



# Soil greenhouse gas emissions from drained and rewetted agricultural bare peat mesocosms are linked to geochemistry

C.K. Nielsen <sup>a,b,\*</sup>, L. Elsgaard <sup>a</sup>, U. Jørgensen <sup>a,b</sup>, P.E. Lærke <sup>a,b</sup>

<sup>a</sup> Department of Agroecology, Faculty of Technology, Aarhus University, Blichers Alle 20, 8830 Tjele, Denmark

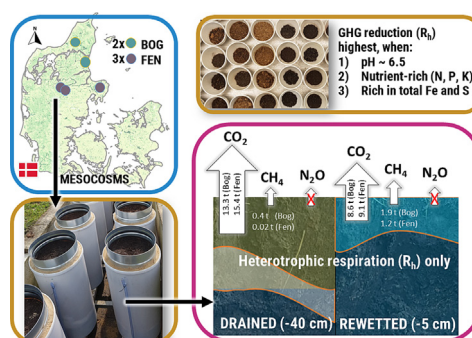
<sup>b</sup> CBIO, Centre for Circular Bioeconomy, Aarhus University, Denmark



## HIGHLIGHTS

- For drained and rewetted peat, emissions were dominated by CO<sub>2</sub>.
- GHG reduction highest on sites with: 1) pH 6.5, 2) rich in nutrients, iron, sulphur
- Rewetting of fen peatlands was most efficient.
- Biogeochemical proxies may be used for prioritising peatland areas for rewetting.

## GRAPHICAL ABSTRACT



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## ABSTRACT

In view of climate considerations regarding the management of peatlands, there is a need to assess whether rewetting can mitigate greenhouse gas (GHG) emissions, and notably how site-specific soil-geochemistry will influence differences in emission magnitudes. However, there are inconsistent results regarding the correlation of soil properties with heterotrophic respiration (R<sub>h</sub>) of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O) from bare peat. In this study, we determined 1) soil-, and site-specific geochemical components as drivers for emissions from R<sub>h</sub> on five Danish fens and bogs, and 2) emission magnitudes under drained and rewetted conditions. For this, a mesocosm experiment was performed under equal exposure to climatic conditions and water table depths controlled to either -40 cm, or -5 cm. For the drained soils, we found that annual cumulative emissions, accounting for all three gases, were dominated by CO<sub>2</sub>, contributing with, on average, 99% to a varying global warming potential (GWP) of 12.2–16.9 t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup>. Rewetting lowered annual cumulative emissions from R<sub>h</sub> by 3.2–5.1 t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup> for fens and bogs, respectively, despite a high variability of site-specific CH<sub>4</sub> emissions, contributing with 0.3–3.4 t CO<sub>2</sub> ha<sup>-1</sup> yr<sup>-1</sup> to the GWP. Overall, analyses using generalized additive models (GAM) showed that emission magnitudes were well explained by geochemical variables. Under drained conditions, significant soil-specific predictor variables for CO<sub>2</sub> flux magnitudes were pH, phosphorus (P), and the soil substrate's relative water holding capacity (WHC). When rewetted, CO<sub>2</sub> and CH<sub>4</sub> emissions from R<sub>h</sub> were affected by pH, WHC, as well as contents of P, total carbon and nitrogen. In conclusion, our results found the highest GHG reduction on fen peatlands, further highlighting that peat nutrient status and acidity, and the potential availability of alternative electron acceptors, might be used as proxies for prioritising peatland areas for GHG mitigation efforts by rewetting.

## 1. Introduction

The Paris Agreement was adopted by 196 Parties, among them the EU and its member states, at the COP 21 meeting in Paris (2015), with the

\* Corresponding author at: Department of Agroecology, Faculty of Technology, Aarhus University, Blichers Alle 20, 8830 Tjele, Denmark.

E-mail address: [claudia@agro.au.dk](mailto:claudia@agro.au.dk) (C.K. Nielsen).

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goal to reduce greenhouse gas (GHG) emissions by 40 % in 2030 as compared to the 1990 baseline and to reach zero-emissions by 2050 (Liobikienė and Butkus, 2017).

One critical tool in achieving this goal is the reduction of GHG emissions from drained peatlands. Peatlands are the dominating wetland type globally (Yu et al., 2010), covering about 3 % of the continental surface (Joosten and Clarke, 2002). A main feature of peatlands in their natural state is that the net primary production exceeds the organic matter decomposition (Lloyd et al., 2013), consequentially leading to the formation of peat, typically at a rate of  $\sim 1 \text{ mm yr}^{-1}$  (Parish et al., 2008). This serves as a critical sink for atmospheric carbon dioxide ( $\text{CO}_2$ ), but also provides the basis for other ecosystem services, such as nutrient retention, water filtration and habitat provision (Mitsch and Gosselink, 2000), thus highlighting the importance of natural peatlands at global and local scales.

However, anthropogenic degradation of peatlands by drainage for agriculture during the last century has led not only to a substantial loss of global peatlands (Joosten and Clarke, 2002) and the associated ecosystem functions (Bonn et al., 2016), but also to emission hotspots. Thus, peatlands release around 5 % of the total anthropogenic emissions in  $\text{CO}_2$  equivalents ( $\text{CO}_2\text{eq}$ ) from only 0.3 % of the total global land area (Joosten, 2016). Drainage, fertilisation and liming practices on peatlands cause the stimulation of microbial oxidative processes thereby enhancing heterotrophic respiration ( $R_h$ ) (Limpens et al., 2008). Carbon (C) losses of up to  $31 \text{ t CO}_2\text{-C ha}^{-1} \text{ y}^{-1}$  and nitrous oxide ( $\text{N}_2\text{O}$ ) emissions of up to  $35 \text{ kg nitrogen (N) ha}^{-1} \text{ y}^{-1}$  have been reported from northern agricultural peatlands (Maljanen et al., 2010). In Denmark, peatlands with an organic carbon content of  $>12 \%$  cover  $129,000 \text{ ha}$  corresponding to approximately 3 % of the total land area (Greve et al., 2021). Of these, 57 % are drained and used for agricultural production, annually losing up to  $16.7 \text{ t C ha}^{-1}$  and up to  $61 \text{ kg N}_2\text{O-N ha}^{-1} \text{ y}^{-1}$  (Elsgaard et al., 2012; Petersen et al., 2012) as a result of peat mineralisation.

Many studies have shown that rewetting of drained organic soils reduces emissions of  $\text{CO}_2$  and  $\text{N}_2\text{O}$  (e.g., Komulainen et al., 1999; Strack and Zuback, 2013), while at the same time facilitating methane ( $\text{CH}_4$ ) emissions due to limited soil aeration (Wilson et al., 2009). Data syntheses show that the net effect of rewetting results in lowered cumulative GHG emissions (Wilson et al., 2016). However, the site-specific climate mitigation potential by rewetting varies and nutrient-rich peatlands, such as the Danish riparian fens, might remain sources of cumulative emissions (in  $\text{CO}_2\text{eq}$ ) even under wet conditions (Höper et al., 2008). In this context, little is known about the geochemical drivers and magnitudes of GHG emissions on the various types of drained agricultural peatlands in Denmark. While temperature (Elsgaard et al., 2012) and water table (Karki et al., 2014) are well known drivers for ecosystem respiration in temperate peatlands, soil-related drivers are rarely assessed. This is in particular true for the component of  $R_h$ , accounting for up to 50 % of total ecosystem respiration in wetlands (Wigand et al., 2009; Jovani-Sancho et al., 2018) and up to 90 % in forest soils (Hu et al., 2016). However, while assessments of whole-ecosystem GHG dynamics (i.e., including soil and plant respiration) are critical in order to account for total C budgets, are quantifications of  $R_h$  necessary to eliminating vegetation-related variations in GHG magnitudes,

potentially adding bias to sound comparisons of soil-specific GHG mitigation potentials. Wilson et al. (2016) proposed a site-specific approach for assessing potential feasibilities of peatland rewetting, including site-specific physical and chemical soil properties. For the majority of studies assessing GHG dynamics following rewetting, standard assessments of peat properties include bulk density, total C and N, as well as pH (Loisel et al., 2014). However, there are inconsistent results regarding the link between soil-geochemical parameters and the emissions of  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  resulting from  $R_h$  from bare and cultivated peatlands. For instance, Weslien et al. (2009) reported high emissions of  $\text{CH}_4$  from peat soils with a low pH in Sweden, whereas Ye et al. (2012) found enhanced  $\text{CO}_2$  and  $\text{CH}_4$  emissions from bogs and fens with a high pH level in Michigan, USA, due to enhanced fermentative activity in the peat. A study by Emsens et al. (2016) on Belgian and Dutch fen peatlands highlighted the negative influence of high soil iron (Fe) content on GHG mitigation by rewetting, which is due to enhanced Fe(III) mediated soil organic matter decomposition under oxygen limitation (Chen et al., 2020). Contrary to this, Saily et al. (2020) reported lower emissions of  $\text{CO}_2$  under the influence of high iron contents in peat.

In relation to the future management of Danish peatlands, there is a desideratum to assess whether rewetting can mitigate high GHG emissions from agriculturally used, and notably how site-specific soil geochemistry will influence GHG magnitudes. Such an assessment might aid in pinpointing priority areas for rewetting to achieve the combined benefits of GHG mitigation, nutrient retention, and habitat creation.

