



## Drained organic soils under agriculture — The more degraded the soil the higher the specific basal respiration

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### ABSTRACT

Drained peatlands are hotspots of carbon dioxide (CO<sub>2</sub>) emissions from agricultural soils. As a consequence of both drainage-induced mineralisation and anthropogenic mixing with mineral soils, large areas of former peatlands under agricultural use underwent a secondary transformation of the peat (e.g. formation of aggregates). These soils show contents of soil organic carbon (SOC) at the boundary between mineral and organic soils. However, the carbon (C) dynamics of such soils have rarely been studied so far. The aim of the present study was to evaluate the vulnerability of soil organic matter (SOM) to decomposition over the whole range of peat-derived soils under agriculture including very carbon rich mineral soils (76–526 g kg<sup>-1</sup> SOC). A total of 62 soil samples covering a broad range of soil and site characteristics were selected from the sample set of the German Agricultural Soil Inventory. Potential CO<sub>2</sub> production was measured by aerobic incubation. Fen and bog peat samples were grouped into disturbance classes according to their soil properties. Specific basal respiration rates (SBR), i.e. CO<sub>2</sub> fluxes per unit SOC, showed the highest values for the most disturbed samples for both fen peat (13.9 ± 6.0 μg CO<sub>2</sub>-C g SOC<sup>-1</sup> h<sup>-1</sup>) and bog peat (10.9 ± 4.7 μg CO<sub>2</sub>-C g SOC<sup>-1</sup> h<sup>-1</sup>). Respiration rates of bog peat increased more strongly with an increasing degree of disturbance than those of fen peat. Perhaps counterintuitively, SOM vulnerability to decomposition thus 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, the variability of the SBR increased drastically with increasing degree of disturbance. The turnover of SOM in less disturbed peat samples tended to be higher in samples with higher nitrogen (N) content, higher pH value and lower C:N ratio, while plant-available phosphorus was important for the mineralisation of more severely disturbed peat. However, clear correlations between a single soil property and SBR could not be identified. The high potential of CO<sub>2</sub> emissions from organic soils with a low SOC content implies that mixing organic soil with mineral soil does not seem to be a promising option for mitigating greenhouse emissions.

### 1. Introduction

Organic soils cover only 2.2 to 3% of the global terrestrial surface (Leifeld and Menichetti, 2018; Tubiello et al., 2016), but store more than one third of global soil organic carbon (SOC) (Scharlemann et al., 2014; Yu et al., 2010). These huge SOC stocks have been built up over

millennia, as intact peatlands under waterlogged conditions are persistent carbon (C) sinks due to higher gross primary production compared to respiration (Clymo et al., 1998). One third of all organic soils are found in Europe (Tubiello et al., 2016), corresponding to 3% of the European landmass (Montanarella et al., 2006). In Germany organic soils cover 4.4% of the land area (Roßkopf et al., 2015). Large areas of

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peatland have been drained for agriculture, forestry and peat mining for energy and horticulture. To date, 25.5 million ha of drained peatlands worldwide are used for agriculture alone, of which around 60% are located in the boreal or temperate zone (Tubiello et al., 2016). The majority of the drained peatlands in Central and Western Europe are used for agricultural purposes, primarily as grassland (Joosten and Tanneberger, 2017). Drainage and agricultural management strongly change the peatlands' hydrological and biogeochemical processes, e.g. by causing strong mineralisation of the soil organic matter (SOM) (Holden et al., 2004). Thus, drainage turns peatlands into hotspots of greenhouse gas (GHG) emissions from soils, which release large quantities of carbon dioxide (CO<sub>2</sub>), but also nitrous oxide (N<sub>2</sub>O) (Maljanen et al., 2010; Tiemeyer et al., 2016).

Drainage considerably alters physical and chemical peat properties. Following drainage, the intrinsic buoyancy of peatlands due to water saturation is immediately lost and the peat is compacted. Mineralisation and pedogenetic transformation of SOM induce the formation of crumbly and, later on, polyhedral and prismatic aggregates, shrinkage cracks and finally results in a dusty, fine-grained ("moorshy") topsoil horizon (Ilnicki and Zeitz, 2003). Consequently, the majority of topsoils of drained agricultural peatlands are strongly decomposed without any recognizable plant remains. Altogether, these processes lead to an increase in bulk density and a decrease in total porosity (Rovdan et al., 2002). Compaction, shrinkage and mineralisation jointly cause subsidence of the soil surface and thus increase risk of flooding and damage to buildings and infrastructure (Gambolati et al., 2005; Holden et al., 2004).

Furthermore, drainage favours carbon over nitrogen (N) mineralisation and microbial N immobilisation during decomposition (Wells and Williams, 1996). Thus, the N content increases, and both the C content and C:N-ratio decrease with increasing degrees of SOM decomposition, especially in the topsoil (Wells and Williams, 1996). As aerobic decomposers preferably use lighter isotopes, the remaining peat is enriched both in <sup>13</sup>C (Ågren et al., 1996) and <sup>15</sup>N (Krüger et al., 2015). The phosphorus (P) content also usually increases after drainage due to ongoing mineralisation of the SOM and concurrent release of previously organically bound P. Under aerobic conditions, P can be immobilized e.g. by Fe(III)-compounds (Sundström et al., 2000; Wells and Williams, 1996; Zak et al., 2010). Furthermore, fertilizer application contributes to the nutrient enrichment of organic soils under agriculture.

Besides drainage, the conversion from pristine peatlands to agricultural land can comprise the active addition of mineral soil to the top peat layer in order to improve trafficability. This can be achieved by mixing with mineral soil layers underlying the peat 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 mixing with mineral soil material, especially topsoils of large areas of former peatlands under agricultural use show SOC contents between those of mineral and organic soils (Schulz and Waldeck, 2015). In Germany, nearly 50% of the peat-derived organic soils cannot be classified as "fen peat" or "bog peat" in the strict sense of the German soil classification (Ad-Hoc-Arbeitsgruppe Boden, 2005) anymore due to deep ploughing, coverage by mineral soil material, low SOC content or shallow depth (Jacobs et al., 2018).

As previous investigations have mainly focused either on mineral soils (< 150 g SOM kg<sup>-1</sup> according to the German definition, Ad-Hoc-Arbeitsgruppe Boden, 2005) or "true" peat soils (> 300 g SOM kg<sup>-1</sup>), there are very few studies on soil properties or SOM dynamics of "low C organic soils" (between 150 and 300 g SOM kg<sup>-1</sup>). However, measurements of CO<sub>2</sub> emissions in the field have shown that peat-derived soils even with a topsoil SOC content as low as 100 g kg<sup>-1</sup> still emit large and similar amounts of CO<sub>2</sub> as "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<sub>2</sub> emissions and SOC content are closely related in mineral soils (Don et al., 2013; Wang et al., 2003). The reasons behind the relatively high CO<sub>2</sub> emissions of the whole continuum of organic soils, including those bordering mineral ones, are not yet clear. Changes in peat properties following water level drawdown and overall SOM quality were found to influence the microbial activity and therefore the CO<sub>2</sub> emissions of drained peatlands (Brouns et al., 2016; Laiho, 2006). Contrarily, a recent study on the SOM decomposability of 21 drained and intensively managed fen soils found only weak correlations between CO<sub>2</sub> emissions and soil properties (Bader et al., 2018). However, the nutrient status of soils is important for microbial activity: microbial P availability have been shown to favor soil respiration (Amador and Jones, 1993; Brake et al., 1999; Säurich et al., 2019) and numerous studies have found an increase in CO<sub>2</sub> emissions after the nutrient content was increased by P, K and N addition (Larmola et al., 2013; Pinsonneault et al., 2016; Sundström et al., 2000).

