Ecosystem respiration, methane and nitrous oxide fluxes from ecotopes in a rewetted extracted peatland in Sweden

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SUMMARY

Ecosystem respiration (carbon dioxide; CO_2), methane (CH_4) and nitrous oxide (N_2O) fluxes to the atmosphere were determined using an opaque closed chamber method within various ecotopes (vegetation covered, bare peat and open water) in a rewetted extracted peatland and within an adjacent open poor fen in Sweden. Ecotopes had a significant impact on CO_2 and CH_4 fluxes to the atmosphere. Ecosystem respiration and CH_4 emissions from the bare peat site, the constructed shallow lake and the open poor fen were low but were much higher from ecotopes with *Eriophorum vaginatum* tussocks and *Eriophorum angustifolium*. A combination of vascular plant cover and high soil temperatures enhanced ecosystem respiration, while a combination of vascular plant cover, high water table levels and high soil temperatures enhanced CH_4 emissions. N_2O emissions contributed little to total greenhouse gas (GHG) fluxes from the soil-plant-water systems to the atmosphere. However, the overall climate impact of CH_4 emissions from the study area did not exceed the impact of soil and plant respiration. With regard to management of extracted peatlands, the construction of a nutrient-poor shallow lake showed great potential for lowering GHG fluxes to the atmosphere.

KEY WORDS: carbon dioxide, constructed water body, greenhouse gases, mire restoration, wetland

INTRODUCTION

When peatlands are drained, e.g. for peat extraction, peat accumulation is terminated and the peat body suffers structural damage (Zeitz & Velty 2002). Simultaneously, drained peatlands are major sources of carbon dioxide (CO_2) and nitrous oxide (N_2O) (Joosten & Clarke 2002, Strack 2008, Berglund *et al.* 2010). Methane (CH_4) emissions are reduced after drainage but may remain high from drainage ditches (Minkkinen *et al.* 2008, IPCC 2014).

Peat extraction for horticulture and combustion has a long tradition in northern Europe and typically takes place at a peatland over a 20-year period, but often even longer. After peat extraction, two types of peatlands can be distinguished: cut-away peatlands, where the peat has been almost completely removed; and cutover peatlands, where a slightly thicker peat layer has been left (Rydin & Jeglum 2006). When peat extraction ceases, one of several post-use alternatives of the area is rewetting (Quinty & Rochefort 1997, 2003; Blankenburg & Tonnis 2004).

Restoration of peatlands after peat extraction has been a global issue for more than 20 years (Vasander *et al.* 2003, Strack 2008). Rewetting, i.e. raising of the water table, is one restoration objective (IPCC 2014) in order to mitigate climate change, water pollution and loss of biodiversity. Rewetting transforms an extracted peatland with aerobic soil conditions to a wetland in which anaerobic conditions prevail, and thus can create suitable conditions for peat-forming plants which could return carbon (C) storage functions and biodiversity (Joosten & Clarke 2002, Rochefort *et al.* 2003, Strack & Zuback 2013). However, there is a need for long-term monitoring of this process (Couwenberg *et al.* 2011, Wilson *et al.* 2016b). Most of the greenhouse gas (GHG) studies conducted to date include only one or two vegetation periods and thus do not adequately capture GHG fluxes to the atmosphere during the transition process from the cessation of peat extraction to the decades after rewetting when hydrology and vegetation are more established (Maljanen *et al.* 2010, Beetz *et al.* 2013, Beyer & Höper 2015).

The changes in soil water conditions and thus soil chemistry and vegetation development after rewetting affect the GHG balance. In general, peatland restoration by rewetting decreases CO_2 and N_2O fluxes to the atmosphere, while CH_4 fluxes to the atmosphere may increase (e.g. Couwenberg 2009, Höper 2015, Wilson *et al.* 2016a). Some studies show that nutrient-poor peatlands could turn into GHG net sinks, but that nutrient-rich peatlands could still be net GHG emitters (Silvan *et al.* 2005, Glatzel *et al.*

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2008, Höper *et al*. 2008), which means that rewetting will not necessarily result in lower GHG fluxes to the atmosphere (Joosten & Clarke 2002).