We hypothesised that soil chemical and physical properties are drivers for differences in site-specific magnitudes of GHG emissions from drained peat soils and for the resulting mitigation potential by rewetting. The aims of this study were to 1) determine soil- and site-specific geochemical drivers for GHG emissions from  $R_h$  and their reduction potential by rewetting, 2) to determine magnitudes of emissions from soil respiration under controlled drained conditions, and 3) to assess the GHG mitigation potential from soil respiration by rewetting of different Danish agriculturally used peatlands.

## 2. Methods

### 2.1. Peatland sites and soil sampling

Intact soil samples were collected from two bog (B) peatlands: Store Vildmose ( $B_{SV}$ ) and Lille Vildmose ( $B_{LV}$ ), and three fen (F) peatlands: Selkær Enge ( $F_{SE}$ ), Øby ( $F_{ØB}$ ), and Vejrumbro ( $F_{VJ}$ ) (Fig. A.1). These sites represent part of the variation that nowadays is found in Danish bog and fen peatlands – both with regard to their original natural state and composition, and their prevailing peat depth and land-use history related to drainage and management (Table 1). Sampling occurred on areas that formerly were used for agricultural production, but now were classified as permanent grassland. All sites were shallow drained at the time of mesocosm collection.

In March 2019, ten intact soil mesocosms were collected from each of the five sites. Soil sampling was performed using PVC pipes (inner diameter, 30 cm; length, 60 cm) with sharpened edge that were mechanically

**Table 1**

Danish agricultural peatland donor sites, their peatland type and information regarding peat depth, land-use, drainage, and peat degradation (on the von Post scale, averaged over a soil profile of 100 cm depth) on their ecosystem- and field-scales.

Name	Type	Scale	Peat depth	Current land-use	Drainage	Von Post	Location	Area
Lille Vildmose ( $B_{LV}$ )	Oligotrophic raised bog	Ecosystem:	1.5–5 m	Perennial grass, peat extraction	1760s - 2016		Northern Jutland	7800 ha
		Field:	1.5–2 m	Perennial grass (grazing)	1940s - 2016	H3	56°54'55"N, 10°12'28"E	6 ha
Øby ( $F_{Ø}$ )	Minerotrophic riparian fen	Ecosystem:	0–4 m	Perennial grass	1930s - 2018		Mid Jutland	139 ha
		Field:	~1.5 m	Perennial grass	1967–2018	H5	56°27'28"N, 9°40'32"E	6 ha
Selkær Enge ( $F_{SE}$ )	Highly degraded minerotrophic fen (former bog)	Ecosystem:	0.2–1 m	Perennial grass	1850s - 2019		Mid Jutland	47 ha
		Field:	0.5–1 m	Perennial grass	1930s - 2019	H8	56°27'47"N, 10°44'38"E	6 ha
Store Vildmose ( $B_{SV}$ )	Highly degraded oligotrophic raised bog	Ecosystem:	0.8–5 m	Perennial grass, potatoes, peat extraction	1920s - now		Northern Jutland	1900 ha
		Field:	1.5 m	Perennial grass (grazing)	1920s - now	H4	57°11'25"N, 9°49'42"E	5 ha
Vejrumbro ( $F_{VJ}$ )	Minerotrophic riparian fen	Ecosystem:	1–3 m	Perennial grass	1930s - now		Mid Jutland	106 ha
		Field:	~2 m	Perennial grass	1950s - 2022	H5	56°26'11"N, 9°33'00"E	10 ha

pressed into the soil and excavated. This resulted in a total of 50 mesocosms that were transported to open-air semi-field facilities at Aarhus University Viborg, Denmark.

## 2.2. Experimental design and set-up

The semi-field study was conducted from 21st of June 2019 to 20th of June 2020. Weather conditions during the study period are shown in Fig. A.2. Briefly, the monthly average temperature ranged between 4.0 and 16.8 °C, with August 2019 as the warmest month. Monthly average precipitation ranged between 32 and 134 mm, with April 2020 as the driest and February 2020 as the wettest month. The average soil temperature in 10 cm depth ranged between 3.5 °C in December 2019 and 17.7 in July 2019 (Fig. A.2).

The GHG mitigation potentials by rewetting of the different peat soils were studied with a generalized complete block design, with treatment (drained or rewetted) as block and site as a nested component. For this, the 10 intact soil mesocosms per site were trimmed by removal of vegetation and the by roots perfoliated upper topsoil layer (5 cm) before the mesocosms were set up in containers for controlled water table depth (WTD) adjustment in the semi-field facility. Removal of the vegetation was done to allow for dark chamber measurement of  $R_h$  in response to rewetting. A steel collar of 10 cm height was permanently placed on the rim of each mesocosm to allow tight placement of opaque chambers for GHG measurements without soil disturbance. The bare soil mesocosms were randomly grouped into two treatments: (i) drained (DRY) with a WTD of -40 cm and (ii) wet (WET) with a WTD of -5 cm. Each treatment had five replicates from each peatland site, resulting in a total of 25 mesocosms for each treatment. The mesocosms were placed in an outer plastic container, filled with gravel in the bottom on which the mesocosm was placed. WTD regulation was established by fitting overflow-tubes to the bottom site of the outer containers with the outlet-end cut at heights corresponding to the WTD treatment. The entire mesocosm setup, modified from Karki et al. (2015) and as schematically shown in Fig. A.3, was placed in two separate ditches (1 m deep x 1 m wide x 8 m long) for each WTD treatment. The soil surface was at ground level elevation and the mesocosms were insulated with seashells to secure robust soil temperature conditions. The mesocosms were rewetted to maintain the selected WTDs using demineralised water, supplied by drip irrigation into the outer containers in intervals of 1 h once every third day during winter months (October to March) to 1 h twice daily during summer months (April to September). Five soil mesocosms per treatment, one for each peatland site, were equipped with a piezometer, time domain reflectometry (TDR) probes, and a soil temperature probe at -10 cm depth (these mesocosms were not used for GHG measurements). The relative water holding capacity (WHC) was measured during each GHG sampling campaign for each site and treatment with the TDR probes. Maximum fluctuations of WTD, due to events of heavy rain or high evapotranspiration, were  $\pm 1.3$  cm (DRY) and  $\pm 2$  cm (WET), resulting in annual averaged WTDs of -40.4 cm and -5.0 cm, respectively. The mesocosms received no fertilisation and were permanently kept free from emerging and invading vegetation by manual weeding.

## 2.3. Soil physical and chemical properties

From each of the studied peatlands, three soil core samples of 5 cm in diameter and 60 cm depth were taken using a Russian peat corer for analysis of soil chemical and physical properties. Soil analyses were performed for the following soil segments: 0–5 cm, 5–20 cm, 20–40 cm, and 40–60 cm. Soil bulk density (BD) was determined by oven drying at 60 °C to constant weight, and soil pH was measured after soaking 5 g of dry soil in 50 mL H<sub>2</sub>O overnight. Total N and C were analysed on a Vario MAX CN (Elementar Analysensysteme GmbH, Hanau, Germany). The contents of Fe, potassium (K), phosphorus (P) and sulphur (S) were determined by inductively coupled plasma optical emission spectroscopy (ICP-OES) as described by Liu et al. (2013). A van Post classification of peat humification

(von Post, 1922; von Post and Granlund, 1926) was performed for soil segments of 10 cm in the upper 20 cm and segments of 20 cm in the remaining 60 cm.

## 2.4. GHG measurements and flux calculation

Measurements of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O fluxes from  $R_h$  took place every two weeks in the study period, resulting in 27 sampling campaigns, performed between 9:30 and 14:30, using opaque PVC chambers with a volume of 41.89 L (diameter, 30 cm; height, 50 cm). For each campaign, the sampling order was randomised in order to account for diurnal variability. The chambers were equipped with a fan to mix headspace air, a vent to ensure pressure equilibrium, and a temperature probe measuring air temperature inside the chamber. Five gas samples per chamber were withdrawn at 0, 5, 10, 25, and 50 min after chamber closure using a syringe (20 mL), connected to the chamber sampling port by a polypropylene tube of 1.2 m length and 4 mm inner diameter. To remove dead volume of the tubing, 16 mL air from the tube and air sampling system were removed with a syringe and discarded prior to taking the gas samples. Eventually, 11 mL of air from the headspace was transferred to pre-evacuated 6 mL glass exetainers (Labco Limited, UK). The exetainers were stored for less than four weeks until gas analysis on an Agilent 7890 gas chromatograph (GC), equipped with an automatic injection system (CTC CombiPAL, Agilent A/S, Nærum, Denmark). Details of the GC and instrument calibration were described by Petersen et al. (2012).