Under field conditions, it is difficult to disentangle interacting effects of climate, hydrology, agricultural management, and soil properties. Thus, there is a lack of any systematic evaluation of the vulnerability to decomposition of a wide range of organic soils, including heavily disturbed ones. Most previous laboratory studies that examined agriculturally used organic soils under controlled conditions mostly incubated samples of a few sites with a rather narrow range of soil properties (Ausec et al., 2009; Bader et al., 2017; Kechavarzi et al., 2010). Bader et al. (2018) incubated a broad variety of disturbed fen peat samples (99 — 499 g kg<sup>-1</sup> SOC) and Säurich et al. (2019) compared respiration rates from intact soil columns of 10 sites with and without sand addition. However, to our best knowledge, there are no laboratory studies including both fen and bog peat and covering a wide range of soil properties.

With our laboratory study under aerobic conditions, we aimed to improve our understanding of the sensitivity of disturbed organic soils to mineralisation. Further, we wanted to elucidate factors governing the vulnerability of the soils' SOM to decomposition. In this context, disturbance was defined as the effect of transformation processes induced by drainage and/or by the mixing of peat with mineral soil. In the present study, 62 samples originating from drained agricultural sites from across Germany were examined, ranging from carbon-rich mineral soil (76 g SOC kg<sup>-1</sup>) to "true" peat (up to 526 g SOC kg<sup>-1</sup>). Given that the samples cover country-scale variability and originated from a large inventory (Jacobs et al., 2018) they were available in dried form. As commonly done (Grover and Baldock, 2012), dried samples were adjusted to standardised water content, pre-incubated and aerobically incubated to determine basal and substrate-induced respiration (Anderson and Domsch, 1978; Heinemeyer et al., 1989).

## 2. Material and methods

### 2.1. Sample selection

The samples used in this study originate from the first German Agricultural Soil Inventory (Jacobs et al., 2018) which aimed at an improved understanding of SOC stocks in agricultural soils. During the inventory, 3104 agricultural soils in Germany were sampled following standardised protocols in an 8 × 8 km grid. For soil sampling and mapping a soil pit was opened at each site down to 1 m. The soil profile was classified according to the German manual of soil mapping (Ad-Hoc-Arbeitsgruppe Boden, 2005) including the degree of decomposition after von Post (von Post, 1922). Soil samples were taken at five depth increments per soil pit (0–10, 10–30, 30–50, 50–70, 70–100 cm). If a depth increment comprised more than one soil horizon, samples were taken from each horizon within this increment. Vice versa, depth increments were divided when they crossed horizon boundaries by > 3 cm. From each increment and/or horizon, volumetric samples were taken in steel rings for the determination of the bulk density, and grab

**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<sub>t</sub>: total nitrogen content, C:N-ratio: carbon to nitrogen ratio, ρ: bulk density, pH-value (CaCl<sub>2</sub>), texture (\*only determined for samples with SOC < 174 g kg<sup>-1</sup>). Additional parameters of this study: P<sub>CAL</sub>: calcium acetate lactate (CAL) extractable phosphorus content and δ<sup>15</sup>N.

Parameter	Median	Min.	Max.
SOC (g kg <sup>-1</sup> )	309.0 ± 18.9	75.7	525.9
N <sub>t</sub> (g kg <sup>-1</sup> )	13.1 ± 0.9	3.4	27.5
C:N-ratio	17.2 ± 1.8	9.9	72.6
ρ (g cm <sup>-3</sup> )	0.24 ± 0.03	0.07	0.99
pH	5.0 ± 0.2	3.1	7.4
Sand content (%)*	44.7 ± 6.2	8.3	87.9
Silt content (%)*	25.0 ± 2.5	6.4	41.8
Clay content (%)*	24.0 ± 4.0	4.8	49.9
P <sub>CAL</sub> (mg kg <sup>-1</sup> )	17.9 ± 9.0	1.3	365.6
δ <sup>15</sup> N (‰)	2.35 ± 0.28	-2.55	9.30

samples for the determination of soil chemical properties. All samples were analysed for SOC and bulk density (ρ), as well as for basic explanatory soil properties (Table 1, see Section 2.2).

For this study, 62 samples from C-rich horizons from 47 sites were selected. The basic criteria were a SOC content > 75 g kg<sup>-1</sup> and a sampling depth > 10 cm. The latter criterion was chosen to reduce the influence of potential fresh plant or root biomass residues in the samples, although roots have been separated by hand. The final sample selection was based on Ward's hierarchical cluster analysis using k-means as partitioning method for 10 clusters. Resulting samples optimally covered the total parameter range (Table 1), as well as land use, major peat substrates (bog/fen) and geographical position. We did not, however, include C-rich samples from organic sediments (e.g. gytja), marsh or other soils without peatland origin (e.g. plaggen soils) here. Sampling sites were used as cropland (18%) and grassland (82%), which corresponds to the dominant agricultural land use of organic soils in Germany. The selected samples were collected between March 2011 and November 2014 and originated from various depth increments (see data.xlsx file in the supplement for detailed information).

## 2.2. Soil properties and degree of disturbance

Samples for soil chemical analysis were dried at 60 °C until constant mass and sieved to < 2 mm. Contents of total C (C<sub>t</sub>) and N (N<sub>t</sub>) as well as the total inorganic carbon content for samples with carbonate (pH<sub>CaCl2</sub> > 6.2) were measured by dry combustion (RC 612, LECO Corporation, St. Joseph, USA). The SOC content was calculated as difference between C<sub>t</sub> and total inorganic carbon.

Stable isotope analysis (δ<sup>15</sup>N) was performed on grinded samples using a mass spectrometer coupled with an elemental analyzer (Isoprime 100 and Vario Isotope, Elementar, Hanau, Germany) via a

**Table 2**

Classification of the anthropogenic disturbance and corresponding mean and standard deviation of soil properties: SOC: soil organic carbon content, C:N-ratio: carbon to nitrogen ratio, δ<sup>15</sup>N, N<sub>t</sub>: total nitrogen content, P<sub>CAL</sub>: calcium acetate lactate (CAL) extractable phosphorus content, pH-value (CaCl<sub>2</sub>), ρ: bulk density.

Degree of disturbance	Description	Peatland type	Label	n	SOC (g kg <sup>-1</sup> )	C:N	δ <sup>15</sup> N (‰)	N <sub>t</sub> (g kg <sup>-1</sup> )	P <sub>CAL</sub> (mg kg <sup>-1</sup> )	pH	ρ (g cm <sup>-3</sup> )
No disturbance	Permanently water-saturated	Fen	D0F	8	426 ± 90	23 ± 8	0.3 ± 1.3	19.8 ± 6.7	8.4 ± 6.0	5.5 ± 1.0	0.13 ± 0.02
		Bog	D0B	4	510 ± 25	52 ± 16	1.5 ± 1.9	10.9 ± 4.7	10.0 ± 11.5	3.2 ± 0.1	0.10 ± 0.02
Slight disturbance	Alternating aerobic-anaerobic conditions	Fen	D1F	10	410 ± 58	24 ± 11	2.2 ± 2.9	19.4 ± 6.1	14.5 ± 14.7	5.3 ± 1.2	0.2 ± 0.04
		Bog	D1B	4	462 ± 34	50 ± 16	1.2 ± 1.7	9.9 ± 3.1	34.6 ± 33.9	3.5 ± 0.2	0.11 ± 0.03
Moderate disturbance	Earthification or moorsh	Fen	D2F	6	283 ± 91	15 ± 2	2.6 ± 1.5	19.6 ± 5.6	28.2 ± 21.3	5.1 ± 0.6	0.44 ± 0.15
		Bog	D2B	6	281 ± 145	26 ± 5	2.4 ± 1.2	11.1 ± 5.9	100.2 ± 52.3	3.9 ± 0.4	0.4 ± 0.3
Strong disturbance	Polyhedral aggregates or subsoil cracks	Fen	D3F	6	307 ± 46	14 ± 2	2.1 ± 1.1	22.0 ± 3.7	35.7 ± 40.8	5.3 ± 1.3	0.26 ± 0.06
Heavy disturbance	Mineral soil addition, low topsoil SOC content	Fen	D4F	18	127 ± 41	15 ± 4	4.3 ± 1.8	9.2 ± 3.2	88.6 ± 108.1	5.9 ± 1.2	0.68 ± 0.20

continuous flow system. The isotope ratio is expressed in per mill relative to atmospheric nitrogen standard.

