, only a few field studies have been carried out and there is therefore very limited knowledge about the separate effects of climate, hydrology and soil properties. The reasons behind the relatively high CO_2 emissions of the whole continuum of organic soils, including those bordering mineral ones, are not yet clear. Peat properties and SOM quality obviously influence the CO_2 emissions of disturbed peatlands (Brouns et al., 2016; Laiho, 2006), but there is a lack of any systematic evaluation of the vulnerability of a wide range of organic soils, including strongly disturbed ones.

The aims of this study, were i) to assess the sensitivity of SOM from anthropogenically disturbed organic soils under agricultural use to mineralisation under aerobic conditions and ii) to determine the indicators and drivers of the vulnerability of SOM. In this context, disturbance was defined as the effect of soil-forming processes induced by drainage and/or by the mixing of peat with mineral soil. For this purpose, 91 samples of soils were examined under cropland and grassland from across Germany, ranging from carbon-rich mineral soil (70 g SOC kg^{-1}) to "true" peatlands (up to 560 g SOC kg^{-1}). As a simulation of the potential effects of drainage, all the samples were aerobically incubated in the laboratory at standardised water content.

2 Material and Methods

2.1 Sample selection

The samples used in this study came from the German Agricultural Soil Inventory, the aim of which is to improve understanding of SOC stocks in agricultural soils. During the soil inventory, agricultural soils in Germany were sampled following standardised protocols in an 8x8 km grid (> 3,000 sites) at seven depth increments per soil pit (10, 30, 50, 70, 100, 150 and 200 cm). All the samples were analysed for SOC and bulk density, as well as for basic explanatory soil properties (Table 1, see section 2.2). 91 samples of organic soil horizons from 67 sites were selected. The basic criteria were a SOC content > 70 g kg^{-1} and a sampling depth > 10 cm to reduce the influence of potential root biomass residues in the samples. Roots have generally been separated by hand, but this might be challenging in organic soils. The final sample selection was based on a cluster analysis to optimally cover the total parameter range, as well as land use, peat type (bog/fen) and geographical position. The selected samples included croplands (19 %) and grasslands (81 %), which correspond to the dominant agricultural land use of organic soils in Germany. In addition to the 91 samples, ten samples of three anthropogenically undisturbed peatlands (bog, transition bog and fen) were sampled.

Table 1: Soil properties of the selected soil samples as medians and standard errors. Standard parameters measured in the German Agricultural Soil Inventory: SOC: soil organic carbon content, N_t: total nitrogen content, $CaCO_3$: calcium carbonate content, C:N-ratio: carbon to nitrogen ratio, ρ: bulk density, pH-value, texture (* only determined for samples with SOC < 172 g kg^{-1}). Additional parameters of this study: Fe_O: oxalate extractable iron oxide content, P_{CAL}: calcium acetate lactate (CAL) extractable phosphorus content, $\delta^{13}C$ and $\delta^{15}N$.

Parameter	Median	Min.	Max.
SOC (g kg^{-1})	257.0 ± 15.5	73.4	568.9
N_t (g kg^{-1})	11.7 ± 0.8	2.9	36.5
$CaCO_3$ (g kg^{-1})	0.0 ± 1.2	0.0	580.0
C:N-ratio	18.0 ± 1.2	9.9	72.6
ρ (g cm^{-3})	0.30 ± 0.03	0.07	0.99
pH $CaCl_2$	4.9 ± 0.1	2.5	7.4
Sand content (%)*	44.7 ± 4.9	2.5	87.9
Silt content (%)*	25.8 ± 2.5	6.4	62.1
Clay content (%)*	20.9 ± 3.1	3.9	62.8
Fe_O (g kg^{-1})	11.8 ± 1.7	0.4	108.3
P_{CAL} (mg kg^{-1})	12.4 ± 5.9	0.4	365.6
$\delta^{13}C$ (‰)	-28.14 ± 0.10	-30.42	-25.47
$\delta^{15}N$ (‰)	2.05 ± 0.24	-2.55	11.23

2.2 Soil properties

Concentrations of total C and N (N_t), as well as the total inorganic carbon content for samples with carbonate (pH_{CaCl_2} > 6.2), were measured by dry combustion (RC 612, LECO Corporation, St. Joseph, USA).
Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) was performed using a mass spectrometer coupled with an elemental analyser (Isoprime 100 and Vario Isotope, Elementar, Hanau, Germany) via a continuous flow system. Samples containing carbonates underwent a carbonate destruction (volatilisation method) on the basis of Hedges and Stern (1984) and Harris et al. (2001) prior to isotope analysis. The isotope ratios are expressed in per mill, $\delta^{13}C$ relative to VPDB standard and $\delta^{15}N$ relative to atmospheric nitrogen standard.
Poorly crystalline and organically-bound iron oxides (Fe_O) were extracted with an acidic ammonium oxalate solution. The extraction took place in the dark to avoid photo-reduction of ferrous iron oxides (Schwertmann, 1964). The concentration of extracted Fe_O was measured by atomic absorption spectrometry (AA-280FS, Varian, Palo Alto, USA).
Plant-available concentrations of phosphorus were determined by calcium acetate lactate (CAL) extraction (Schüller, 1969). P_{CAL} concentrations were measured using the molybdenum blue method (Murphy and Riley 1962).
The fractions of the texture classes sand, silt and clay were quantified by a semi-automated sieve-pipette machine (Sedimat 4-12, UGT, Müncheberg, Germany) after aggregate destruction and the removal of salt and SOM using H_2O_2 (Vos et al., 2016). Undisturbed soil samples in rings were dried at 105 °C until constant mass and subsequently weighed to determine bulk density (ρ). The pH values were measured using 0.01 mol/L $CaCl_2$ and a glass electrode. Electrical conductivity (EC) was determined in a water solution.

2.3 Incubation experiments: Basal respiration and substrate-induced respiration

The soil samples were incubated aerobically under optimum moisture and constant temperature (23 °C) conditions to determine basal soil respiration (BR) and substrate-induced respiration (SIR), which was used to calculate microbial biomass (Anderson and Domsch, 1978).
The dried (40 °C) and 2 mm sieved soil samples were moistened to a standardised water content of 60 % water-filled pore space. The apparent porosity of the dried and sieved sample was determined from the bulk density of the loose sample. The necessary amount of water to reach 60 % water-filled pore space was then applied to the soil samples under continuous stirring to ensure uniform rewetting. Afterwards, the moistened samples were stored in darkness under aerobic conditions for 7 days at 6 °C and then for a further 7 days at 23 °C for pre-incubation. On day 14, the soil samples were prepared for incubation in a semi-automatic incubation device using its flow-through mode (Heinemeyer et al., 1989). Three replicates (20 g dry wt.) of each sample were put loosely in acrylic glass tubes (4 cm diameter) and enclosed at both ends with polystyrene foam stoppers. Humidified ambient air flowed through 24 independent lines containing the soil samples at flow rates between 160 and 180 ml min^{-1}. An infrared CO_2 gas analyser (ADC-255-MK3, Analytical Development Co. Ltd.,

Hoddesdon, UK) was used to measure CO_2 concentrations. Each replicate sample was measured hourly over an incubation time of at least 40 h or until a relatively constant BR was reached (up to 90 h).

Afterwards soil samples were amended with a mixture of 100 mg glucose and 100 mg talcum using an electronic stir for 30 s to determine the active microbial biomass using the SIR method. The mixture was then incubated again for 6 h to obtain the maximal initial respiratory response of the microbial biomass (Anderson et al., 1995).

2.4 Data analysis

Statistical analysis was performed using the R software environment (version R-3.1.3, R Core Team, 2015).