Gas fluxes were calculated using linear regression within the package *flux* (Jurasiński et al. (2014) version 0.3–0) in the statistical program R (R Core Team (2020) Version 4.1.2 – “Bird Hippie”), based on best linear fits according to the smallest normalised root mean square error (NRMSE), calculated on at least four out of the five gas concentration measurements. Additional quality checks for the individual fluxes included  $R^2$ , a defined quality range for concentration measurements, the number of measurements below ambient (NOMBA) as well as a GC quality flag to indicate observed errors resulting from the GC analysis. Further, fluxes of CH<sub>4</sub> and N<sub>2</sub>O were tested for chamber leakage or gas sampling errors based on a control against CO<sub>2</sub> concentration data, resulting in no fluxes discarded. CO<sub>2</sub> fluxes were accepted when all three assumptions were met: 1) no quality flags were violated, 2)  $R^2 > 0.95$ , and 3) significant regression for flux estimation ( $p < 0.05$ ). Due to frequent CH<sub>4</sub> and N<sub>2</sub>O fluxes near zero, fluxes were accepted when the following criteria were met: 1) no quality flags were violated, and 2)  $R^2 > 0.90$ . Further, fluxes of all gases beyond the 2.0 percentile tail of a log-norm-distribution were regarded as outliers and discarded ( $n = 29$ ). In addition, nine CH<sub>4</sub> fluxes indicating an uptake rate  $> 0.5$  mg m<sup>-2</sup> h<sup>-1</sup> were discarded according to Hütsch (2001) who found no CH<sub>4</sub> uptake rates  $> 0.3$  mg m<sup>-2</sup> h<sup>-1</sup> in any ecosystems. Hence, out of initially 1080 fluxes for each gas, 90 %, 79 % and 90 % of measured CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O fluxes, respectively, met our quality criteria and were included in all further calculations and analyses. Summer fluxes were defined as those in the period from April to September, whereas winter fluxes were those from October to March.

## 2.5. Interpolation to annual gas fluxes

Fluxes of CO<sub>2</sub> from all mesocosms and treatments were interpolated to annual values using the function *budget.reco* in the *flux* package (Jurasiński et al., 2014). Based on the relationship between soil temperature and measured fluxes, hourly values for CO<sub>2</sub> were modelled using an exponential regression model of Arrhenius-type, as modified by Lloyd and Taylor (1994), with hourly soil temperature from the semi-field facility as driver (Eq. (1)):

$$R = \theta_1 * \exp \left( E_0 * \left( \frac{1}{T_{ref} - T_0} - \frac{1}{Temp - T_0} \right) \right) \quad (1)$$

where  $R$  is the soil respiration flux rate,  $\theta_1$  is the base respiration rate (in  $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ) at the reference temperature ( $T_{ref}$ ) of 10 °C,  $E_0$  is the



parameter of temperature sensitivity of  $R$ ,  $T_0$  is the theoretical lower temperature limit for the soil respiration (here constrained to  $-46.02$  °C) and  $Temp$  is the soil temperature (°C). Hourly values were summed up to determine annual  $CO_2$  emissions as well as summertime and wintertime emissions.

Annual cumulative balances of  $CH_4$  were calculated by modelling hourly values using a simple linear regression model, based on soil temperature fits as applied for  $CO_2$ :

$$R = \theta_1 * \theta_2 * T \quad (2)$$

where  $R$  is the soil respiration flux rate,  $\theta_1$  is the base respiration rate (in  $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ) at the reference temperature ( $T_{ref}$ ) of 10 °C,  $\theta_2$  is the bias coefficient of  $0.08 \pm 0.01$  and  $Temp$  is the soil temperature (°C).

Both  $CO_2$  and  $CH_4$  interpolation models were quality checked regarding their fit by posteriori analyses of model performance and passed at  $p < 0.01$  and  $R^2 > 0.8$ .

Annual  $N_2O$  emissions for each mesocosm and treatment were calculated following a Monte Carlo permutation procedure, as described in detail by Huth et al. (2013). Annual  $CH_4$  and  $N_2O$  fluxes were converted into  $CO_2\text{eq}$  using the 100-yr global warming potentials (GWP) of 28 and 265, respectively (Myhre et al., 2013; Evans et al., 2021).

## 2.6. Environmental variables, soil moisture and water table depth

Hourly average air temperatures during GHG sampling campaigns, daily temperature means, and daily average precipitation were gathered from a meteorological station located 1.3 km from the semi-field site. Soil temperature within the mesocosms was automatically logged hourly during the entire study period. During each GHG sampling campaign, water table depth (WTD) was monitored in the pre-installed piezometers (one replicate per site and treatment), while the electrical conductivity to obtain WHC was measured in the soil mesocosms with the pre-installed TDR probes.

## 2.7. Statistical analysis

To estimate the influence of covariates, including biogeochemical properties, on gas fluxes of  $CO_2$  and  $CH_4$ , we used generalized additive models (GAMs) with a Gaussian distribution and an identity link function for the log or square root transformed response variables, thereby fitting mean and variance on the log scale. The usage of GAMs was chosen, since GAMs allow for an estimation of non-linear and smooth relationships in a flexible modelling approach based on individual data-derived penalties (Marra and Wood, 2011; Wood, 2011; Wood et al., 2016). GAMs were performed with the package *mgcv* (Wood, Version 1.8–38, 2021) in R, using restricted marginal likelihood for all model coefficients and penalties, in which the following model was used:

$$y_i \sim N(\mu, \sigma^2)$$

$$y_i = \alpha + f_1(t.\text{air}_i, t.\text{soil}_i) + f_2(\text{intrannual}(\text{date}_i)) + f_3(\text{tdr}_i) + f_4(S_i) + f_5(\text{Fe}_i) + f_6(\text{P}_i) + f_7(\text{pH}_i) + f_8(\text{BD}_i) + f_9(\text{TC}_i) + f_{10}(\text{TN}_i) + f_{11}(K_i) + \beta_1 x_1 + \varepsilon_i, \varepsilon_i \sim N(\mu, \sigma^2).$$

where  $y_i$  is the log or square root transformed observed dependent variable and  $\mu$  is the overall mean, affected by  $f_1$ : the isotropic product smooth representing the marginal effects and interaction of temperature ( $t.\text{air}$  and  $t.\text{soil}$ ),  $f_2$ : intrannual(date), i.e., the penalised cyclical smooth term of data where spline end points are equal,  $f_3 - f_{11}$ : smooth functions of the various covariates for the  $i$ th sample, and  $x_1$ , the categorical predictor variable of peatland type (bog or fen).  $\alpha$  is the intercept and  $\sigma^2$  denotes the experimental error. Prior to model fitting, variables were controlled for multicollinearity by estimating the Pearson product moment correlation

coefficient. The final model was checked for concurvity and model residuals were inspected for normality and homoscedasticity. To test for significance of differences between means, a one-way ANOVA with post-hoc Tukey HSD at 95 % confidence level was performed. Correlation effects between site specific soil properties and the various annual cumulative GHG balances and reduction potentials by rewetting were determined by multiple linear regression using Pearson's correlation. Measures of central tendency are given as means and dispersion around the means are given as standard error ( $n = 4$ ) unless otherwise specified. For all statistical analyses, averaged soil properties for the depth of  $-5$  cm to  $-25$  cm were used.

## 3. Results

### 3.1. Soil properties

Content gradients (in g per kg) with depth were observed for all soil chemical and physical parameters (Table A.1), which in particular were pronounced for TC, K, and P. TC was lowest in fen soils and highest in bog soils and ranged on average from 35.2 % ( $F_V$ ) to 51.3 % ( $B_{SV}$ ) across depth. In contrast, TN was highest in fen peat soils (2.6–2.9 %) and lowest in bog peat soils (1.3–1.4 %). TC increased with depth for all sites, whereas TN showed a decline for bogs and was stable for fens. Across depth in the fen peat soils, the average contents of Fe, P and S ( $\text{kg}^{-1}$  DM) ranged from 8.0 to 10.7 g Fe, 1.1–1.3 g P, and 7.1–11.5 g S, whereas the bog peat soils showed 2–10 times lower contents. Averaged pH ranged from 4.6 to 6.4 and differed significantly ( $p < 0.001$ ) between fens and bogs, with bogs being more acidic than fens.