Contents of plant-available phosphorus were determined by calcium acetate lactate (CAL) extraction (P<sub>CAL</sub>) (Schüller, 1969). P<sub>CAL</sub> contents were measured using the molybdenum blue method. The ammonium molybdate solution and the phosphate ions form a blue compound which is then measured with a spectrophotometer (Murphy and Riley, 1962). The pH values were measured using 5 mL soil and 25 mL of a 0.01 mol/L CaCl<sub>2</sub> and a glass electrode.

The fractions of the texture classes sand, silt and clay of samples with SOC < 174 g kg<sup>-1</sup> 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<sub>2</sub>O<sub>2</sub> (DIN ISO 11277, 1998). Bulk density was determined by drying the volumetric samples at 105 °C until constant mass and subsequent weighing.

Here, we use a classification of anthropogenic disturbance based on the mapped soil horizons (Ad-Hoc-Arbeitsgruppe Boden, 2005, see also Ilnicki and Zeitz (2003)) and further soil properties (details in Table S1). Fen (F) and bog (B) peat samples were divided into five and three disturbance classes, respectively, according to the severity of secondary pedogenetic transformation (Table 2): 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. As the transformation sequence of a drained peatland starts with the formation of an earthified topsoil horizon, these horizons are defined as "moderately disturbed". Under intensified drainage, the subsoil peat starts to develop secondary pedogenetic features, characterised by blocky to prismatic aggregates and/or the formation of shrinkage cracks, therefore they are defined as "strongly disturbed" horizons. In the present sample set, this level of disturbance only occurred in fen peat. "Heavily disturbed" samples all originate from the topsoil and cannot be classified as peat anymore due to mineralisation and addition of mineral soil material. Given that this classification was developed after the sample selection, the distribution among the groups is not uniform.

## 2.3. Incubation experiments: Basal respiration and substrate-induced respiration

The soil samples were incubated aerobically under optimum moisture conditions and constant temperature (23 °C) to determine basal soil respiration (BR) and substrate-induced respiration (SIR). The latter was in turn used to calculate microbial biomass (Anderson and Domsch, 1978).

An optimum standardised water content of 60% water-filled pore space was determined by pre-tests. To calculate the necessary amount of water, the apparent porosity φ of the dried and sieved sample was

calculated as follows:

$$\Phi = 1 - \frac{\rho_{loose}}{\rho_s}, \quad (1)$$

where  $\rho_{loose}$  [ $\text{g cm}^{-3}$ ] is the bulk density of the loose sample and  $\rho_s$  [ $\text{g cm}^{-3}$ ] is the particle density. The particle density  $\rho_s$  was estimated according to eq. (2) for organic soils given by Bohne (2005):

$$\rho_s = 0.086 * AC + 1.44, \quad (2)$$

where AC [%] is the ash content of the sample. The water was then applied to the soil samples (70 g dry wt.) under continuous stirring to ensure uniform rewetting. Afterwards, the moistened samples were pre-incubated in darkness under aerobic conditions for 7 days at 6 °C and then for a further 7 days at 23 °C (Jones et al., 2019). On day 14, the soil samples were adjusted in their water content if necessary and transferred to 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<sup>-1</sup>. Three of the lines were ran as blanks. An infrared CO<sub>2</sub> gas analyzer (ADC-255-MK3, Analytical Development Co. Ltd., Hoddesdon, UK) was used to measure CO<sub>2</sub> concentrations. Each tube 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 by the SIR method. The mixture was then incubated and measured again for 6 h to obtain the maximal initial respiratory response of the microbial biomass (Anderson et al., 1995).

## 2.4. Data analysis

Data and statistical analysis was performed using the R software environment (version R-3.5.0, R Core Team, 2018).

### 2.4.1. Determination of basal and specific basal soil respiration

The basal respiration (BR) is expressed as  $\mu\text{g CO}_2\text{-C g soil}^{-1} \text{h}^{-1}$  and the specific basal respiration (SBR) is normalized by the sample's SOC content into  $\mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ . An exponential model was fitted simultaneously to all three incubation replicates to determine the equilibrium values of the SBR (Fig. S1):

$$\text{CO}_2 - C(t) = a - (a - \text{SBR})(1 - e^{-k*t}), \quad (3)$$

where  $\text{CO}_2\text{-C}(t)$  [ $\mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ] is the specific CO<sub>2</sub> production per hour,  $a$  [ $\mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ] is the initial respiration and  $k$  [ $\text{h}^{-1}$ ] is the change rate of SBR. SBR is the asymptotic value of Eq. 3.

To achieve an objective quantification of the basal and 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 behavioral from non-behavioral 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., 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 of the SBR.

For the evaluation of the SIR, the value of the maximum initial respiratory response was identified manually and then transcribed via a conversion factor to microbial biomass (SIR-C<sub>mic</sub>) [ $\mu\text{g g}^{-1} \text{soil}$ ] as follows (Kaiser et al., 1992):

$$\text{SIR} - C_{\text{mic}} = \mu\text{l CO}_2 \text{ g}^{-1} \text{soil h}^{-1} * 30. \quad (4)$$

As in the case of BR, we normalized SIR-C<sub>mic</sub> by the samples' SOC content. This is referred to as “specific SIR-C<sub>mic</sub>” in the following. To quantify the efficiency of microbial respiration per unit biomass, the metabolic or respiratory quotient  $q(\text{CO}_2)$  [ $\text{mg CO}_2\text{-C h}^{-1} \text{g}^{-1} \text{biomass SIR-C}_{\text{mic}}$ ] was calculated by dividing the BR by the SIR-C<sub>mic</sub> (Anderson and Domsch, 1985):

$$q(\text{CO}_2) = \frac{\text{BR}}{\text{SIR} - C_{\text{mic}}/1000} \quad (5)$$

The metabolic quotient  $q(\text{CO}_2)$  indicates the efficiency of soil microorganisms in acquiring organic carbon (Dilly and Munch, 1998) and depends, among other factors, on nitrogen availability and pH (e.g. Spohn, 2015).

### 2.4.2. Statistical analysis

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. Correlation coefficients of  $0.3 \geq r_s \geq 0.7$  will be referred to as “moderate correlation” and  $r_s > 0.7$  as “strong correlation” in the following.

Differences in BR, SBR, specific SIR-C<sub>mic</sub> and  $q(\text{CO}_2)$  between the disturbance classes and in SBR between sample with the same degree of decomposition (H) were determined by using a generalized least squares (gls) model with the varident variance structure from the R package “nlme” (Pinheiro et al., 2015). This variance structure allows for handling the unbalanced data of the present study by taking into account the specific variances of the different classification factors.  $P$ -values were computed with the Tukey's honest significant differences test ( $\alpha = 0.05$ ) and adjusted with the Bonferroni correction using the R package “multcomp” (Hothorn et al., 2008).