2.4.1 Determination of basal soil respiration

The measured BR is expressed as µg CO_2-C g soil^{-1} h^{-1} and the specific basal respiration (SBR) is normalised by the sample's SOC content into µg CO_2-C g SOC^{-1} h^{-1}. An exponential model was fitted simultaneously to all three incubation replicates to determine the equilibrium values of the SBR (Figure):

$$\mathrm{CO_2 - C\,(t) = a - (a - SBR)\,(1 - e^{-k*t})}, \qquad (1)$$

where CO_2-C (t) [µg CO_2-C g SOC^{-1} h^{-1}] is the specific CO_2 production per hour, *a* [µg CO_2-C g SOC^{-1} h^{-1}] is the initial respiration and *k* [h^{-1}] is the change rate of SBR.

To achieve an objective quantification of the (specific) basal respiration and its uncertainty, the R package "dream" was used (Guillaume and Andrews, 2012), which is based on the iterative Markov Chain Monte Carlo (MCMC) approach. This method is basically a Markov chain that generates a random walk through the high-probability-density region in the parameter space, separating behavioural from non-behavioural solutions following the probability distribution (Vrugt et al., 2009b). The differential evolution adaptive metropolis (DREAM) algorithm is an efficient MCMC sampler that runs multiple Markov chains simultaneously for global exploration of the parameter space. In doing so, DREAM uses a differential algorithm for population evolution and a metropolis selection rule to decide whether a population of candidate points is accepted or not. After the burn-in period, the convergence of individual chains is checked using the Gelman and Rubin (1992) convergence criterion, which examines the variance between and within chains (Vrugt et al., 2008, 2009a).

Once the convergence criterion of Gelman and Rubin was < 1.01, another 500,000 simulations were run to determine the posterior probability density functions of the model parameters, which were used to calculate the median and the 2.5 and 97.5 % quantiles.

For the evaluation of the SIR experiment, the value of the maximum initial respiratory response was identified manually and then transcribed to microbial biomass (SIR-C_{mic}) [µg g^{-1} soil] as follows (Kaiser et al., 1992):

$$\mathrm{SIR\text{-}C_{mic}} = \mu\mathrm{l\,CO_2\,g^{-1}\,soil} * 30. \qquad (2)$$

To quantify the efficiency of microbial respiration per unit biomass, the metabolic or respiratory quotient $q(CO_2)$ [mg CO_2-C h^{-1} g^{-1} biomass SIR-C_{mic}] was calculated by dividing the BR by the SIR-C_{mic} (Anderson and Domsch, 1985):

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$$q(CO_2) = \frac{BR}{\mathrm{SIR{-}C_{mic}}/1000}. \tag{3}$$

The higher the value of $q(CO_2)$, the higher the CO_2 emissions per unit microbial biomass, indicating a lack of available C for metabolism in the soil.

2.4.2 Degree of disturbance

The present classification of anthropogenic disturbance is based on the mapped soil horizons from which the samples originated. The soil horizons and the degree of decomposition after von Post were mapped according to the German manual of soil mapping (Ad-Hoc-AG Boden, 2005). While the original von Post scale was developed for undrained peat, the German classification frequently uses the von Post scale for drained peat as well. The samples of peatland genesis were divided into five different disturbance classes according to the severity of disturbance and (Table 2, based on Ilnicki and Zeitz (2003) and Ad-Hoc-AG Boden (2005)): no disturbance (D0F/D0B), slight disturbance (D1F/D1B), moderate disturbance (D2F/D2B), strong disturbance (D3F) and heavy disturbance (D4F). Slightly disturbed horizons experience drainage and are influenced by a fluctuating water table, thus they are temporarily subjected to aerobic conditions but there has not yet been a secondary transformation of the peat structure. Earthified topsoils are defined as “moderately disturbed”. Strong disturbance is characterised by blocky to prismatic aggregates and/or the formation of shrinkage cracks, and is only found in subsoils. In the present sample set, this level of disturbance only occurred in fen peat. Finally, both highly decomposed dusty “moorsh” and mixtures of peat and mineral soil have been defined as “heavily disturbed”. This class also only occurred in fen peat. Overall there are five fen classes, three bog classes, and one class each for *gyttja* (organic or calcareous sediments) and *other* samples. Samples from the class *other* were organic marsh soils or could not be assigned to any disturbance class (e.g. buried organic soils). For further information see Table A1 in the appendix. Given that this classification was developed after the sample selection, the distribution among the groups is not uniform. The von Post scale from H1 to H10 was altered by adding H11 for low C organic soils deriving from peat. G*yttja* and other remaining samples were not included in the van Post scale.

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Table 2: Classification of the anthropogenic disturbance and corresponding median and standard error of soil properties: SOC: soil organic carbon content, C:N-ratio: carbon to nitrogen ratio, $\delta^{15}N$, N_t: total nitrogen content, P_{CAL}: calcium acetate lactate (CAL) extractable phosphorus content, pH-value, EC: electrical conductivity, Fe_O: oxalate extractable iron content, ρ: bulk density

Degree of disturbance	Description	Peatland type	Label	n	SOC (g kg^{-1})	C:N	$\delta^{15}N$ (‰)	N_t (g kg^{-1})	P_{CAL} (mg kg^{-1})	pH	EC (µS cm^{-1})	Fe_O (g kg^{-1})	ρ (g cm^{-3})
No disturbance	Pristine or nearly natural	Fen	D0F	12	462 ± 37	23 ± 3	0.3 ± 0.5	19.4 ± 2.6	7.9 ± 2.2	5.5 ± 0.4	140 ± 38	5.5 ± 1.1	0.13 ± 0.01
		Bog	D0B	9	521 ± 13	57 ± 8	1.2 ± 1.0	9.1 ± 2.4	5.7 ± 5.7	3.2 ± 0.1	92 ± 23	0.9 ± 1.7	0.10 ± 0.01
Slight disturbance	Alternating aerobic-anaerobic conditions	Fen	D1F	9	426 ± 19	18 ± 4	1.2 ± 1.0	21.8 ± 2.0	6.6 ± 3.9	5.2 ± 0.4	282 ± 124	13.4 ± 2.7	0.20 ± 0.02
		Bog	D1B	5	473 ± 13	46 ± 7	0.5 ± 0.7	10.7 ± 1.5	41.8 ± 13.2	3.5 ± 0.1	70 ± 11	3.3 ± 2.8	0.12 ± 0.02
Moderate disturbance	Earthification	Fen	D2F	7	340 ± 32	17 ± 1	1.2 ± 0.6	21.0 ± 1.9	12.4 ± 8.6	5.2 ± 0.2	292 ± 276	21.0 ± 4.7	0.30 ± 0.05
		Bog	D2B	6	333 ± 52	23 ± 2	2.0 ± 0.5	14.2 ± 2.6	77.3 ± 27.0	3.8 ± 0.3	121 ± 10	9.3 ± 1.8	0.18 ± 0.10
Strong disturbance	Polyhedral aggregates or cracks	Fen	D3F	5	320 ± 19	14 ± 1	1.9 ± 0.5	24.0 ± 1.8	24.2 ± 19.9	5.6 ± 0.6	271 ± 55	24.4 ± 14.1	0.26 ± 0.07
Heavy disturbance	Dusty moorsh or high content of mineral soil	Fen	D4F	19	142 ± 12	14 ± 1	3.3 ± 0.4	10.0 ± 1.1	30.9 ± 24.5	5.4 ± 0.3	209 ± 153	19.6 ± 2.7	0.65 ± 0.05
Gyttja	Organic or calcareous sediments	-	G	12	100 ± 19	20 ± 3	1.7 ± 0.6	5.4 ± 0.7	14.2 ± 7.5	4.7 ± 0.4	253 ± 206	17.1 ± 9.1	0.51 ± 0.08
Other	e.g. organic marsh soils, buried horizons	-	O	17	124 ± 15	16 ± 2	3.5 ± 0.5	7.0 ± 0.7	11.3 ± 6.1	5.2 ± 0.3	124 ± 146	21.8 ± 3.9	0.54 ± 0.05

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2.4.3 Statistical and multivariate analysis

In a first step, Spearman's rank correlation coefficient r_s was evaluated for the specific basal respiration and all measured explanatory variables using the R package "Hmisc" (Harrell, 2016). The p-values were adjusted using the method after Bonferroni. Differences between the results of disturbance classes for BR, SBR, SIR-C_{mic} and $q(CO_2)$ were determined using an analysis of variance. P-values were computed with the Tukey 'honest significant differences' test ($\alpha = 0.05$) and adjusted with the Bonferroni correction using the R package "multcomp" (Hothorn et al., 2008). Correlation coefficients were classified as follows: $0.3 \geq r_s \geq 0.7$ is a moderate correlation and $r_s > 0.7$ a strong correlation.