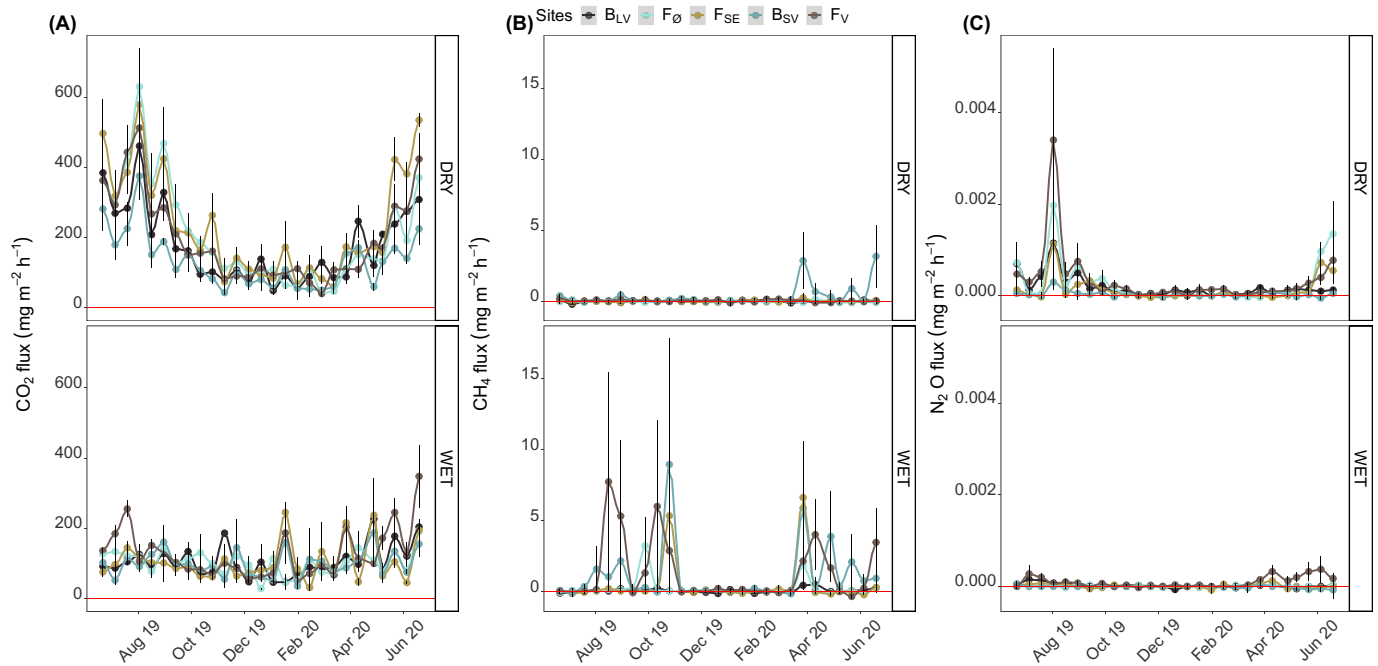
### 3.2. Fluxes of GHG from heterotrophic respiration

#### 3.2.1. Measured and modelled $CO_2$ fluxes

Mid-day heterotrophic soil respiration across all sites was 52 % lower in WET as compared to DRY on an average annual basis (Fig. 1A). Flux magnitudes from fen peatlands were highly similar. Soil from  $F_{SE}$  showed the highest emission among the five DRY sites ( $237 \pm 37 \text{ mg } CO_2 \text{ m}^{-2} \text{ h}^{-1}$ ), whereas  $F_V$  had the highest emissions among WET treatments ( $128 \pm 26 \text{ mg } CO_2 \text{ m}^{-2} \text{ h}^{-1}$ ). For treatment DRY, the lowest average fluxes over the sampling period ( $133 \pm 26 \text{ mg } CO_2 \text{ m}^{-2} \text{ h}^{-1}$ ) were detected from  $B_{SV}$ . For treatment WET the lowest average fluxes were from  $B_{SV}$  ( $101 \pm 28 \text{ mg } CO_2 \text{ m}^{-2} \text{ h}^{-1}$ ). Under drained conditions, fen peatland soils emitted on average  $214 \pm 38 \text{ mg } CO_2 \text{ m}^{-2} \text{ h}^{-1}$ , which was 37 % more ( $p < 0.001$ ) than bog peatlands ( $156 \pm 30 \text{ mg } CO_2 \text{ m}^{-2} \text{ h}^{-1}$ ). For treatment WET, there was no difference in  $CO_2$  emissions between the five soil types, with the exception of  $F_V$ , showing on average 34 % higher soil respiration as compared to the other sites. Summer fluxes (mean temperature: 13.1 °C) across all sites were on average 54 % (WET) - 65 % (DRY) higher as compared to winter fluxes (mean temperature: 5.3 °C), indicating the high temperature dependency. Treatment WET reduced average  $CO_2$  fluxes during the summer months by 40 % ( $B_{SV}$ ) - 72 % ( $F_{SE}$ ) as compared to DRY. The reduction of annual average  $CO_2$  flux by raising the WTD from  $-40$  cm to  $-5$  cm ranged between 38 % ( $B_{SV}$ ) to 69 % ( $F_{SE}$ ). Modelled hourly rates of ( $R_H$ ) showed a strong seasonality (Fig. A.4), with low and near-zero fluxes during winter months for all soils on treatments DRY and WET.

#### 3.2.2. $CH_4$ fluxes

Annual methane fluxes were generally low for all sites in treatment DRY, with  $B_{SV}$  showing the highest annual emissions ( $0.4 \pm 0.3 \text{ mg } CH_4 \text{ m}^{-2} \text{ h}^{-1}$ ). Dry soils from  $B_{LV}$  and  $F_0$  were characterised by a minor uptake of  $CH_4$ . Rewetting raised annual fluxes significantly ( $p < 0.001$ ) for all soils (Fig. 1B) with, on average, similar resulting fluxes from fens ( $0.7 \pm 0.6 \text{ mg } CH_4 \text{ m}^{-2} \text{ h}^{-1}$ ) and bogs ( $0.6 \pm 0.4 \text{ mg } CH_4 \text{ m}^{-2} \text{ h}^{-1}$ ). However, we observed high variabilities across sites of the same peatland type. For instance, annual methane emissions for fens were highest from  $F_V$  ( $1.3 \pm 1.1 \text{ mg } CH_4 \text{ m}^{-2} \text{ h}^{-1}$ ), as compared with  $F_0$  and  $F_{SE}$  (means,  $<0.5 \text{ mg } CH_4 \text{ m}^{-2} \text{ h}^{-1}$ ). For bogs,  $B_{SV}$  emitted  $1.1 \pm 0.8 \text{ mg } CH_4 \text{ m}^{-2} \text{ h}^{-1}$ , which was significantly



**Fig. 1.** Measured fluxes (in  $\text{mg m}^{-2} \text{h}^{-1}$ ) for the study sites Lille Vildmose ( $B_{LV}$ ), Øby ( $F_{\emptyset}$ ), Selkær Enge ( $F_{SE}$ ), Store Vildmose ( $B_{SV}$ ) and Vejrumbro ( $F_V$ ) of A) carbon dioxide ( $\text{CO}_2$ ), B) methane ( $\text{CH}_4$ ) and C) nitrous oxide ( $\text{N}_2\text{O}$ ) for the dry (top panels) and wet (bottom panels) treatments. Grey shaded lines for the various soil types show averaged flux values at the specific sampling campaigns from the replicates ( $n = 4$ ) with standard errors showing the variation. Red lines indicate zero.

( $p < 0.001$ ) more than  $B_{LV}$  ( $0.1 \pm 0.1 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ ). Summer emissions of  $\text{CH}_4$  at WET were for  $B_{LV}$ ,  $F_{\emptyset}$  and  $F_V$  higher than those during the colder winter half-year. However, due to high methane emissions ( $>5.4 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ ) on the 25.10.2019 and 27.03.2020, the integrated rates were highest during winter for soils from  $F_{SE}$  and  $B_{SV}$ .

### 3.2.3. $\text{N}_2\text{O}$ fluxes

Nitrous oxide fluxes were generally low and close to zero in the majority of occasions, with the highest overall flux of  $3.4 \pm 2.0 \mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$  observed for soils from  $F_V$  on treatment DRY.  $\text{N}_2\text{O}$  fluxes for DRY showed an annual average between  $0.04 \pm 0.04$  ( $B_{SV}$ ) and  $0.34 \pm 0.18 \mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$  ( $F_V$ ), with the highest contribution during summer months (Fig. 1C). Rewetting reduced annual average  $\text{N}_2\text{O}$  fluxes by 72 % ( $F_V$ ) to 97 ( $F_{\emptyset}$ ) % or even resulted in small net  $\text{N}_2\text{O}$  uptake ( $B_{SV}$ ), resulting in fluxes between  $-0.01 \pm 0.03$  ( $B_{SV}$ ) and  $0.10 \pm 0.06$  ( $F_V$ )  $\mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$ .

### 3.3. Annual balances and the GWP of soil respiration

Annual cumulative emissions from  $R_h$ , when accounting for all three gases, were for all DRY soils significantly dominated by  $\text{CO}_2$ , ranging

between  $11.4 \pm 0.8$  ( $B_{SV}$ ) and  $16.8 \pm 0.6$  ( $F_{SE}$ )  $\text{t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$  (Table 2). The contribution of  $\text{N}_2\text{O}$  to the GWP was below 0.01 % and hence negligible.  $\text{CH}_4$  contributed with  $0.8 \pm 0.5 \text{ t CO}_2 \text{ eq ha}^{-1} \text{ yr}^{-1}$  most to the cumulative annual emissions from  $B_{SV}$  while soils from  $B_{LV}$  and  $F_{\emptyset}$  were characterised by a minor uptake of  $\text{CH}_4$ . On average, drained bog sites emitted 13.7 % less  $\text{CO}_2 \text{ eq ha}^{-1} \text{ yr}^{-1}$  than fens (Table 3). Rewetting raised the share of  $\text{CH}_4$  to total emissions on all sites, thus contributing 3 % ( $B_{LV}$ ) – 30 % ( $B_{SV}$ ) of the overall GWP, while  $\text{CO}_2$  emissions were significantly ( $p < 0.001$ ) lowered by 3.3 ( $B_{SV}$ ) to 9.2 ( $F_{SE}$ )  $\text{t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ . The contribution of  $\text{N}_2\text{O}$  to the GWP was even lower under rewetted than drained conditions. When accounting for all three gases, annual cumulative emissions in  $\text{t CO}_2 \text{ eq ha}^{-1}$  on treatment DRY ranged from  $12.2 \pm 1.2$  ( $B_{SV}$ ) to  $16.9 \pm 0.6$  ( $F_{SE}$ ). Rewetting reduced the annual cumulative emissions of all soils by 6 % ( $B_{SV}$ ) to 48 % ( $F_{SE}$ ) to values ranging from  $8.7 \pm 1.1$  ( $F_{SE}$ ) to  $12.6 \pm 1.4$  ( $F_V$ )  $\text{t CO}_2 \text{ eq ha}^{-1} \text{ yr}^{-1}$ . However, there was no statistical difference in annual cumulative emissions between fen and bog peatlands on both treatments DRY and WET (Fig. 2). Nonetheless, significant reductions of cumulative emissions from  $R_h$  following rewetting were found for soils from  $B_{LV}$ ,  $F_{\emptyset}$  and  $F_{SE}$ , and also across fen peatlands (Table 4). Generally, we