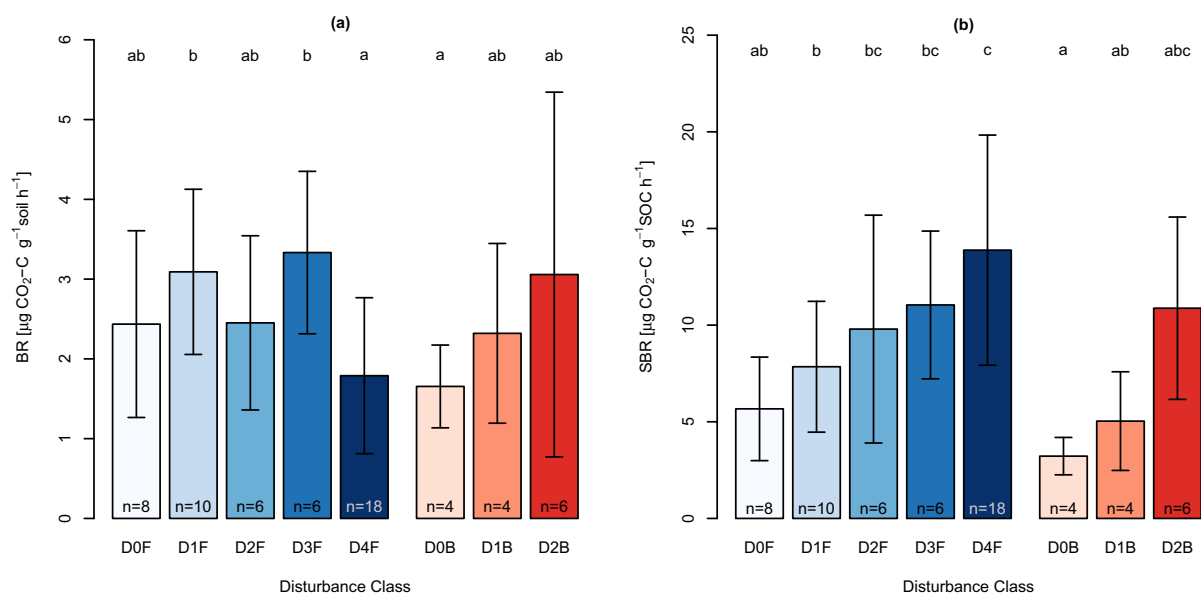
The results for every disturbance class given below are means with standard deviations, unless otherwise stated.

## 3. Results

### 3.1. Vulnerability of SOM to decomposition as determined by respiration rates

Basal respiration (BR) of all samples was highly variable, ranging from 0.5 to 7.0  $\mu\text{g CO}_2\text{-C g soil}^{-1} \text{h}^{-1}$ . Overall, bog and fen samples had similar BR rates of  $2.5 \pm 1.7 \mu\text{g CO}_2\text{-C g soil}^{-1} \text{h}^{-1}$  and  $2.4 \pm 1.2 \mu\text{g CO}_2\text{-C g soil}^{-1} \text{h}^{-1}$  respectively. Furthermore, there were no consistent patterns of BR and disturbance rates (Fig. 1a, Table S2). In the case of fen peat, the BR rates of heavily disturbed samples were significantly lower compared to strongly and slightly disturbed samples, but not compared to moderately and undisturbed ones.

Normalizing BR to SOC content resulted in highly variable specific basal respiration (SBR) rates between and within classes, which ranged from 1.5 to 23.8  $\mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ . Overall, fen samples had higher SBR rates ( $10.4 \pm 5.6 \mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ) than bog samples ( $7.0 \pm 4.8 \mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ; Fig. 1b). However, SBR of moderately disturbed D2B samples, i.e. the strongest disturbance assigned to bog peat samples, was comparable to strongly and heavily disturbed fen samples (D3F, D4F; Table S2). In contrast to BR, there were strong patterns as SBR rates clearly increased with increasing soil disturbance for both fen and bog peat. Significant differences could be found between undisturbed bog samples (D0B) and the disturbed fen sample



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

classes D3F and D4F ( $p < 0.001$ ) and D1F and D2F ( $p < 0.01$ , all further  $p$  values are given in Table S3 and Table S4). The heavily disturbed fen samples (D4F) reached the highest SBR rates that were significantly higher than the undisturbed and slightly disturbed samples of both fen and bog peat. The highest variability of SBR also occurred for the most disturbed fen and bog peat samples, respectively (Fig. 1b, Table S2).

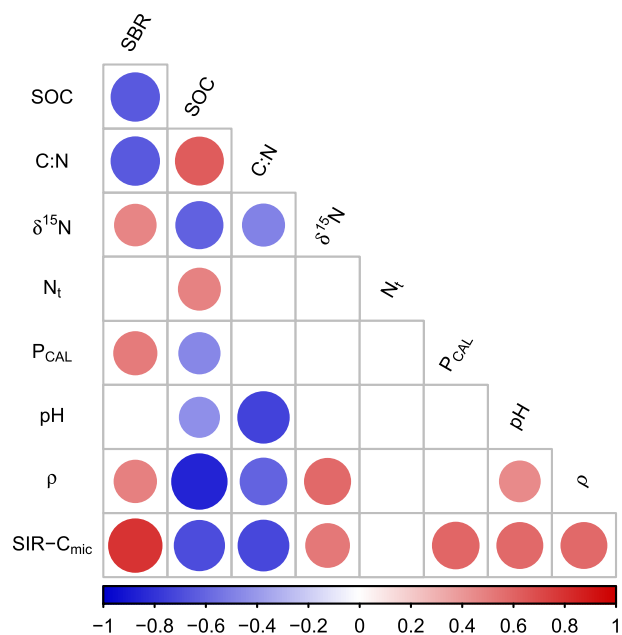
### 3.2. Influence of organic matter quality and soil characteristics

The BR rates for the whole dataset could hardly be explained by any of the measured soil characteristics (Fig. S2, Table S3) as there was only a moderate positive, but significant correlation with  $N_t$ , but not with SOC. Soil properties also correlated with each other, for example there were strong negative correlations between SOC and  $\rho$  as well as between C:N-ratio and pH value (Fig. S2, Table S3). In the following, we will limit results on SBR rates as these are assumed to be better indicators for the SOM vulnerability to decomposition than BR rates.

In the case of SBR rates of the whole dataset (Fig. 2, Table S3) moderate positive correlations with  $\delta^{15}N$  values, phosphorus content and bulk density were observed. Significant negative relationships were found between SBR and SOC content and the C:N-ratio.

Fig. 3 shows soil characteristics and SBR rates of individual samples grouped by disturbance classes. Consistent with the increase of SBR rates with disturbance classes (Fig. 1b) the SBR rates were significantly higher ( $p < 0.001$ ) at higher degrees of decomposition (von Post values, Fig. 3a). Slightly and moderately decomposed samples, i.e. those with von Post values of H3 and H5, had significantly lower SBR rates ( $5.8 \pm 3.6$  and  $6.7 \pm 3.2 \mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$  respectively) than strongly decomposed samples mapped as H10 ( $13.0 \pm 3.7 \mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ) or low C organic soils deriving from peat (NA;  $13.5 \pm 6.3 \mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ).