In a second step, multi-variate linear regression was applied to identify the most crucial factors and interactions influencing the specific basal respiration. The generalised least squares (gls) model was used with the exponential variance structure following the protocol of Zuur et al. (2009) using the R package "nlme" (Pinheiro et al., 2015). The SBR was set as the dependent variable, with the explanatory variables of SOC, N_t, C:N-ratio, P_{CAL}, carbonate ($CaCO_3$), pH, $\delta^{13}C$, $\delta^{15}N$, Fe_O, ρ, soil depth and EC as well as the categorical variables of the degree of decomposition (von Post, 1924), the degree of disturbance and peatland type. Important meaningful interactions were also incorporated. To achieve homoscedasticity of residuals, the data of EC and P_{CAL} were log10 transformed and the C:N-ratio log-transformed. Applying the top-down strategy for the model selection, the complete generalised least squares model was run first and variables stepwise removed until all the variables were significant with a p-value < 0.001 obtained by t-statistics. To identify the best model, Akaike's information criterion (AIC) was compared with the full model for all calculated models after each parameter drop. Afterwards, the best model was cross-validated using the "leave-one-site-out" approach.

All the results given below are medians with standard errors, unless otherwise stated.

3 Results

3.1 Vulnerability of SOM as determined by respiration rates

For all classes, BR was highly variable, ranging from 0.3 to 7.0 µg CO_2-C g soil^{-1} h^{-1} (Fig. 1a). The BR rates of fen samples decreased with an increasing degree of disturbance due to concomitantly decreasing SOC content (Table 2), while bog samples behaved inversely. Overall, bog samples (2.0 ± 0.3 µg CO_2-C g soil^{-1} h^{-1}) had similar BR rates to fen samples (2.5 ± 0.2 µg CO_2-C g soil^{-1} h^{-1}). *Gyttja* (1.3 ± 0.3 µg CO_2-C g soil^{-1} h^{-1}) and *other* samples (1.1 ± 0.2 µg CO_2-C g soil^{-1} h^{-1}) showed significantly lower BR rates than undisturbed, slightly and strongly disturbed fen samples (D0F, D1F, D3F).

Overall, fen samples had significantly higher ($p < 0.01$) average SBR rates of 8.3 ± 0.7 µg CO_2-C g SOC^{-1} h^{-1} than bog samples (5.1 ± 0.9 µg CO_2-C g SOC^{-1} h^{-1}). This difference was especially clear for undisturbed and slightly disturbed samples. SBR rates were also highly variable between and within classes, and ranging from 1.5 to 25.1 µg CO_2-C g SOC^{-1} h^{-1} (Fig. 1b). SBR rates tended to increase with increasing soil disturbance for both fen and bog. D0B samples had significantly lower ($p < 0.01$) SBR rates than the classes D4F, *gyttja* and *other* with 3.7 ± 0.6 µg CO_2-C g SOC^{-1} h^{-1}. The moderately disturbed D2B samples showed much higher SBR rates (10.1 ± 2.1 µg CO_2-C g soil-SOC^{-1} h^{-1}) than the other two bog classes, and were comparable to strongly and heavily disturbed fen samples (D3F, D4F). Both *gyttja* and *other* showed high and variable SBR rates with 14.2 ± 2.4 µg CO_2-SOC g SOC^{-1} h^{-1} and 10.8 ± 1.5 µg CO_2-C g SOC^{-1} h^{-1} respectively.

3.2. Organic matter quality and soil characteristics determining SOM vulnerability

The significant Spearman correlation coefficients indicated moderate positive correlations between SBR rates and phosphorus concentration ($r_s = 0.52$), pH value ($r_s = 0.42$), iron oxides ($r_s = 0.42$) and carbonate concentration ($r_s = 0.36$). Significant negative dependence was found between SBR and the C:N-ratio ($r_s = -0.62$) and SOC content ($r_s = -0.49$) (Fig. 2). The most influencing factors on SBR rates as indicated by the best fitted *gls* model were SOC, C:N-ratio, P_{CAL} and ρ (all $p < 0.001$). With these four parameters the cross-validated model explained 42 % of the variability of the measured SBR rates.

While the correlation matrix shown in Fig. 2 gives a general overview on potential explanatory variables, a closer look is taken at some selected variables and their interaction with the disturbance classes (Figs. 3 and 4).

Overall, the variability and magnitude of SBR rates increased with decreasing SOC content (Fig. 3a) and an increasing degree of decomposition (Fig. 3b). The rates were highest and most variable for soil samples with a low SOC content, comprising the D4F, *gyttja* and *other* samples. Within disturbance classes, the strength of the negative correlations between SBR and SOC content tended to increase with increasing disturbance for fen peat, but became slightly positive for heavily disturbed D4F samples (Fig. 4). In contrast, bog, *gyttja* and *other* samples showed only weak correlations between SBR and SOC.

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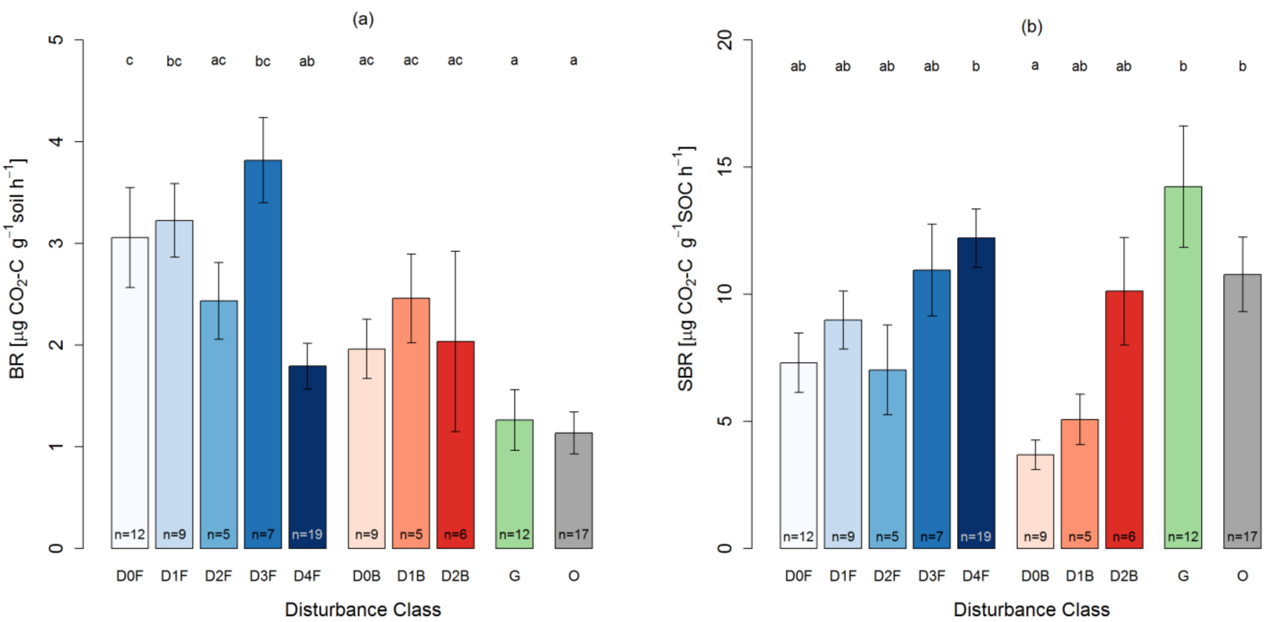

Figure 1: a) Median of basal respiration (BR) rates and b) specific basal respiration (SBR) rates for all disturbance classes: F=fen, B=bog, G=gyttja, O=other, D0=no disturbance, D1=slight disturbance, D2=moderate disturbance, D3=strong disturbance, D4=heavy disturbance. Bars show the standard error. Different letters represent significant differences (Tukey's test, $p < 0.05$).