**Table 2**

Average annual cumulative emissions of carbon dioxide ( $\text{CO}_2$ ), methane ( $\text{CH}_4$ ), nitrous oxide ( $\text{N}_2\text{O}$ ) as well as their summed global warming potential for a 100-year time horizon (GWP). All values in  $\text{t CO}_2 \text{ eq ha}^{-1} \text{ yr}^{-1}$  with a global warming potential conversion factor of 28 for  $\text{CH}_4$  and 265 for  $\text{N}_2\text{O}$ . Values are given for soil mesocosms from Lille Vildmose ( $B_{LV}$ ), Øby ( $F_{\emptyset}$ ), Selkær Enge ( $F_{SE}$ ), Store Vildmose ( $B_{SV}$ ) and Vejrumbro ( $F_V$ ) for each of the treatments: dry and bare (DRY) and wet and bare (WET). Standard error is reported in brackets. Letters indicate differences between means, where treatments with the same letter are not significantly different.

	DRY					WET				
	$B_{LV}$	$F_{\emptyset}$	$F_{SE}$	$B_{SV}$	$F_V$	$B_{LV}$	$F_{\emptyset}$	$F_{SE}$	$B_{SV}$	$F_V$
$\text{CO}_2$	15.13 ( $\pm 1.37$ )ab	14.07 ( $\pm 1.17$ )ab	16.82 ( $\pm 0.64$ )a	11.40 ( $\pm 0.75$ )b	15.22 ( $\pm 1.56$ )ab	9.16 ( $\pm 0.2$ )a	8.90 ( $\pm 0.45$ )a	7.65 ( $\pm 0.92$ )a	8.09 ( $\pm 1.09$ )a	10.77 ( $\pm 0.86$ )a
$\text{CH}_4$	-0.01 ( $\pm 0.03$ )a	-0.04 ( $\pm 0.03$ )a	0.03 ( $\pm 0.04$ )a	0.75 ( $\pm 0.47$ )a	0.08 ( $\pm 0.07$ )a	0.32 ( $\pm 0.22$ )a	0.64 ( $\pm 0.32$ )a	1.09 ( $\pm 0.73$ )a	3.40 ( $\pm 2.06$ )a	1.82 ( $\pm 0.52$ )a
$\text{N}_2\text{O}$	0.004 ( $\pm 0.001$ )a	0.005 ( $\pm 0.002$ )a	0.003 ( $\pm 0.001$ )a	0.001 ( $\pm 0.001$ )a	0.008 ( $\pm 0.003$ )a	<0.001 ( $\pm <0.001$ )ab	<0.001 ( $\pm <0.001$ )b	<0.001 ( $\pm <0.001$ )b	<0.001 ( $\pm <0.001$ )b	0.002 ( $\pm 0.001$ )a
GWP	15.13 ( $\pm 1.36$ )a	14.03 ( $\pm 1.15$ )a	16.85 ( $\pm 0.62$ )a	12.16 ( $\pm 1.15$ )a	15.31 ( $\pm 1.52$ )a	9.48 ( $\pm 0.31$ )a	9.54 ( $\pm 0.7$ )a	8.73 ( $\pm 1.14$ )a	11.49 ( $\pm 2.18$ )a	12.59 ( $\pm 1.37$ )a

**Table 3**

Average annual cumulative emissions of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), nitrous oxide (N<sub>2</sub>O) as well as their summed global warming potential for a 100-year time horizon (GWP). All values in t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup> with a global warming potential conversion factor of 28 for CH<sub>4</sub> and 265 for N<sub>2</sub>O. Values are given as means across sites per peatland type for each of the treatments: dry and bare (DRY) and wet and bare (WET). Standard error is reported in brackets. Letters indicate differences between means, where treatments with the same letter are not significantly different. The average reduction of cumulative emissions per gas from WET as compared to DRY is given as a negative (-) or positive (+) change in percentage, without variation.

	DRY		WET		Change (%)	
	Bog	Fen	Bog	Fen	Bog	Fen
CO <sub>2</sub>	13.27 (± 1.01) a	15.37 (± 0.71) a	8.62 (± 0.55) a	9.11 (± 0.56) a	- 35.04	- 40.73
CH <sub>4</sub>	0.37 (± 0.26) a	0.02 (± 0.03) a	1.86 (± 1.12) a	1.18 (± 0.32) a	+ 402.70	+ 5800
N <sub>2</sub> O	<0.001 (± < 0.001) a	0.001 (± < 0.001) a	<0.001 (± < 0.001) a	<0.001 (± < 0.001) a	0	0
GWP	13.64 (± 1.0) a	15.40 (± 0.7) a	10.49 (± 1.09) a	10.29 (± 0.76) a	- 23.09	- 33.18

observed high variations of GWP across replicates for the various sites and peatland types for both the DRY and WET treatments (Fig. 3A). The contribution of CO<sub>2</sub> to the within-site variation (Fig. 3B) was for both treatments more pronounced than the contribution from CH<sub>4</sub> (Fig. 3C).

### 3.4. The effect of site-specific soil properties and environmental variables on GHG fluxes

#### 3.4.1. Drained conditions

For both CO<sub>2</sub> and CH<sub>4</sub> fluxes, the GAM analysis showed that fluxes from treatment DRY, were well explained by peatland type ( $p < 0.001$ ) (Table A.2). Further, flux magnitudes were significantly ( $p < 0.001$ ) affected by the WHC, soil and air temperatures, and date. Soil specific predictor variables of high importance for CO<sub>2</sub> were pH ( $p < 0.001$ ), P ( $p < 0.01$ ), and to a lesser extent TN ( $p < 0.05$ ). The GAM was able to explain 92 % of the CO<sub>2</sub> variation, showing that the lowest CO<sub>2</sub> fluxes under drained conditions occurred from peatland sites where pH, P, TN and WHC were low (Fig. B.1). For CH<sub>4</sub>, the GAM detected that site-specific BD ( $p < 0.001$ ), K, TN and pH (all  $p < 0.01$ ) were important predictor variables for flux magnitudes. However, contrary to fluxes of CO<sub>2</sub>, the highest CH<sub>4</sub> fluxes occurred at sites with low pH but higher BD, high K, and high TN (Fig. B.2). Aside from pH, our findings also demonstrated such contrasting behaviour between drivers for CO<sub>2</sub> and CH<sub>4</sub> fluxes for the isotropic smooth interaction of soil and air temperatures. Here the GAM indicated that a rise in air temperature affected magnitudes of CO<sub>2</sub> emissions, while fluxes of CH<sub>4</sub> showed a higher dependency on soil temperatures (Figs. B.3, 4). Overall, the GAM

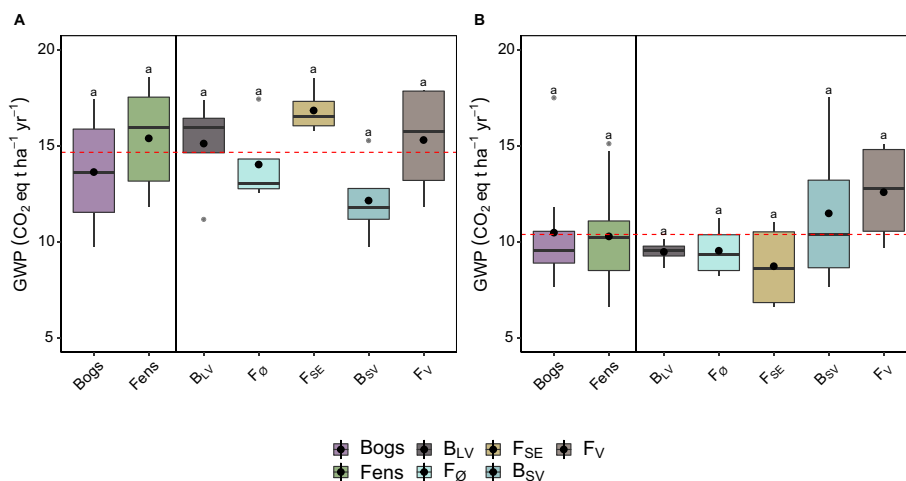
for CH<sub>4</sub> fluxes under drained conditions allowed us to detect non-linear trends with 83 % of the deviance explained.