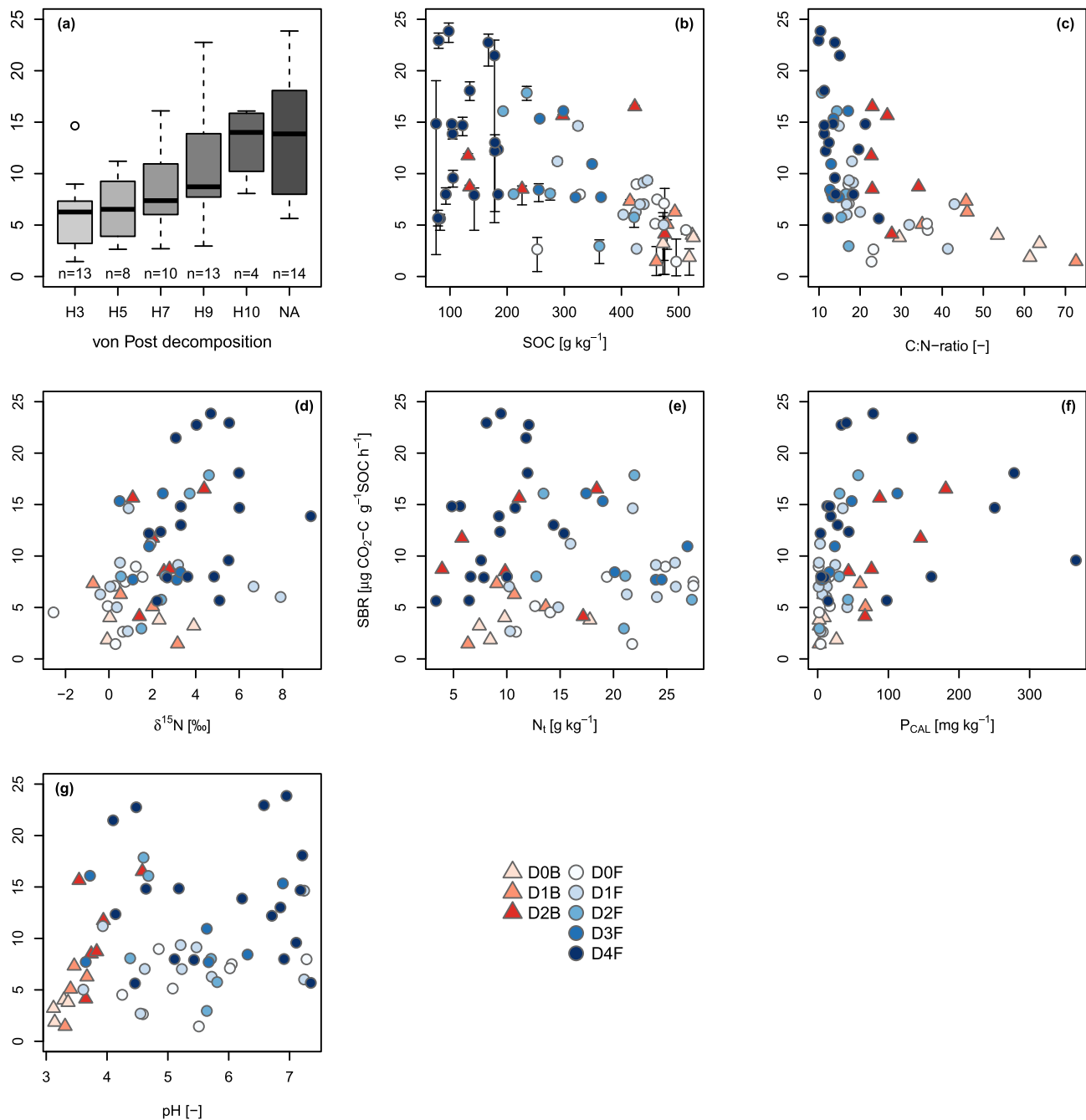
Furthermore, both variability and magnitude of SBR rates increased with decreasing SOC content (Fig. 3b), i.e. SBR rates were highest and most variable for soil samples with a low SOC content (mainly heavily disturbed fen peat samples; see Table 2). This negative relationship between SOC and SBR remained also apparent when correlating soil characteristics separately for each disturbance class (Fig. 4, Table S4). Fig. 3b also exemplarily shows the 2.5 and 97.5% quantiles of the DREAM-fit, i.e. the uncertainty of the calculated SBR rates. While there



**Fig. 2.** Significant ( $p < 0.05$ ) correlation coefficients after Spearman for specific basal respiration rates (SBR) with 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 and  $\rho$ : bulk density) and specific microbial biomass (SIR-C<sub>mic</sub>).

were several samples mainly of the D4F class for which SBR rates could only be determined with large uncertainties, most quantile ranges were small and thus partially invisible in Fig. 3b. Even disregarding the samples with large uncertainties would not change the overall picture of high and highly variable SBR rates at low SOC content.

With decreasing C:N-ratios, SBR rates increased in an exponential manner (Fig. 3c). However, when splitting the sample set at C:N = 25 into two groups, there was no longer any correlation for neither group. Again, the highest and most variable rates of  $11.1 \pm 5.4 \mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$  were measured for mostly highly disturbed samples with low C:N ratios ( $< 25$ ), which mainly belong to all fen classes and D2B



**Fig. 3.** Specific basal respiration (SBR) rates of all samples classified in disturbance classes (F = fen, B = bog, D0 = no disturbance, D1 = slight disturbance, D2 = moderate disturbance, D3 = strong disturbance, D4 = heavy disturbance) versus (a) decomposition degree after von Post (H1 = completely undecomposed, H10 = completely decomposed, NA = “not applicable” as the von Post scale cannot be applied for low C organic soils deriving from peat), (b) soil organic carbon content, (c) carbon to nitrogen ratio, (d)  $\delta^{15}\text{N}$ , (e) total nitrogen content, (f) calcium acetate lactate (CAL) extractable phosphorus content, (g) pH value. Bars in (b) show 2.5 and 97.5% quantiles of the DREAM-fit.

(see Table 2). In contrast, samples with a C:N-ratio  $> 25$  were bog samples with low or minimal disturbance, which had clearly lower and less variable SBR rates of  $5.4 \pm 3.4 \mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ . In detail, there was a strong negative correlation between SBR rates and the C:N-ratio for D2F samples and moderate negative correlations were found for D0F, D1F, D4F, D0B and D1B, although none of these correlations were significant (Fig. 4, Table S4).

There was a clear difference in  $\delta^{15}\text{N}$  values between samples from undisturbed and disturbed horizons (Fig. 3d). The values for undisturbed or slightly disturbed horizons were  $1.5 \pm 1.9\text{‰}$  (D0B),  $1.2 \pm 1.7\text{‰}$  (D1B),  $0.3 \pm 1.2\text{‰}$  (D0F) and  $2.2 \pm 2.9\text{‰}$  (D1F)

respectively. All the other disturbance classes showed higher  $\delta^{15}\text{N}$  values up to  $9.3\text{‰}$ , and a significant overall increase in SBR rates with increasing  $\delta^{15}\text{N}$  (Fig. 2). There were positive correlations between  $\delta^{15}\text{N}$  and SBR rates for D0F and D2F (Fig. 4, Table S4). In contrast to the overall trend (Fig. 2), there was a significant negative correlation between  $\delta^{15}\text{N}$  and SBR rates in the case of slightly disturbed D1B samples.

Even though there was no significant correlation between  $\text{N}_t$  and SBR rates (Fig. 2),  $\text{N}_t$  contents were positively correlated with the SBR rates of the disturbance classes D0F, D4F and D0B (Fig. 4, Table S4). In contrast, the SBR rates of D3F were negatively correlated with  $\text{N}_t$  contents.