With increasing von Post values, SBR rates showed a significantly linear increase ($p < 0.001$, Fig. 3b). Soil samples with a von Post decomposition degree of H3 and H7 had significantly lower ($p < 0.05$) SBR rates of 6.3 ± 1.0 µg CO_2-C g SOC^{-1} h^{-1} and 7.8 ± 0.8 µg CO_2-C g SOC^{-1} h^{-1}, respectively, than samples mapped as H10 (13.4 ± 1.2 µg CO_2-C g SOC^{-1} h^{-1}). With decreasing C:N-ratios, SBR rates increased in an exponential manner (Fig. 3c). However, when splitting the samples into two groups at C:N = 25, there was no longer any correlation for any of the groups. Again, the highest and most variable rates of 10.4 ± 0.6 µg CO_2-C g SOC^{-1} h^{-1} were measured for highly disturbed samples with low C:N ratios < 25, which mainly belong to all fen classes, *gyttja*, D2B and *other* (see Table 2). In contrast, samples with a C:N-ratio > 25 were bog samples with low or minimal disturbance, which had significantly lower ($p < 0.001$) and less variable SBR rates of 4.1 ± 0.6 µg CO_2-C g SOC^{-1} h^{-1}. In detail, there was a strong negative correlation between SBR rates and the C:N-ratio for D0F ($r_s = -0.73$) and *gyttja* samples ($r_s = -0.85$, $p < 0.05$). Moderate correlations were found for *other* ($r_s = -0.56$), D1F ($r_s = -0.47$), D2F ($r_s = -0.32$) and D0B ($r_s = -0.47$) but these correlations were not significant (Fig. 4).

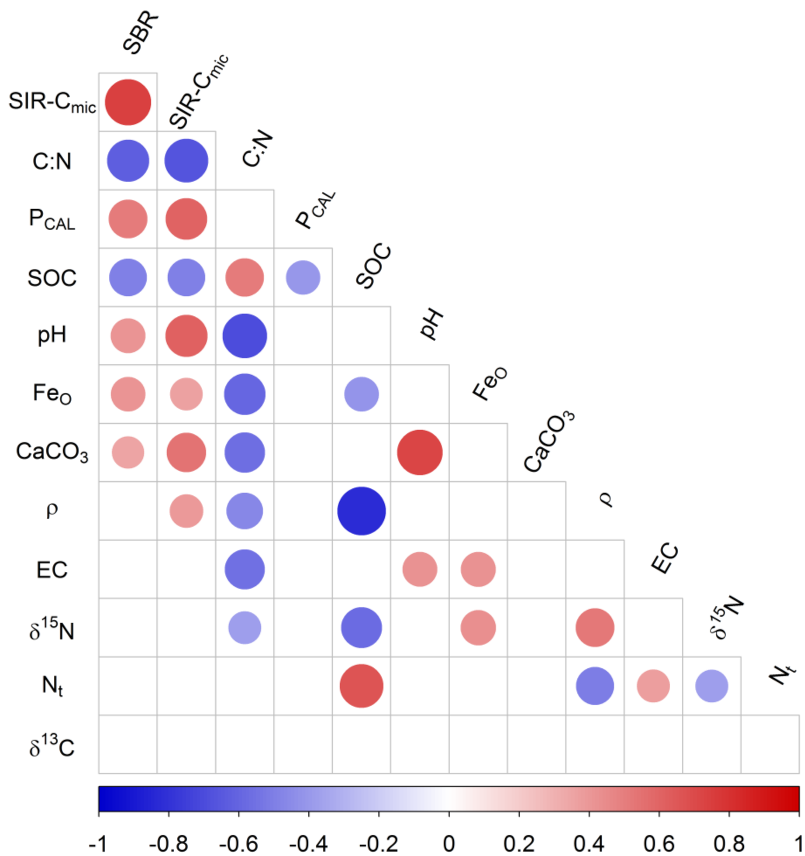

Figure 2: Significant ($p < 0.05$) correlation coefficients after Spearman for the specific basal respiration rates (SBR) as well as the determined specific microbial biomass ($SIR\text{-}C_{mic}$) and all determined soil properties: C:N-ratio: carbon to nitrogen ratio, P_{CAL}: calcium acetate lactate (CAL) extractable phosphorus content, SOC: soil organic carbon content, pH-value, Fe_O: oxalate extractable iron content, $CaCO_3$: calcium carbonate content, ρ: bulk density, EC: electrical conductivity, $\delta^{15}N$, N_t: total nitrogen content and $\delta^{13}C$

Even though there was no general relationship between N_t and SBR rates (Fig. 3d), N_t concentrations were positively correlated with the respiration rates of the disturbance classes D0F ($r_s = 0.57$), D4F ($r_s = 0.37$), D0B ($r_s = 0.47$) and *gyttja* samples ($r_s = 0.55$) (Fig. 4). In contrast, the samples of D3F ($r_s = -0.6$) were negatively correlated.

There was a significant ($p < 0.001$) difference in $\delta^{15}N$ values between samples from undisturbed and disturbed horizons (Fig. 3e). The mean values for undisturbed horizons were 0.0 ± 0.6 ‰ (D0B) and -0.3 ± 0.4 ‰ (D0F) respectively. All the other disturbance classes showed higher $\delta^{15}N$ values up to 11.2 ‰, and a slight overall increase in SBR rates with increasing $\delta^{15}N$. However, mainly within (relatively) undisturbed classes, there were negative correlations between $\delta^{15}N$ and SBR rates for D0B ($r_s = -0.5$), D1B ($r_s = -0.7$) and D3F ($r_s = -0.3$) (Fig. 4). In contrast, there were slightly positive correlations in the case of heavily disturbed D4F samples ($r_s = 0.33$).

Overall, P_{CAL} showed significant positive correlations with the SBR rates (Fig. 2) and, furthermore, P_{CAL} was the explanatory variable with the highest number of positive correlations with SBR over all disturbance classes. This is visualised by the linear increase of SBR with P_{CAL} (Fig. 3f). In the case of bogs, the correlation increased with increasing disturbance (D0B: $r_s = 0.42$, D1B: $r_s = 0.5$, D2B: $r_s = 0.77$, Fig. 4). Overall the bog samples ($r_s = 0.71$, $p < 0.05$) had a significantly strong dependence and the fen samples ($r_s = 0.49$, $p < 0.01$) a significantly moderate dependence on P_{CAL}. The effect of the disturbance class was less consistent in the case of fens compared to bogs, with the strongest correlation in D3F ($r_s = 1$, $p < 0.001$).

Considering all the samples, SBR rates increased linearly with increasing pH (Fig. 3g), reflecting the general differences between bogs and fens. This increase in SBR was most distinctive for D0F ($r_s = 0.85$, $p < 0.05$), D1B ($r_s = 0.5$) and *gyttja* samples ($r_s = 0.78$). The correlation with pH values was moderate for D0B ($r_s = 0.47$), *other* ($r_s = 0.37$) and D2F samples ($r_s = -0.46$), which were negatively correlated (Fig. 4). Overall, the SBR rates of bog samples correlated strongly with pH ($r_s = 0.74$, $p < 0.05$), even though bog samples covered only a small range (3.5 ± 0.1) of the overall pH values, whereas *other* samples had the widest range (5.2 ± 0.3) followed by *gyttja* (4.8 ± 0.4) and *fen* samples (5.6 ± 0.2).

The concentration of iron oxides had a linear positive relationship with SBR rates (Fig. 2), which was especially noticeable in the strong correlation with D2F samples ($r_s = 0.96$, $p < 0.05$). Furthermore, rates of D1F ($r_s = 0.37$), D1B ($r_s = 0.4$) and *other* samples ($r_s = 0.36$) showed moderate positive dependence on Fe_O (Fig. 3h; Fig. 4). However, this effect was not systematic as the SBR rates of samples of disturbance class D3F ($r_s = -0.5$) were negatively correlated with iron concentration.