#### 3.4.2. Rewetted conditions

Concerning fluxes of CO<sub>2</sub> for treatment WET, the GAM explained 78 % of the deviance (Table A.3). As also for DRY, the smooth predictor variables of temperature, date, WHC, as well as the parametric coefficients of peatland type, had a significant influence (all  $p < 0.001$ ) on flux magnitudes. In addition, CO<sub>2</sub> fluxes displayed a negative response with increasing pH ( $p < 0.001$ ), while fluxes increased with higher P contents ( $p < 0.001$ ) and lower WHC ( $p < 0.001$ ) (Fig. B.5). Regarding CH<sub>4</sub>, we were able to explain 75 % of the deviance, with bog peatland type, WHC, temperatures, date, and TN (all  $p < 0.001$ ), as well as pH ( $p < 0.05$ ) and TC ( $p < 0.01$ ) affecting emission magnitudes. The GAM analysis showed that high CH<sub>4</sub> fluxes under rewetted conditions occurred predominantly on soils with high contents of TC ( $p < 0.001$ ) but low TN ( $p < 0.001$ ), and low pH ( $p < 0.05$ ) (Fig. B.6). Also, for the WET treatments, the GAMs detected similar, though not as pronounced, contrasting responses of CO<sub>2</sub> and CH<sub>4</sub> fluxes to air and soil temperatures as under drained conditions (Figs. B.7, 8).

#### 3.4.3. Correlation of soil properties and annual cumulative emissions

The Pearson's correlation detected significant correlations between average soil properties at the depth of -5 cm to -25 cm and average annual GHG emissions from R<sub>h</sub> across the different peatland sites for treatments DRY and WET (Table A.4), with the majority of correlations between the various annual cumulative emissions and GWP. Annual CO<sub>2</sub> emissions



**Fig. 2.** Boxplot showing the global warming potential (GWP) in annual cumulative emissions (t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup>) for the study sites Lille Vildmose (BLV), Øby (FØ), Selkær Enge (FSE), Store Vildmose (BSV) and Vejrumbrø (FV), as well as across the peatland types bog and fen for the treatments DRY (panel A) and WET (panel B). Bold black dots represent the mean for each site, based on four replicates, while the interior line represents the median. The boxes bound the interquartile range (IQR) (25th to 75th quartile). The whiskers extend to 1.5 times the IQR, and their ends show the highest and lowest value excluding outliers, which are represented by dark grey dots. Red dashed lines indicate averages across all sites and letters indicate differences between means, where treatments with the same letter are not significantly different.

**Table 4**

Table showing significant differences of annual cumulative emissions of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), nitrous oxide (N<sub>2</sub>O) as well as their summed global warming potential for a 100-year time horizon (GWP) between the treatments dry and bare (DRY) and wet and bare (WET) for soil mesocosms from Lille Vildmose (B<sub>LV</sub>), Øby (F<sub>Ø</sub>), Selkær Enge (F<sub>SE</sub>), Store Vildmose (B<sub>SV</sub>) and Vejrumbro (F<sub>V</sub>) as well as per peatland type. Letters indicate differences between means, where treatments with the same letter are not significantly different.

	Bog		Fen		B <sub>LV</sub>		F <sub>Ø</sub>		F <sub>SE</sub>		B <sub>SV</sub>		F <sub>V</sub>	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
CO <sub>2</sub>	a	b	a	b	a	b	a	b	a	b	a	b	a	b
CH <sub>4</sub>	a	a	b	a	a	a	a	a	a	a	a	a	b	a
N <sub>2</sub> O	a	b	a	b	a	b	a	a	a	a	a	a	a	a
GWP	a	a	a	b	a	b	a	b	a	b	a	a	a	a

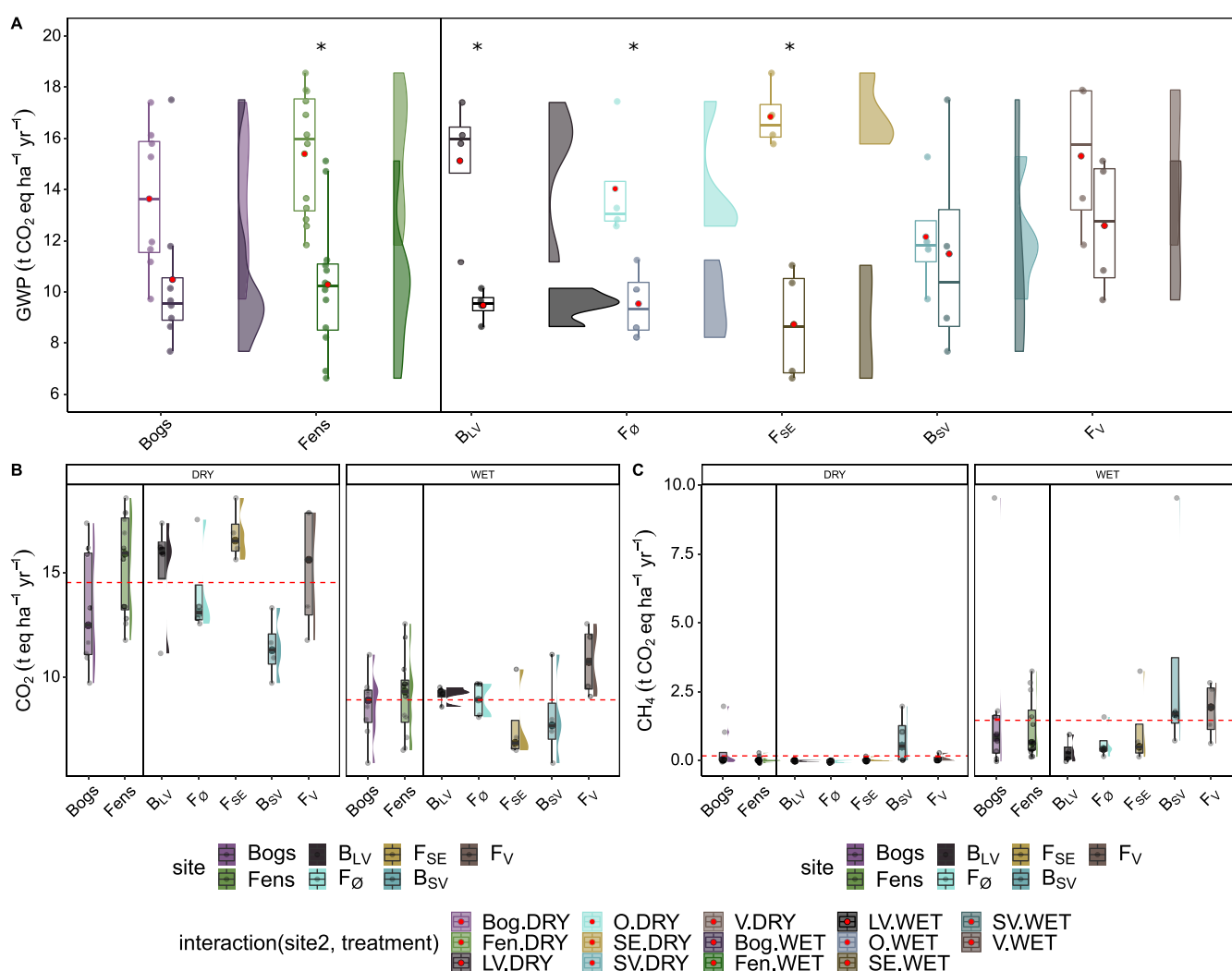
were for both treatments correlated with N<sub>2</sub>O. The GWP was highly correlated with all other annual cumulative values for the various gases on treatment WET, while no correlations were found for DRY. For CH<sub>4</sub>,

the only significant ( $p < 0.001$ ) relationship was found with the GWP on treatment WET.

Regarding correlations of GHG with average soil properties, we only found minor significant ( $p < 0.05$ ) correlations for DRY between CO<sub>2</sub> and the soil properties BD, Fe, and TC. The negative correlation between CO<sub>2</sub> and TC was also observed between GWP (DRY) and TC.