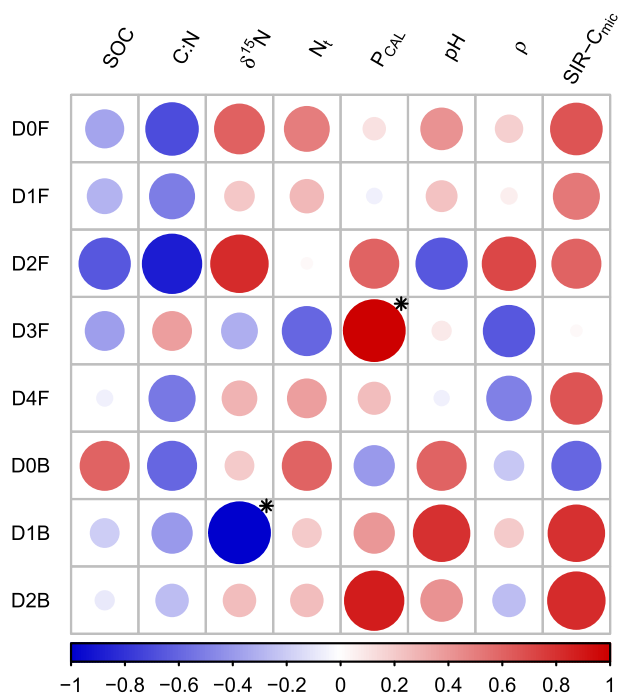


Fig. 4. Correlation coefficients after Spearman (significant correlations ( $p < 0.05$ ) are marked with asterisks) for the specific basal respiration rates separated into the disturbance classes (F = fen, B = bog, D0 = no disturbance, D1 = slight disturbance, D2 = moderate disturbance, D3 = strong disturbance, D4 = heavy disturbance) and soil properties: SOC: soil organic carbon content, C:N-ratio: carbon to nitrogen ratio,  $\delta^{15}\text{N}$ ,  $\text{N}_t$ : total nitrogen content,  $\text{P}_{\text{CAL}}$ : calcium acetate lactate (CAL) extractable phosphorus content, pH-value,  $\rho$ : bulk density and the specific microbial biomass ( $\text{SIR-C}_{\text{mic}}$ ).

Overall,  $\text{P}_{\text{CAL}}$  showed significant positive correlations with the SBR rates (Fig. 2, Table S3) and, furthermore,  $\text{P}_{\text{CAL}}$  was the explanatory variable with the highest number of positive correlations with SBR over all disturbance classes. This can also be derived from the increase of SBR with  $\text{P}_{\text{CAL}}$  in Fig. 3f. In the case of bogs, the correlation increased with increasing disturbance (Fig. 4, Table S4). When combining all bog peat samples and all fen peat samples, respectively, there was also a stronger correlation of  $\text{P}_{\text{CAL}}$  and SBR rates for bog peat ( $r_s = 0.84$ ,  $p < 0.05$ ) than for fen peat ( $r_s = 0.53$ ,  $p < 0.01$ ). The effect of the disturbance class was less consistent in the case of fens compared to bogs, with the strongest correlation in D3F.

Considering all samples, SBR rates and pH did not show a significant correlation, but the general differences between bogs and fens were visible (Fig. 3g). Even though bog samples covered only a small range ( $3.6 \pm 0.4$ ) of the overall pH values compared to fen samples ( $5.5 \pm 1.1$ ) the increase in SBR was most distinctive for all disturbance classes of bog samples D0B, D1B and D2B. The correlation between D2F samples and pH values was moderately negative (Fig. 4, Table S4).

As texture was only measured for those samples with  $\text{SOC} < 174 \text{ g kg}^{-1}$ , correlations could only be determined for  $n = 16$  samples. There was neither a significant correlation between sand content and SBR nor between clay content and SBR or BR rates (data not shown).

### 3.3. Microbial biomass and mineralisation rates

The specific microbial biomass ( $\text{SIR-C}_{\text{mic}}$ ) was significantly and strongly correlated with SBR ( $r_s = 0.79$ , the highest correlation coefficient for the complete data set).  $\text{SIR-C}_{\text{mic}}$  and SBR thus showed similar relationships with explanatory variables (Fig. 2, Table S3) as well as comparable patterns across disturbance classes (Fig. 1b, Fig. 5a). Overall,  $\text{SIR-C}_{\text{mic}}$  was highest for D4F samples followed by D2B, D2F

and D3F samples. Values of  $\text{SIR-C}_{\text{mic}}$  were higher for fen peat samples than for bog peat samples and tended to increase with increasing disturbance, especially in the case of bog peat samples. With a closer look to individual disturbance classes, there were still moderate to strong positive correlations between  $\text{SIR-C}_{\text{mic}}$  and SBR, except for D0B and D3F (Fig. 4, Table S4). Samples of the classes D1B and D2B showed the highest correlations.

The metabolic quotient was significantly negatively correlated with  $\text{P}_{\text{CAL}}$  and pH values and positively with C:N-ratios (data not shown). There were no significant differences in the metabolic quotient between disturbance classes (Fig. 5b, Table S2). Samples of class D0B showed the highest values. All other classes had lower values in similar range. However, there was a slight tendency for decreasing metabolic quotients with increasing disturbance for bog samples.

## 4. Discussion

### 4.1. Methodological aspects

Sieving and drying obviously affects soil structure and micro-organisms. Given that the samples cover country-scale variability and originate from a large inventory (Jacobs et al., 2018), they were only available in dried form. The dried soil samples were adjusted to standardised water content and aerobically incubated in the laboratory after pre-incubation. The usage of rewetted soil samples might be seen as a shortcoming of the present study, however, it allowed for an analysis of a sample set of organic soils of unprecedented coverage of land use variability in Germany. Rewetting dried samples is a common approach for soil incubation experiments and numerous studies have shown that effects of drying and rewetting are minor (Grover and Baldock, 2012; Haney et al., 2004; Meisner et al., 2013). Even when samples have been dry for more than three decades respiration rates of rewetted samples matched fresh samples already after some hours for Alfisols and Vertisols (Jones et al., 2019). Unfortunately, there is to our best knowledge no comparable study for organic soils available in literature for which effects might be different. If a sufficient pre-incubation time of the soil samples is maintained such as in our study, rewetting effects will be minimized (Jones et al., 2019), and we assume that this will also be the case for organic soils. Furthermore, the incubation time of this study was based on the standard procedure for this kind of incubation experiment which is 24 to 40 h (Blagodatskaya et al., 2014; Böhme et al., 2005; Dilly and Munch, 1998; Kautz et al., 2004; Müller and Höper, 2004). As pre-experiments have shown that this is too short for some samples to reach quasi-steady state respiration rates we increased the incubation time up to 90 h for SOC rich samples. The range of SBR rates measured in our study ( $0.03$  to  $0.6 \text{ mg CO}_2\text{-C g SOC}^{-1} \text{ d}^{-1}$ ) agreed well with Bader et al. (2018) who provided a literature review on respiration rates from incubation experiments on mineral and peat soil samples, which also stresses the validity of our results.

Thus, our approach allowed to simulate the potential effects of (ongoing) drainage and to compare under standardised and controlled conditions basal respiration rates of samples that experienced different degrees of anthropogenic disturbance comprising both pedogenetic transformation and addition of mineral soil material.