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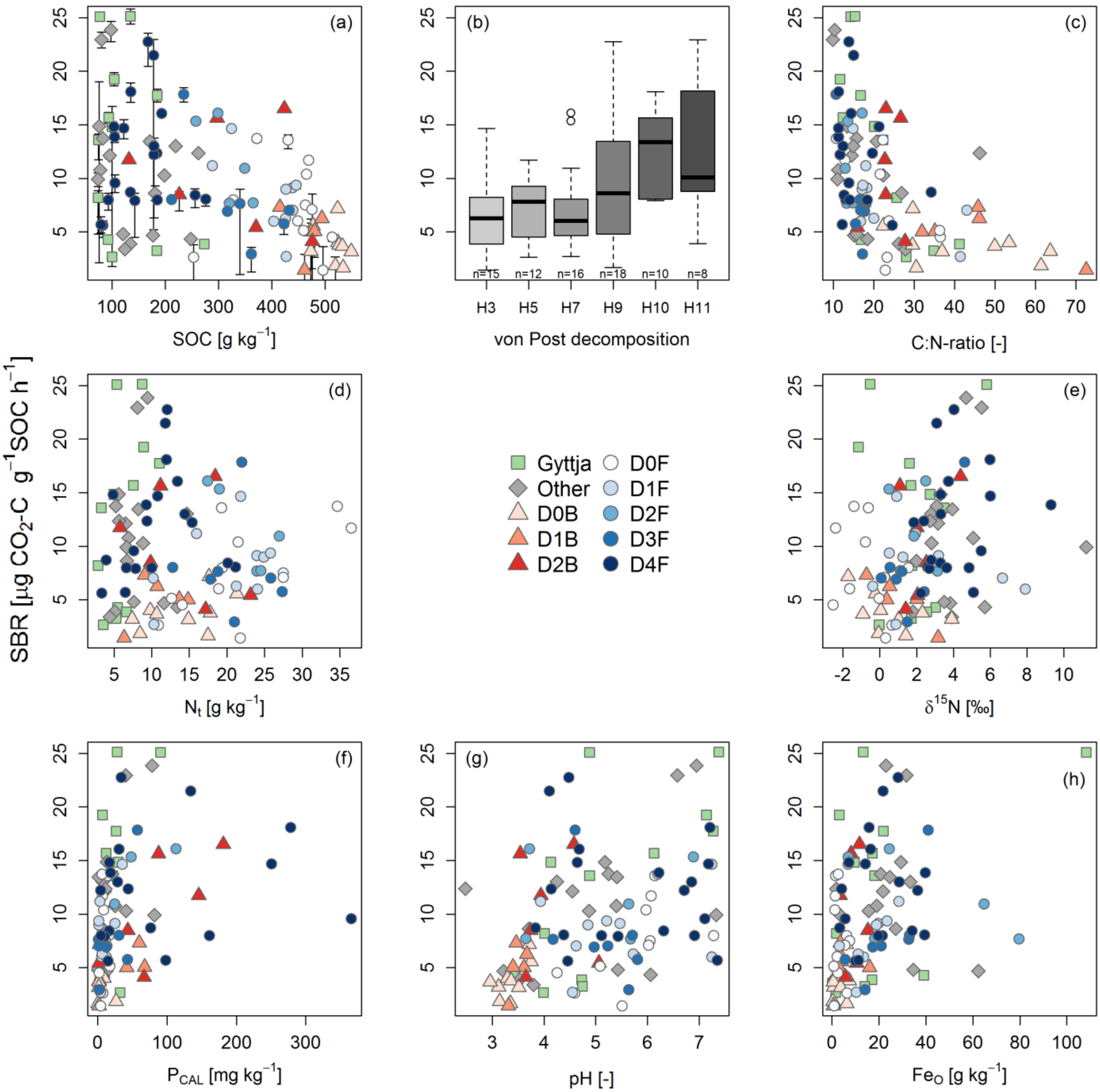

Figure 3: Specific basal respiration (SBR) rates of all samples classified in disturbance classes (F=fen, B=bog, G=gyttja, O=other, D0=no disturbance, D1=slight disturbance, D2=moderate disturbance, D3=strong disturbance, D4=heavy disturbance) versus (a) soil organic carbon content, (b) decomposition degree after von Post, (c) carbon-to-nitrogen ratio, (d) total nitrogen content, (e) $\delta^{15}N$, (f) calcium acetate lactate (CAL) extractable phosphorus content, (g) pH value, (h) oxalate extractable iron content. Bars in (a) show 2.5 and 97.5 % quantiles of the DREAM-fit.

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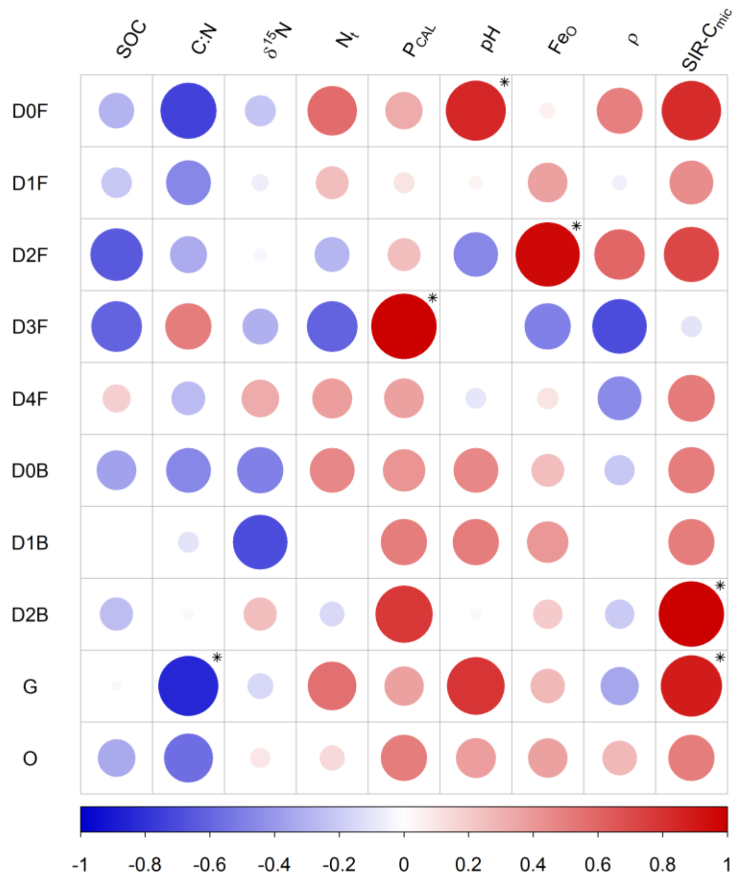

Figure 4: Correlation coefficients after Spearman (significant correlations ($p < 0.05$) are marked with asterisks) for the specific basal respiration rates separated into the disturbance classes (F=fen, B=bog, G=gyttja, O=other, D0=no disturbance, D1=slight disturbance, D2=moderate disturbance, D3=strong disturbance, D4=heavy disturbance) and soil properties: SOC: soil organic carbon content, C:N-ratio: carbon to nitrogen ratio, $\delta^{15}N$, N_t: total nitrogen content, P_{CAL}: calcium acetate lactate (CAL) extractable phosphorus content, pH-value, Fe_O: oxalate extractable iron content, ρ: bulk density, as well as the determined specific microbial biomass ($SIR\text{-}C_{mic}$)

3.3 Relation between microbial biomass and mineralisation rates

Overall, the specific microbial biomass (Fig. 5a) was positively correlated with SBR ($r_s = 0.75$) and thus followed a similar pattern to SBR (Fig. 1b) across disturbance classes: values were higher for fen samples than for bog samples and tended to increase with increasing disturbance, especially in the case of bog samples. There were strong positive correlations between $SIR\text{-}C_{mic}$ and SBR for all disturbance classes (Fig. 4), except D2F ($r_s = 0.45$), which was moderately correlated with $SIR\text{-}C_{mic}$ and D3F. Samples of the classes D2B ($r_s = 1$, $p < 0.001$) and *gyttja* ($r_s = 0.88$, $p < 0.05$) showed the highest dependencies. Overall, specific $SIR\text{-}C_{mic}$ was highest for D4F samples (3249 ± 411 µg C g^{-1} SOC) followed by D3F (2293 ± 612 µg C g^{-1} SOC) and D2B samples (2265 ± 400 µg C g^{-1} SOC). *Gyttja* (1907 ± 339 µg C g^{-1} SOC) and *other* samples

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(1528 ± 533 µg C g^{-1} SOC) had relatively high values of microbial specific SIR-C_{mic}, with the latter being the most variable of all the groups.