**4. Discussion**

The present study assessed differences in soil respiration for different Danish agriculturally used peatlands under drained (WTD, -40 cm) and rewetted (WTD, -5 cm) conditions, focusing on potential site-specific geochemical drivers for emissions resulting from R<sub>h</sub> and their effects on the GHG mitigation potential by rewetting. As expected, and widely known from previous research, CO<sub>2</sub> and CH<sub>4</sub> fluxes for both treatments were strongly affected by environmental factors, in particular ambient temperatures, as well as the soil-specific WHC. However, for both gases were not only those covariates, but, in



**Fig. 3.** Combined raincloud and boxplots showing the within and in-between site variation of annual cumulative greenhouse gas emissions, based on the individual contributions of CO<sub>2</sub> and CH<sub>4</sub> per replicate. Panel A): Vertical raincloud plot illustrating the data distribution (the “cloud”) with jittered raw data (the dots) from each replicate, and data statistics (the boxplots) for the study sites Lille Vildmose (B<sub>LV</sub>), Øby (F<sub>Ø</sub>), Selkær Enge (F<sub>SE</sub>), Store Vildmose (B<sub>SV</sub>) and Vejrumbro (F<sub>V</sub>), as well as across the peatland types bog and fen. Paler colours show the global warming potential (GWP) in annual cumulative emissions (t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup>) for treatment DRY, while darker colours show the GWP for treatment WET. Stars denote significant differences between treatments for the various sites. Panel B): Boxplot showing annual cumulative emissions of carbon dioxide (CO<sub>2</sub>) in t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup> for the various sites and types for treatment DRY and WET. Panel C): Boxplot showing annual cumulative emissions of methane (CH<sub>4</sub>) in t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup> for the various sites and types for treatment DRY and WET. In all boxplots on the panels, bold red or black dots represent the mean for each site, based on four replicates, while the interior line represents the median. The boxes bound the interquartile range (IQR) (25th to 75th quartile). The whiskers extend to 1.5 times the IQR, and their ends show the highest and lowest value excluding outliers, which are represented by colored (panel A) or dark grey (panels B and C) dots. Red dashed lines indicate averages across all sites.



particular, site-specific soil properties detected as critical by the GAM models.

#### 4.1. Emission reductions across sites were similar following rewetting

The spatial variability of GHG fluxes and annual cumulative emissions in drained and rewetted agricultural and natural peatlands is to a large extent controlled by environmental factors, such as temperature (Elsgaard et al., 2012), seasonal patterns of precipitation (Barel et al., 2021), vegetation communities (Couwenberg et al., 2011), and groundwater levels (Evans et al., 2021). However, most studies so far focused on assessing the controls on a site-specific GWP under drained and rewetted conditions, of either 1) net ecosystem exchange or net ecosystem carbon balance (e.g., Tiemeyer et al., 2020); 2) those of  $R_h$  but in differing climatic zones, such as the tropics (e.g., Hergoualch et al., 2017), or 3) with a focus on the effects of abiotic factors (e.g., Järveoja et al., 2020). Thus, a sound comparison of the site-specific values for  $R_h$  obtained in this study to those from other sites in similar climatic settings is difficult to perform, in particular regarding fen peatlands where emission factors from bare peat soil are scarce.

Nonetheless, one option is to examine reported emission factors for drained bog peatlands undergoing active peat extraction for e.g., horticulture. Both bogs assessed in our study have been subject to peat extraction for horticulture and fuel in the past, with activities ceasing last on  $B_{SV}$ . Hence, comparing the GWPs for these peatlands with the range of reported values for active peat extraction sites (4.0–16.0 t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup> (IPCC, 2014); 11.3 t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup> (Wilson et al., 2016); 2.6–5.0 t CO<sub>2</sub> ha<sup>-1</sup> yr<sup>-1</sup> (Shurpali et al., 2008)), showed that observed  $R_h$  was in the upper range, with the main contributor to the overall GWP being CO<sub>2</sub>. However, both bogs also have shown differences regarding their GHG emission potentials under drained and rewetted conditions. While  $B_{LV}$  was characterised by a GWP of  $15.1 \pm 1.3$  t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup> under drained conditions, which was significantly ( $p < 0.001$ ) reduced by 37 % following rewetting, were cumulative annual emissions from  $R_h$  for  $B_{SV}$  similar, independent of the soils water saturation. This discrepancy between the potential for emission reduction might be found in their site-specific record regarding duration and, therefore, depth of peat extraction, affecting the intrinsic recalcitrance of the peat substrate (Kleber, 2010) which also has been recently highlighted by Clark et al. (2023).

Nonetheless, our study under equal environmental conditions, and controlled WTDs for all soil sites, only showed significant differences of flux magnitudes and annual cumulative CO<sub>2</sub> emissions between  $F_{SE}$  and  $B_{SV}$ . Beyond that, emission magnitudes and budgets from  $R_h$ , were similar across sites, peatland types, and stages of water saturation. Further, although original vegetation, including top-soil roots, has been removed for the mesocosms in this study, decomposing fine roots in the deeper soil layers were likely to have caused the partially high CO<sub>2</sub> emissions in the drained state (Iversen et al., 2018; Dezzeeo et al., 2021).

However, while the contribution of CO<sub>2</sub> from WET to the annual GWP was similar across sites, we observed considerable differences regarding CH<sub>4</sub> emissions from  $R_h$ , ranging from 0.3 ( $B_{LV}$ ) to 3.4 ( $B_{SV}$ ) t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup>. In fact, from  $B_{LV}$  and  $F_0$  they even were as low as CH<sub>4</sub> emissions reported following topsoil removal and sphagnum introduction (Huth et al., 2020), both associated with low CH<sub>4</sub> emissions (Larmola et al., 2010). In our study, the removal of the upper, by roots foliated, topsoil layer might contribute with a causation to the low observed CH<sub>4</sub> fluxes at high WTD. In addition, years of drainage or peat extraction might contribute to a potential lag-time effect regarding the potential for CH<sub>4</sub> recovery as seen on the example of  $B_{SV}$ , expressing the potential for methanogenic activity at the end of the study period and following heavy rainfall events. Nonetheless, differences and irregularities of CH<sub>4</sub> emissions for drained and rewetted peatlands have already been reported elsewhere (e.g., Vybornova et al., 2019), thus highlighting the importance of peat substrate quality for the determination of soil related GHG mitigation potentials.

Nonetheless, contrary to most other studies, we were able to measure GHG emissions from  $R_h$  at permanently controlled WTD levels, thereby

being independent from environmental fluctuations, usually significantly affecting fluxes in natural ecosystems and agroecosystems (Evans et al., 2021). Further, due to our study set-up, the soil mesocosms were equally exposed to ambient temperatures, known to affect CH<sub>4</sub> production and oxidation potentials (Zhang et al., 2021). Being able to eliminate these critical factors for site-specific differences in emission magnitudes, the question regarding a causation for observed differences in CH<sub>4</sub> emissions, both between and within sites, remains, though the divergent nature of CH<sub>4</sub> fluxes in wetlands is commonly acknowledged (Knox et al., 2019). We observed this strong variability also across replicates for the various sites and peatland types for both, the DRY and WET treatments, confirming the transient and divergent nature of methane even on micro-spatial scale.

Across peat soil types, the average emission reduction of 4.1 t CO<sub>2</sub>eq ha<sup>-1</sup> yr<sup>-1</sup> following rewetting is lower than usually reported values for whole-ecosystem fluxes (e.g., Höper et al., 2008), highlighting the importance of vegetation for belowground C accumulation and therewith GHG mitigation. However, even small differences in mean WTD (Moore and Dalva, 1993) in correlation with inter-annual variability in weather conditions (Aslan-Sungur et al., 2016; Mikhaylov et al., 2019), differing vegetation cover (Couwenberg et al., 2011), and time since rewetting (Wilson et al., 2016) pose difficulties for robust comparisons between different studies, in particular those covering larger WTD intervals. A large number of previous studies, though mainly on vegetated peatland ecosystems, are in line with our observation: although rewetting did not lead to a re-establishment of a carbon-sink function, the ecosystems were clearly characterised by significant emission reductions as compared to the state prior to rewetting (e.g. Strack and Zuback, 2013; Günther et al., 2015; Renou-Wilson et al., 2016; Franz et al., 2016).

Although the presented results have restricted validity in the context of ecosystem-scale emission magnitudes, our study design allowed to accurately compare flux magnitudes from  $R_h$  for different Danish peatland sites in the year following rewetting. Here we were able to demonstrate a GHG reduction efficiency of -33 % for fen peatlands and -23 % for bogs. Interestingly, independent of the average emission magnitudes for the drained state, the emission factors for all sites were within a similar range when rewetted.

Due to the lack of plants in this study and the associated lack of C allocation to belowground biomass parts, naturally, no CO<sub>2</sub> sink function was re-established following rewetting. At the same time though, the lack of aerenchymatous plants on the rewetted mesocosms might partly explain the low observed CH<sub>4</sub> emissions, since vegetation can form a major pathway for methane emissions due to plant-mediated CH<sub>4</sub> transport, allowing methane to bypass the oxidative zone in unsaturated peat substrate (van den Berg et al., 2020). In addition, Galand et al. (2005) has highlighted the importance of peatland-vegetation for the supply of substrate, like acetate, for methanogenesis. On the other hand, *Sphagnum* peat mosses are linked to methanotrophy and CH<sub>4</sub> reduction on fully-saturated peatlands (Kox et al., 2021). Considering this, there is a high potential that the sites assessed in this study might show differing magnitudes of GHG under rewetting in an ecosystem-setting including the presence of typical wetland vegetation (e.g., *Typha* spp., *Phragmites* spp., *Sphagnum* spp.) in restoration or paludiculture practices.