### 4.2. Enhanced variability of respiration rates with increasing disturbance of peat

The most striking result of the present experiment was that specific basal respiration (SBR) rates increased both in magnitude and variability with increasing disturbance of the peat soils, irrespectively of whether this transformation was expressed as a von Post value, a disturbance class or C:N ratio (Figs. 3 and 4). Second, while overall SBR rates of fen peat exceeded those of bog peat, SBR of moderately disturbed bog peat was comparable to moderately, strong and heavily

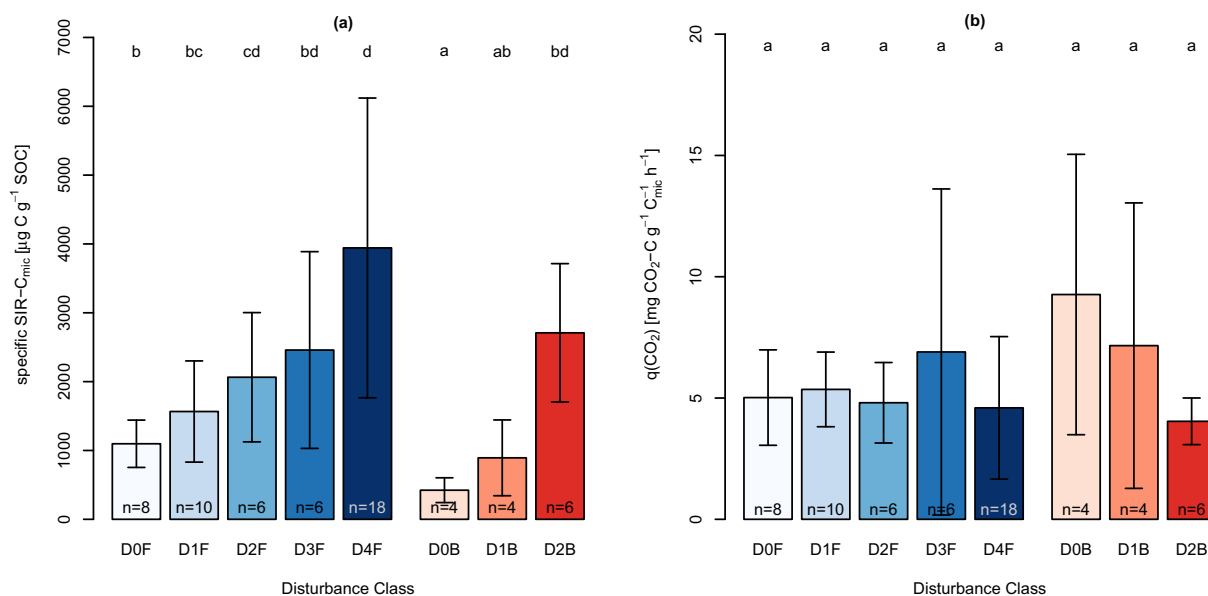


Fig. 5. Mean of a) specific microbial biomass (SIR-C<sub>mic</sub>) determined via substrate induced respiration (SIR) and b) metabolic quotient ( $q(\text{CO}_2)$ ) for different disturbance classes: F = fen, B = bog, D0 = no disturbance, D1 = slight disturbance, D2 = moderate disturbance, D3 = strong disturbance, D4 = heavy disturbance. Bars show the standard deviation. Different letters represent significant differences (Tukey's test,  $p < 0.05$ ).

disturbed fen peat (Fig. 1b), indicating a strong vulnerability of bog peat to decomposition. Third, in contrast to less disturbed peat samples, it proved to be practically impossible to describe SBR or specific microbial biomass (SIR-C<sub>mic</sub>) for heavily disturbed fen samples with the set of available explanatory variables (Fig. 4). Fourth, in contrast to SBR, the basal respiration (BR) rates did not show any consistent patterns (Fig. 1a, Fig. S2).

Several previous studies also tried to relate respiration rates to different measures of disturbance. Brake et al. (1999), for example, conducted a study on drained bog peat. As in our study, they found higher SBR rates for disturbed peat samples. In contrast, Glatzel et al. (2004) measured lower rates of aerobic respiration for stronger decomposed bog peat samples, i.e. those with higher von Post values. In this context, it is important to stress 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 (and also in the present study) applied to drained peatlands as well. When taking into account the occasional problematic nature of the von Post value, the results of Glatzel et al. (2004) only contradict our results at first view: Their undecomposed samples are fresh peat from the acrotelm, while samples with a higher degree of decomposition originate from deeper soil layers. Thus, the latter samples are rather comparable with our D0B samples, which also showed low SBR (and BR) rates. This is also consistent with further studies on managed and unmanaged organic soils which found lower SBR rates for samples from deeper soil layers (Bader et al., 2018; Brake et al., 1999; Hardie et al., 2011; Hogg et al., 1992; Säurich et al., 2019). Reasons might be lower abundance of fresh plant biomass, lower nutrient levels and decreasing availability of labile compounds with depth (see Section 4.4).

Inicki and Zeitz (2003) reported on highly disturbed fen peat and found lower  $\text{CO}_2$  production rates for samples with a high degree of decomposition, especially for moorshy peat soils. In our study, the high variability of SBR, especially of strongly and heavily disturbed fen peat, also comprise samples with such low respiration rates (Fig. 3b). However, these samples are rarely pure moorshy peat, but always contain mineral soil, which might improve aeration of the soil and thus increase respiration rates. Physical disturbance of peat, i.e. the destruction of the original structure and mixing with mineral soil, has been previously

found to increase  $\text{CO}_2$  release in laboratory experiments (Ross and Malcolm, 1988; Rovdan et al., 2002). Similarly, Säurich et al. (2019) measured SBR rates for peat-sand mixtures and strongly decomposed peat in a long-term incubation experiment with intact soil cores, indicating comparable or even increased SOM vulnerability to decomposition with sand addition.

As mentioned above, strong correlations between soil properties and SBR or SIR-C<sub>mic</sub> for these heavily disturbed fens samples (D4F, Fig. 4) were not found. Since these soils have a comparably low SOC content ( $127 \pm 41 \text{ g kg}^{-1}$ , 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. Numerous studies have shown SOM stabilisation on clay minerals (Hassink, 1997; Saidy et al., 2012; Six et al., 2016). However, there was no correlation between clay content and SBR in the present set of samples, despite the wide range of clay content in the heavily disturbed samples (5 to 50%).

The generally higher SBR rates of fen peat compared to bog peat have already been observed in previous studies (Bridgman and Richardson, 1992; Urbanová and Bárta, 2015) and was expected here. Usually, 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). Urbanová and Bárta (2015) found that the microbial communities in bogs increased in richness and diversity upon drainage, but decreased in fens, indicating high sensitivity of bogs to anthropogenic impacts. The same authors also found that fens and bogs became more similar after long-term drainage as their characteristic differences in biogeochemical properties and microbial composition decreased upon drainage. This is in line with our results: We found significantly lower SIR-C<sub>mic</sub> in undisturbed bog peat than in fen peat, but under disturbed conditions SIR-C<sub>mic</sub> became comparable. This points – together with the stronger increase of SBR with disturbance – to a higher vulnerability of bog peat. All these previous findings corroborate our results that SBR rates of bog and fen peat become more similar, but generally higher with stronger degree of disturbance.

Overall, the structural and chemical changes of the peat properties seem to induce destabilising positive feedback processes.



#### 4.3. SOM quality as an indicator for respiration rates

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 characterize SOM quality, C:N-ratio, degree of decomposition and  $\delta^{15}\text{N}$  stable isotope values were available for 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. SBR rates increased rapidly with lower C:N-ratios, at least over 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 seems to be 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  $\delta^{15}\text{N}$  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  $^{15}\text{N}$  enrichment (Nadelhoffer et al., 1996). The positive correlation between specific basal respiration and  $\delta^{15}\text{N}$  (Fig. 2, Fig. 3e) indicated that increased microbial transformation under aerobic conditions altered the stable N isotope signature of SOM. Mineralisation will therefore result in both increased  $\delta^{15}\text{N}$  values and increased respiration rates, making it difficult to distinguish between cause and effect.