Specific SIR-C_{mic} showed similar relationships with explanatory variables as SBR (Fig. 2).

There were no significant differences in the metabolic quotient between disturbance classes (Fig. 5b). The values of the classes D0F, D1F, D2F, D4F and D2B were slightly lower than those of the other classes, and there was a slight tendency for a decreasing metabolic quotient with increasing disturbance for bog samples.

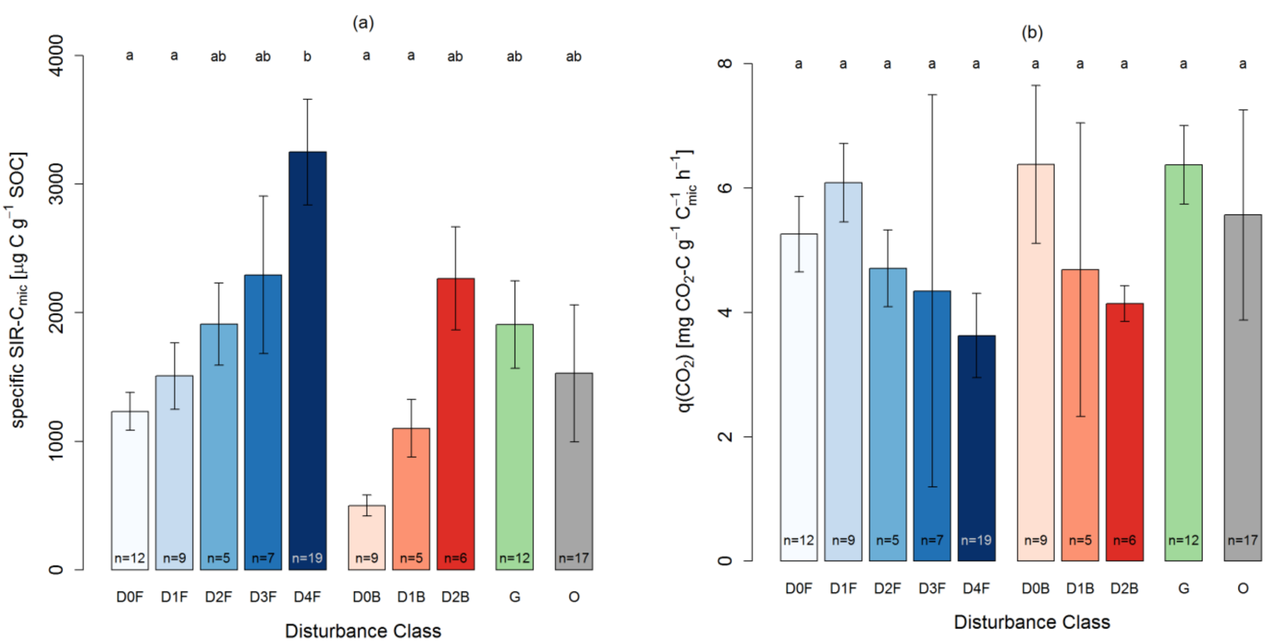

Figure 5: a) Median of specific microbial biomass (SIR-C_{mic}) determined via substrate induced respiration (SIR) and b) metabolic quotient ($q(CO_2)$) for different disturbance classes: F=fen, B=bog, G=gyttja, O=other, D0=no disturbance, D1=slight disturbance, D2=moderate disturbance, D3=strong disturbance, D4=heavy disturbance. Bars show the standard error. Different letters represent significant differences (Tukey's test, $p < 0.05$)

4 Discussion

4.1 Enhanced SOM vulnerability to decomposition with increasing disturbance of peat

The most striking result of the present experiment was that specific basal respiration rates increased both in magnitude and variability with increasing degradation and disturbance of the peat soils, irrespective of whether this degradation was expressed as a von Post value, a disturbance class or SOC content (Figs. 3 and 4). This finding was best illustrated in the bog samples and manifested itself in the more variable specific basal respiration rates with a smaller SOC content. Second, in contrast to less disturbed peat samples, it proved to be practically impossible to describe the specific basal respiration or specific microbial biomass for heavily disturbed fen samples with the set of explanatory variables used here (Fig. 4). In contrast to specific basal respiration, it is noteworthy that the basal respiration rates tended to increase with increasing disturbance for bog samples, while there was a significant decrease for fen samples, i.e. the effects of disturbance on total basal respiration were soil specific (Fig. 1a).

Glatzel et al. (2004) refer to the importance of the von Post value as an indicator of CO_2 production, however they identified a negative correlation. Similarly Ilnicki and Zeitz (2003) found lower CO_2 production rates for samples with a high degree of decomposition and the lowest rates for moorshy peat soils. However, Brake et al. (1999) found increasing specific basal respiration rates for increasingly disturbed peat samples. The most probable reason for the discrepancies is that the von Post scale was originally developed for natural peatlands, where strong decomposition is caused by age as well as climatic conditions during peat formation and peatland development, and not by anthropogenic impacts. Due to the lack of better, widely accepted indicators, the von Post scale is frequently applied to drained peatlands as well. Consequently, the naturally strongly decomposed peat of the study of Glatzel et al. (2004) underwent a completely different pedogenesis than the samples from the drained peatlands in the present study. With regard to the results of Ilnicki and Zeitz (2003), the high variability in the specific basal respiration of the strongly disturbed samples in the present study also includes “moorshy” samples with low respiration rates.

The higher specific basal respiration rates of fen samples compared to bog samples of similar disturbance, has been observed in previous studies (e.g. Bridgham and Richardson, 1992; Urbanova and Barta, 2015) and was expected here. Generally, faster decomposition processes occur under minerotrophic conditions and in peat dominated by vascular plants (Blodau, 2002). Undisturbed bogs are characterised by a lack of nutrients, strong acidity and peat substrates that hinder rapid mineralisation due to their chemical composition (Urbanová and Bárta, 2014; Verhoeven and Liefveld, 1997).

It has been found that after drainage the microbial communities increase in richness and diversity in bogs, but in contrast decrease for fens (Urbanová and Bárta, 2015), indicating the high sensitivity of bogs to anthropogenic impacts. The same authors also found that fens and bogs become more similar after long-term drainage as their characteristic differences in biogeochemical properties and microbial composition reduce. This could explain our observation that strong disturbance diminished differences in specific basal respiration rates between bog and fen peat. Additionally, increased nutrient supply

(Wells and Williams, 1996) and effects of physical disturbance (Ross and Malcolm, 1988; Rovdan et al., 2002) might contribute to this effect. Furthermore disturbance might reactivate enzymes that were previously inactive, thus enhancing mineralisation rates under favourable conditions (Freeman et al., 1996, 2001). Freeman et al. (2001) found that the enzyme phenol oxidase has a tremendous effect on increasing the peat decomposition under aerobic conditions. These effects might cause the strong increase in specific basal respiration rates and specific microbial biomass values from undisturbed/slightly disturbed to moderately disturbed bog samples.