#### 4.2. Soil nutrient stocks and acidity explain part of the variation in emissions

The large differences observed between annual CO<sub>2</sub> and CH<sub>4</sub> emissions between sites, but also for the replicates per site, might be linked to differences regarding their drainage and land-use history, consequently affecting peat substrate quality also on a micro-scale. This was pronounced for the assessed bog sites, where sphagnum moss plant litter was the main peat building compound, where differences between replicates also have been observed regarding the von Post scale. Knowing that plant litter quality affects magnitudes of GHG emissions (Kreyling et al., 2021), numerous studies have demonstrated the high recalcitrance of sphagnum mosses and sphagnum peat (Hobbie et al., 2000; Straková et al., 2011; Kasimir et al., 2021) which are structurally more complex and hence require higher



energy demands of decomposing microorganisms (Sjögersten et al., 2016). We hence hypothesise that the biochemistry of plant litter might explain differences in soil respiration for  $B_{SV}$  and  $B_{LV}$  in the drained and rewetted treatments.

In our study, we focused on simple geochemical indicators for correlations with emissions. Our findings highlighted that, for  $CO_2$ , in particular the nutrient contents of P, N, and K, frequently applied to agriculturally managed peatlands by fertilisation, and as indirectly enriched as a result of peat oxidation, as well as the soil pH, frequently affected as a result of liming, were main variables of significance. Our results show, that, for drained soils, an increase in pH above 5.5 is accompanied by an increase in  $CO_2$  emission magnitudes, regardless of nutrient availability, which is in line with a study by Urbanová and Bárta (2020), highlighting the correlation of peat acidity and low emissions. However, under wet conditions we observed a contrary pattern, where a higher pH was correlated with lower fluxes of  $R_h$ . This is contrary to findings by Ye et al. (2012) who found an increase in  $CO_2$  production with increasing pH also under anaerobic conditions. However, for our sites, P availability played a major role, with pH controlling the P utilisation efficiency (Luo et al., 2021), implying that with increasing pH a higher P content is required to increase respiration activity. A similar statement has been made by Ye et al. (2012), where respiratory activity was inhibited in correlation with humic substances besides pH. The overall importance of nutrients for SOM decomposition, and hence respiration rates, has been highlighted in previous studies on bog peatlands (e.g. Larmola et al., 2013; Pinsonneault et al., 2016) and numerous studies found an increase in soil respiration with higher P availability (e.g. Brake et al., 1999; Säurich et al., 2019). For TN content, we did not find clear correlations to  $CO_2$  emissions on neither the drained nor the rewetted peatlands. In this context, we assign the slightly significant ( $p < 0.05$ ) effect of TN on respiration rates from the drained treatment, as detected by the GAM analysis, to the general difference of emission magnitudes for the distinction between nutrient rich fen peatlands, and the nutrient poorer bogs.

In recent research (e.g., Knorr et al., 2009; Deng et al., 2017; de Jong et al., 2020), a variety of inhibitory effects were highlighted to potentially affect methanogenesis, mainly the presence of alternative electron acceptors (e.g. nitrate, ferric iron, sulfate), which are thermodynamically favoured in anaerobic respiration (Zhang et al., 2021). For instance, for  $B_{LV}$ , we observed the lowest annual  $CH_4$  emissions of all sites, accounting for only  $0.2 \text{ t } CO_2eq \text{ ha}^{-1} \text{ yr}^{-1}$ . Particular for  $B_{LV}$ , as compared to  $B_{SV}$ , is a higher content of Fe in the top 25 cm of the soil column, potentially indicating the presence of Fe(III) as a preferred electron acceptor, inhibiting optimal methanogenic conditions. Van Diggelen et al. (2020) highlighted that rewetting of formerly drained coastal wetlands, such as  $B_{LV}$ , will lead to enhanced sulfate and ferric oxyhydroxide reduction rates, the latter historically known to be found on  $B_{LV}$  as “bog ore”, initially lowering  $CH_4$  production. Further, bulk density, a soil property previously negatively correlated with methane production (Putkinen et al., 2018), was in the top 25 cm, with on average  $0.13 \text{ g cm}^{-3}$ , twice as high as compared to  $B_{SV}$ .

We found the highest overall GHG reductions following rewetting of soil from  $F_{SE}$  with an average reduction rate of  $8.1 \text{ t } CO_2eq \text{ ha}^{-1} \text{ yr}^{-1}$ .  $F_{SE}$  is characterised with the highest pH of all assessed sites as well as with the highest content of S in soil. In addition, as observed for all three fen peatlands, high amounts of Fe were prevailing on these sites. Interestingly, we found that higher GHG reductions, based on the mitigation of  $CO_2$  emissions, were obtained on sites rich in Fe, while we assume that the high contents of S might have indicated the availability of  $SO_4^{2-}$  and therewith the potential for inhibited  $CH_4$  production (Van Diggelen et al., 2020; de Jong et al., 2020) on  $F_{SE}$  and  $F_0$  under anaerobic conditions. However, there is no consensus yet on whether iron availability in soils is correlated with GHG mitigation potentials. For instance, Chen et al. (2020), though in a study on subtropical agricultural Ultisol soils under fluctuating redox conditions, found that Fe-addition under anoxic conditions increased SOM mineralisation, and consequently  $CO_2$  emissions. Contrary to that, Hall et al. (2016) reported a significantly decreased mineralisation of lignin methoxyl derived carbon following Fe addition, which is in line with the

results by Wen et al. (2019), highlighting the role of iron in protecting peat soil organic carbon from mineralisation. However, in our study we did not assess how the iron redox cycle between the ferric and ferrous state was affected by time since rewetting. Emsens et al. (2016) proposed a higher effectiveness of rewetting for Fe-poor fen peatlands, due to lower decomposition rates of organic matter, related to anaerobic iron reduction. However, since P, found as positively affecting GHG emissions in our study, but also S, can be bound to Fe-compounds (Smolders et al., 2006; Geurts et al., 2008; Zak et al., 2010), we hypothesise that a potential trade-off between iron-reduction induced  $CO_2$  emissions from previously stabilised SOM and iron-prevented mobilisation of P, lowering  $CO_2$  emissions, was balanced on our assessed fens. Nonetheless, an assessment of the potential influence of alternative electron acceptors on emissions of  $CH_4$  and  $CO_2$  was beyond the scope of this study, focussing on simple geochemical variables, and the hypotheses regarding inhibitory effects need to be confirmed in future studies.

#### 4.3. Implications for future management of agricultural peatlands

Peatland rewetting measures for climate and biodiversity considerations are a hot topic on global, regional, and national scales. However, cost-related hurdles for implementation (Artz et al., 2018) and the question of landownership and technical feasibility are likely to hamper current visions of meeting the climate components of legally binding international treaties by peatland rewetting. In addition, uncertainties regarding the effect of rewetting degraded peatlands on GHG balances remain.

Hence, in order to maximise the mitigation efficiency of adverse land-atmosphere carbon exchange from agriculturally used peatlands, it is critical to focus rewetting initiatives not only on areas with ideal hydrological infrastructure (Grygoruk et al., 2015; Stachowicz et al., 2022) but also on “hotspot” areas with the highest expected mitigation potential as affected by soil properties. In this context, our results present both an opportunity and a challenge. Across sites and peatland types, we were able to demonstrate a GHG reduction from heterotrophic soil respiration of approximately 28 % following rewetting, not taking biomass C budgets into account. On the other hand, independent on the initial cumulative GHG emissions in the drained state, all sites had a similar GWP following rewetting of between  $8.7$  and  $12.6 \text{ t } CO_2eq \text{ ha}^{-1} \text{ yr}^{-1}$ .

Across peat soil types, we found that the mitigation potential of  $CO_2$  by rewetting was highest on sites that are rich in nutrients, iron and sulphur, in particular, if characterised by a near-neutral pH as well as a higher state of peat degradation. Thus, we found a higher GHG mitigation efficiency for the assessed fen peatlands. However, more similarly controlled studies on a larger variety of peatland sites are needed to make more robust predictions regarding the site-specific drivers for GHG emissions from soil respiration and their mitigation potential by rewetting. These studies will hopefully be able to further define how contents of soil nutrients, iron, sulphur, and peat acidity, as our study indicated, can be used as robust proxies for GHG mitigation efficiencies.

## 5. Conclusion

In our study, we focused on simple geochemical indicators for correlations with emission magnitudes. Our findings highlighted that, for  $CO_2$ , in particular the nutrient contents of P, N, and to a lesser extent K, frequently applied on agriculturally managed peatlands by fertilisation, as well as the soil pH were main variables of significance. In conclusion, overall and equal for drained and rewetted treatments, the annual cumulative GWP of the carbon-rich sites were controlled by  $CO_2$  emissions, with  $CH_4$  having a variable, but minor contribution and  $N_2O$  emissions being negligible. Across peat soil types, we found an indication that nutrient status, peat acidity, as well as contents of iron and sulphur, indicating the potential availability of electron acceptors, might be used as proxies for the GHG mitigation efficiency by peatland rewetting. Thus, we found an indication for prioritising drained fen peatlands for rewetting measures if quick emission reductions are required in the context of the Paris Agreement. However, more solid

quantification of the expected effects, in particular when considering whole-ecosystem emission dynamics, will require more data from a larger representation of site-specific peatland biogeochemistry.

### CRedit authorship contribution statement

CN developed and performed the study design and experimental work, the analysis of the data, and the writing of the manuscript. All authors contributed to the study design and the writing and reading of the manuscript and approved the final manuscript.

### Data availability

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

### Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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### Appendix A. Supplementary data

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