The greater the disturbance, the harder it was to find possible correlative patterns of SOM quality parameters and SBR, especially in the case of fen peat samples. One reason for this could be that chemical and physical changes during decomposition differed between peat-forming plants (Bohlin et al., 1989). These are generally more diverse in fens than in bogs, but could no longer be identified. Furthermore, the class of heavily disturbed fen samples combined samples that have been amended by mineral soil by different processes (e.g. ploughing, application from external sources, or natural sedimentation in riverine fens). This adds another level of complexity (see Section 4.2), which might contribute to the high variability of SBR rates. Finally, the DREAM-fits showed the largest uncertainty for some of the samples of the class D4F (Fig. 3b), which might have added to the difficulty in finding appropriate explanatory variables. However, even when excluding those samples with large uncertainties, the general picture of high SBR rates and a high variability remained valid. Explaining respiration rates from disturbed organic soils thus remains challenging, especially when moving beyond samples from one peatland or one region. This problem is not unique to our study, as other authors faced similar problems when trying to relate respiration rates to soil properties. For example, the incubation study on disturbed fen peat by Bader et al. (2018) only found weak relationships between  $\text{CO}_2$  fluxes and soil chemical and physical properties, even though they incubated fresh samples for a much longer time (6 months).

#### 4.4. Nutrient availability and acidity as indicators for respiration rates

Agriculturally used peat soils drained for a long time are often enriched in N and (labile) P contents (Laiho et al., 1998; Schlichting et al., 2002; Sundström et al., 2000) due to ongoing mineralisation of SOM, fertilisation and, in the case of P, sorption of the resulting inorganic P forms to Fe(III) compounds (Zak et al., 2010). Such enrichment is also visible in the present sample set (Table 2). As P is needed for microbial growth, a lack of labile phosphorus limits the decomposition of SOM. Due to the low pH and low iron contents, natural bogs are frequently P-limited (Verhoeven et al., 1990), which is reflected by the low content of plant-available phosphorus ( $P_{\text{CAL}}$ ) of the undisturbed bog peat samples. However, disturbed bog samples showed much higher  $P_{\text{CAL}}$  contents than the respective fen classes, which likely originated from past

fertilisation. Results of the present study showed that  $P_{\text{CAL}}$  was indeed the most important explanatory variable for SBR rates across all disturbance classes. This confirms the results of Brake et al. (1999) who also found that P strongly correlates with the respiration rates of disturbed bog samples. Furthermore, an incubation experiment with undisturbed peat cores also showed both surprisingly high  $P_{\text{CAL}}$  contents of bog peat and  $P_{\text{CAL}}$  as a major explanatory variable for  $\text{CO}_2$  fluxes across peat types and sampling depths (Säurich et al., 2019).

Nitrogen contents of all disturbance classes were comparable (except for D4F) and higher in fen peat than in bog peat (Table 2), while C:N-ratios decreased with disturbance. As indicated by Fig. 4, SBR rates seem to be positively influenced by N contents in the case of undisturbed samples only. 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.

Especially in the case of bogs, there was also a positive correlation between SBR rates and pH values (Fig. 3g), probably reflecting lower microbial activity in an undisturbed acidic environment (D0B, Fig. 5a). Earlier studies have, counterintuitively, sometimes detected a negative correlation (Ausec et al., 2009; Fisk et al., 2003) between pH and respiration. 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, however, contradicts the common observation that fens show higher respiration rates than bogs (Bridgman and Richardson, 1992; Urbanova and Barta, 2015). However, with increasing disturbance any influence of the pH-value vanishes in the present sample set, possibly due to better nutrient availability and increased overall pH-values.

#### 4.5. Microbial biomass and activity

The specific microbial biomass ( $\text{SIR-C}_{\text{mic}}$ ) increased with the increasing degree of anthropogenic disturbance for both fen and bog samples (Fig. 5a). While topsoils frequently show higher microbial activity than subsoils (Brake et al., 1999; Fisk et al., 2003; Preston et al., 2012; Säurich et al., 2019), it is surprising that heavily degraded topsoils (D4F) had higher  $\text{SIR-C}_{\text{mic}}$  than less disturbed topsoils (D2F) since the remaining SOM of such degraded peat should be energetically less attractive for microorganisms than better preserved peat (Fisk et al., 2003). One reason might be the improved availability of nutrients due to long-term aerobic decomposition (and possibly fertilisation), which might cause 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  $\text{SIR-C}_{\text{mic}}$  with pH value and  $P_{\text{CAL}}$  as well as negative correlations with C:N-ratios (Fig. 2).

The metabolic quotient, i.e. the ratio of basal respiration to microbial biomass, indicates the efficiency of microorganisms to transform SOM into microbial biomass. Overall, there were no significant differences in the metabolic quotient between disturbance classes (Fig. 5b). The slight tendency towards lower metabolic quotients of strongly disturbed bog and fen samples compared to undisturbed samples might indicate that these microorganisms are more efficient at using SOM for growth, possibly due to better nutrient availability.

#### 4.6. Implications for peatland management

Both the high basal respiration and the high specific basal respiration rates of heavily disturbed samples confirm the vulnerability of “low C organic soils” to decomposition 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. We expected that below some unknown SOC content such former peat soils would behave like mineral soils, i.e. with respiration rates related to SOC or clay content.

However, this threshold does not seem to be within the studied SOC range of 76 to 526 g kg<sup>-1</sup>. Additionally, the high variability of respiration rates of heavily disturbed samples (Fig. 3b) also agrees with the finding that the variability of CO<sub>2</sub> emissions from “low C organic soils” field studies is high (Tiemeyer et al., 2016). Therefore, mixing organic soil with mineral soil does not seem to mitigate respiration rates, but on average increases the vulnerability of SOM to decomposition. Similar effects have been found in field studies (Maljanen et al., 2004) as well as in laboratory studies with intact cores (Säurich et al., 2019). However, for specific samples the respiration rates remains still rather unpredictable. By mixing peat with mineral soil, a whole new soil horizon develops that may include modified microbial communities and potentially fresh SOM due to aggregate destruction (Ross and Malcolm, 1988). Increased availability of nutrients (especially of P) by fertilisation might also contribute to increased respiration rates (Fig. 3f, Amador and Jones, 1993; Brake et al., 1999). However, it should be stressed that we did not carry out fertilisation experiments here. Liming of acidic 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. Raising the water table may prevent further decomposition and, under optimum conditions, reinstate the typical peatland environment, however, severe disturbance might have a long-lasting effect on the biogeochemistry of rewetted peatlands.

## 5. Conclusions

This study examined the vulnerability of SOM of organic soils to decomposition by determining the basal respiration and specific basal respiration (SBR) rates under aerobic conditions in the laboratory. It could be shown that SBR increased in magnitude and variability with increasing disturbance, and that it was highest and most variable at the boundary between mineral and organic soils. Thus, there was a trend towards higher SBR with lower SOC content. Furthermore, bog peat samples seemed to be more sensitive to anthropogenic disturbance than fen peat samples as indicated by a stronger increase of SBR rates with increasing disturbance. Overall, the most important indicators for the vulnerability of SOM to decomposition identified in the present study were narrow C:N-ratios, low SOC content, high pH-values, and – most important – high contents of plant-available phosphorus. There seems to be a positive feedback loop of disturbance and increased mineralisation. However, we could not explain the very high variability of SBR rates of heavily disturbed samples with the available soil properties. Given the continued drainage and disturbance of peatlands and the considerable potential of high CO<sub>2</sub> emissions even 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 mitigation option.

## Declaration of competing interest

The authors declare that they have no conflict of interest.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2019.113911>.

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