Surprisingly, *gyttja* and *other* organic soils showed similarly high specific basal respiration rates as the heavily disturbed peat samples. To the authors' knowledge, there are no studies that have determined the respiration rates of gyttja before, as gyttja soils are most often covered by peat soils. However, organic gyttja soils have similar physical soil properties to heavily disturbed peat, including high bulk density, a high degree of decomposition and low pore volume (Chmieleski, 2006). Intensive microbial processes in drained organic gyttja soils as well as the presence of easily degradable SOM (Chmieleski, 2006) could explain the high respiration rates.

Overall, the structural and chemical changes of the peat properties seems to cause destabilising positive feedback processes, as shown in specific basal respiration and, in the case of bogs, the absolute values of respiration increase as well.

4.2 SOM quality as an indicator of SOM vulnerability

While SOM quality is closely linked to the mineralisation of SOM, there is no commonly accepted quality index for SOM (Reiche et al., 2010). To characterise SOM quality, C:N-ratio, degree of decomposition and $\delta^{15}N$ stable isotope values were used in this study, as they are all indicators of the transformation stage of organic matter (Bohlin et al., 1989; Glatzel et al., 2004; Krüger et al., 2014; Reiche et al., 2010). The results pointed to a faster turnover of SOM in samples with a narrow C:N-ratio, especially in fen samples. Specific basal respiration rates increased rapidly with falling C:N-ratios below a threshold value of 25 (Fig. 3c). However this may only be an effect of preferential C release during decomposition at sufficient N supply (Kuhry and Vitt, 1996), i.e. a narrow C:N-ratio is also a product of fast turnover. In contrast, wider C:N-ratios seem to indicate a more stable SOM pool. This indicates that there is surprisingly no increased stabilisation with increased degradation due to selective preservation of more stable SOC components (Lehmann and Kleber, 2015) that are unattractive for decay, such as waxes, polyphenols, lignins and tannins (Verhoeven and Liefveld, 1997). Low $\delta^{15}N$ values appear to be a good indicator of undisturbed or fresh SOM, especially in bog peat, due to the lack of SOM turnover processes that usually result in ^{15}N enrichment (Nadelhoffer et al., 1996). For the increasingly disturbed samples, the correlation between specific basal respiration and $\delta^{15}N$ became positive (Fig. 4), indicating that increased microbial transformation under aerobic conditions altered the stable isotope signature of SOM. Mineralisation will therefore result in both increased $\delta^{15}N$ values and increased respiration rates, making it difficult to distinguish between cause and effect.

Overall, the greater the disturbance, the harder it proved to be to find possible patterns of SOM quality parameters and specific basal respiration, especially in the case of fen samples. One reason for this could be that chemical and physical changes during decomposition differ between peat-forming plants (Bohlin et al., 1989), that can no longer be identified and are more diverse in bogs than in fens. Furthermore, the class of heavily disturbed fen samples combines samples which have been amended by mineral soil by different processes (e.g. ploughing, application from external sources, or natural sedimentation in riverine fens) and those which have become "moorshy", but were not amended. To disentangle different processes, a larger number of samples and more detailed information on the sites' history will be required in future studies. Finally, the DREAM-fits showed the largest uncertainty for some of the samples of the class D4F (Fig. 3a), which might have contributed to the difficulty in finding appropriate explanatory variables.

4.3 Nutrients and acidity as indicators of SOM vulnerability

Agriculturally used peats drained for a long time are often enriched in N and (labile) P concentrations (Laiho et al., 1998; Schlichting et al., 2002; Sundström et al., 2000) due to ongoing mineralisation of SOM and sorption of the resulting inorganic P forms to Fe(III) compounds (Zak et al., 2010). As P is needed for microbial growth, a lack of labile phosphorus limits the decomposition of SOM, and this limitation may be due to both low P contents as well as sorption and fixation of P to iron, calcium or aluminium minerals (Wells and Williams, 1996). This was also the case in the present sample set (Table 2). The results of the present study show that plant-available phosphorus (P_{CAL}) was the most important explanatory variable for specific basal respiration rates, especially for bog samples. This confirms the results of Brake et al. (1999) who also found that P strongly correlates with the respiration rates of disturbed bog samples. Due to the low pH and iron concentrations, bogs are frequently P-limited (Verhoeven et al., 1990), which is reflected in the correlation between specific basal respiration and P_{CAL} (Fig. 4) Depending on the iron concentration (Zak et al., 2010), deeper and less disturbed peat layers are potentially threatened by enhanced P mobilisation and leaching.

Nitrogen concentrations only increased for moderately disturbed bog samples, and even decreased for heavily disturbed fen samples compared to undisturbed or slightly disturbed samples (Table 2). This might be due to accelerated N-mineralisation (Williams and Wheatley, 1988) or increased immobilisation of N since peat plants are decomposed under increasing oxygen supply and disturbance levels (Wells and Williams, 1996). As indicated by the correlations (Fig. 4) specific basal respiration rates seem only to be positively influenced by N concentrations in the case of undisturbed samples and *gyttja*. *Gyttja* samples are fairly undisturbed in most cases too, due to the soil depth. This might indicate a shift from N to P limitation in the course of degradation processes since ongoing mineralisation increases the N supply. Furthermore Toberman et al. (2015) found a positive correlation between N and P content in *Sphagnum* peat, pointing to the important role of P availability in N fixation.

Beside nutrient impacts, there was also a positive correlation between specific basal respiration rates and the pH of *gyttja*, undisturbed fen and bog and slightly disturbed bog samples, probably reflecting lower microbial activity in an acidic environment (Fig. 5a). The present study's findings of a positive relationship between specific basal respiration rates and pH value of undisturbed, slightly and moderately disturbed peat samples (Figs. 2 and 3g) are in an apparent contradiction to earlier reports that have detected a negative correlation (Ausec et al., 2009; Fisk et al., 2003). The authors explain the

negative relationship by a restricted efficiency of C metabolism of the microbial biomass in bogs due to the acidic environment, which was however not the case in the present study's samples set (see section 4.4; Fig. 5b), and contradict the common observation that bogs show higher respiration rates than fens (e.g. Bridgham and Richardson, 1992; Urbanova and Barta, 2015). Although all three studies used undisturbed peatland sites, their samples had a smaller pH range and they only sampled to a depth of 30 cm, instead of up to 200 cm as in the present study. This and the fact that a broader sampling site basis was used here could explain the contrasting correlation. However, with increasing disturbance the influence of pH diminishes in the present samples, possibly due to better nutrient availability and increased pH-values overall in bogs.
As already mentioned, it was impossible to identify any strong correlations between soil properties and specific basal respiration or SIR-C_{mic} of heavily disturbed fens samples (D4F Fig. 4). Since these soils have a comparably low SOC content (142 ± 12 g kg^{-1}, Table 2), they have become increasingly similar to mineral soils. It could therefore be expected that stabilisation mechanisms for SOM become more similar to mineral soils. However, Fe_O, which has been shown to be important for SOM stabilisation (Wagai and Mayer, 2007 and references therein), is of minor importance for specific basal respiration, even for samples at the boundary of mineral and organic soils (Fig. 4). Furthermore, numerous studies have shown SOM stabilisation on clay minerals (e.g. Hassink, 1997; Saidy et al., 2012; Six et al., 2016). However, there was no correlation between clay content and specific basal respiration in the present set of samples, despite the wide range of clay content in the heavily disturbed samples (5-50 %).

4.4 Microbial biomass and activity

The specific microbial biomass increased with the increasing degree of anthropogenic disturbance for both fen and bog samples (Fig. 5a). This is surprising since highly degraded peat should be energetically less attractive for microorganisms than well conserved peat (Fisk et al., 2003). The transition from anaerobic to aerobic conditions increases mineralisation (Bridgham and Richardson 1992; Glatzel et al. 2004; Holden et al. 2004 and references therein), and therefore improves the availability of nutrients as well as readily available SOM since fertilisation causes changes in the community and in the amount of microbial biomass (Amador and Jones, 1993; Brouns et al., 2016). This is reflected in positive correlations of specific microbial biomass with pH value and negative correlations with C:N-ratios. The metabolic quotient, i.e. the ratio of basal respiration and microbial biomass, indicates the efficiency of microorganisms to transform SOM into microbial biomass. Overall, there were no significant differences in the metabolic quotient between disturbances classes (Fig. 5b). However, *gyttja* and *other* samples have a high potential of respiring CO_2 although they have low microbial biomass and SOC contents. In contrast, the slight tendency towards lower metabolic quotients of strongly disturbed bog and fen samples compared to undisturbed samples indicate that these microorganisms are more efficient at using SOM for growth. Although the metabolic quotients were lower compared to the undisturbed samples, the high amount of microbial active biomass and the high specific respiration rates point towards accelerated mineralisation rates in the strongly and heavily disturbed peat samples.

4.5 Implications for peatland management

The high specific basal respiration rates of heavily disturbed samples confirm the vulnerability of "low C organic soils" that has already been identified in field studies (Leiber-Sauheitl et al., 2014; Tiemeyer et al., 2016). Potential emissions do not reach a constant level, and do not always decrease or stop with increasing disturbance. The SOC content below which such soils behave like mineral soils does not seem to be within the studied SOC range. However, there were heavily disturbed samples in this present study that showed low potential emissions which agrees with the finding that the variability of CO_2 emissions from "low C organic soils" field studies is high. Therefore mixing organic soil with mineral soil does not seem to mitigate respiration rates by the potential stabilisation effect of clay, but on average increases the vulnerability of SOM. However, for specific samples the respiration rates are still rather unpredictable. By ploughing mineral soil into the peat layer, a whole new soil horizon develops, that may include modified microbial communities and potentially fresh SOM after disaggregation of the peat takes place (Ross and Malcolm, 1988). Applying N and especially P fertilisers on peatlands might increase the specific basal respiration rates (Amador and Jones, 1993), because lower respiration rates of less disturbed peat samples might be primarily caused by their nutrient limitation. However, it should be stressed that additional experiments that could provide clearer answers to such questions were not carried out. Similarly, liming of acidy peat soils might have a similar effect because increasing the pH value generates favourable microbial conditions for decomposition (Andersson and Nilsson, 2001; Fuentes et al., 2006). Finally, degradation of the topsoil might even influence the mineralisation of deeper peat layers due to leaching of nutrients and dissolved organic matter. Rising water tables may prevent further decomposition and reinstate the typical peatland environment, however severe disturbance might have a long-lasting effect on the biogeochemistry of rewetted peatlands.

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5 Conclusions

This study examined the vulnerability of SOM of organic soils to decomposition by determining the specific basal respiration rates under aerobic conditions in the laboratory. It was shown that the specific basal respiration increased in magnitude and variability with increasing disturbance, and that it was at its highest and most variable at the boundary between mineral and organic soils. At this boundary heavily degraded organic soil or peat soils mixed with mineral soil prevailed, and therefore it was surprising that a decreasing trend of specific basal respiration with higher SOC was identified. Furthermore, bog samples seemed to be more sensitive to anthropogenic disturbance than fen samples as indicated by a stronger increase of specific respiration rates with increasing disturbance. Overall, the most important indicators for the vulnerability of SOM identified in the present study were narrow C:N-ratios, higher pH-values, lower SOC content, and higher concentrations of available phosphorus. There seems to be a positive feedback loop of disturbance and increased mineralisation. However no explanation could be found for the very variable specific basal respiration of heavily disturbed ("moorshy") fen peat and mineral soil-peat mixtures. For these types of soils, more sophisticated indicators of vulnerability still need to be identified. Given the continued drainage and disturbance of peatlands and the considerable potential of CO_2 emissions from heavily disturbed organic soil presented here, future research needs to be concentrated on identifying hotspots within these very heterogeneous soils for correctly targeting mitigation measures. Furthermore mixing peat with mineral soils does not seem to be a promising option to mitigate emissions.

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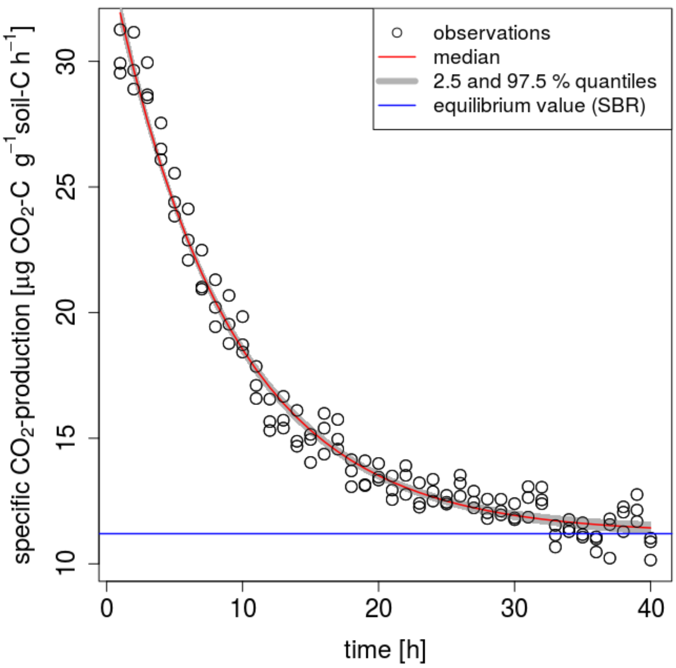
Data availability

Results of the incubation experiment and the soil properties of the samples are available as supplementary data.

489 **Appendix A**



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491 **Figure A1:** Specific CO_2 production of three incubation replicates over time. Corresponding median including quantiles (2.5 and 97.5 %)
492 and the equilibrium value of the SBR, as determined by the exponential model

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Table A1: Classification of the degree of disturbance with corresponding soil horizons and description (Ad-Hoc-AG Boden, 2005; TGL 24300/04 in Succow and Joosten, 2001); abbreviations of soil horizons according to KA5 (Ad-Hoc-AG Boden, 2005)

Degree of disturbance	Soil horizon*	Description
No disturbance	Hr	Permanently saturated and anaerobic ("reduced") conditions, not altered by secondary pedogenetic processes, peat substrates can be identified. "Undisturbed horizons" may not be confused with "undisturbed peatlands" as such horizons may appear at greater depth of drained sites.
Slight disturbance	Hw	Alternating saturated-unsaturated conditions and thus temporarily subjected to aerobic conditions, peat structure not yet altered by secondary pedogenetic processes.
Moderate disturbance	Hv	Topsoil horizon of moderately drained sites, earthified, crumbly structure caused by aerobic decomposition, plant residuals not visible anymore, not dusty when dry.
Strong disturbance	Ht, Ha	Subsoil horizon of intensively drained sites, polyhedral aggregates caused by swelling and shrinkage, crumbly when dry (Ha) OR prismatic aggregates with vertical cracks (Ht) as transition horizon to underlying peat. Aggregate and shrinkage horizons have been combined in this class due to the very low number (n = 2) of shrinkage horizons in our sample set.
Heavy disturbance	Hm, Aa, Hvp	Topsoil horizon of intensively drained sites, "moorshy", dusty or small-grained structure when dry, intensive aerobic decomposition, plant residuals not visible anymore ("Mulm") OR horizons with a high content of mineral soil due to ploughing, mineralization, anthropogenic addition from external sources, or addition from natural sources (sedimentation in riverine fens or translocation by wind). All earthified ploughed horizons (Hvp) in our dataset had a low SOC content pointing to mixing with mineral soil and were thus classified as "heavily disturbed". Due to the strongly disturbed conditions of these topsoils, it was impossible to distinguish between the underlying different processes.
Gyttja	fF	Organic or calcareous lacustrine sediments mainly in terrestrialization peatlands. Due to the lack of an English translation of the German term "Mudde", the term "gyttja" was used here for all these sediments, although it describes calcareous sediments only in the German classification system.
Other	e.g.	Organic marsh soils, buried horizons, horizons without peatland genesis, but with SOC > 8%.

*Basic horizon symbols without additional geogenetic or pedogenetic attributes or combined horizons, for details see supplementary data S1

Competing interests

The authors declare that they have no conflict of interest.

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