Numerous studies have characterised GHG fluxes from various peatland types in the Nordic countries, but only a few consider CO_2, CH_4 and N_2O at the same time (Maljanen *et al*. 2010). However, to assess the overall climate impact, it is important to consider all three gases. For rewetted peat extraction areas there have been some well-documented investigations (e.g. Tuittila *et al*. 2000, Wilson *et al*. 2013, Strack *et al*. 2016), but research on GHG fluxes from different ecotopes (e.g. constructed lakes, bare peat and vegetated shore and littoral zones) in rewetted peatlands is still limited overall. Therefore, the aims of this study were to:

- quantify CO_2, CH_4 (including ebullition) and N_2O fluxes to the atmosphere in various ecotopes, such as vegetation-covered, bare peat and open water, within a rewetted extracted peatland;
- compare these fluxes to the atmosphere against those from a nearby open poor fen not subject to peat extraction; and
- investigate the influence of soil temperature and soil water conditions on gas fluxes from the various ecotopes.

Monitoring was conducted to obtain multi-year data on CO_2, CH_4 and N_2O fluxes from ecotopes in a rewetted peatland after peat extraction, but not to prepare annual GHG budgets. The study was carried out in sub-boreal central Sweden and was part of the long-term project *"Restoration of terminated peat cuttings by rewetting"* (Jordan *et al*. 2009, Kozlov *et al*. 2016, Lundin *et al*. 2016).

METHODS

Site description

This study was carried out at the Porla peatland (place name: Porlamossen), which includes a rewetted extracted section and an open nutrient-poor fen (59° 01' N, 14° 38' E; 74.1 ha, 85 m above sea level), in Laxå municipality, 50 km south-west of Örebro city, Sweden (Figure 1a). The climate is semi-humid and maritime (Köppen 1936), with a mean annual temperature (1961–1990; Raab & Vedin 1995) of 5.7 °C and a growing season length (temperature > 5 °C for four days; Odin *et al*. 1983) of 200 days. Precipitation is 690 mm yr^{-1} (1961–1990; Raab & Vedin 1995). During the years after rewetting (2000–2013), precipitation was 9 % higher and air temperature was 0.7 °C warmer (4 × 4 km gridded data; SMHI 2014) than the regional 30-year average (1961–1990).

Block peat extraction started in 1889 and continued until 1958. A second era of milled peat extraction (mean annual volume of 30,000 m^3) started in 1980 and ended in 1999. A section of the extracted area was prepared for rewetting in 1999. The outlet from this section was closed and a device (outlet monk) was installed to control the water level. In this rewetted section, the thickness of the remaining peat on the underlying moraine (sandy-silty till) at that time varied between 0 and 2 m and mostly comprised *Carex*/*Eriophorum* peat, but also *Sphagnum* peat in the top horizons where peat thickness was greater. The degree of peat decomposition (H; von Post 1924) was H4–6 for the *Carex*/*Eriophorum* peat and H3–5 for the *Sphagnum* peat. Rewetting established two shallow lakes (5 and 12 ha, respectively) with a maximum water depth of 1.5 m. The Porla study site (Figure 1b) covers the southern part of the rewetted section, including the 12 ha lake, and the remaining open poor fen. The general downward slope of the study area is in a northward direction and the poor fen slopes towards the lake. The poor fen was not disturbed by peat extraction but subsidence cracks are still visible approximately 20 m from the edge at the northern margins. The studied poor fen ecotope sub-area ("mire") was located approximately 100 m further south and was unaffected by drainage.

During the fifteen years of rewetting, *Sphagnum* spp. cover has started to establish on the loose peat shores of the lake. Simultaneously, *Eriophorum angustifolium* has vanished from the nutrient-poor parts but has expanded in the more nutrient-rich parts (formed by blocked drainage ditches).

Investigation of ecotopes

Seven ecotopes with typical wetland and peatland characteristics (Table 1) were selected for the present study. Within each of the ecotopes, sub-areas were chosen for investigation (Figure 1b). Boardwalks were installed in 2008 to prevent disturbance to the peat from trampling. A total of 45 flux measurement positions were established in the seven sub-areas. CO_2, CH_4 and N_2O fluxes to the atmosphere were measured on ten occasions during daytime in the snow-free period (April–October) from 2009 to 2012. On every measurement occasion, soil or water temperature at 10 cm depth was determined adjacent to each GHG flux measurement position. Concomitantly, soil water conditions were classed into one of four categories; dry, wet, saturated and inundated (field estimation according to Ad-hoc-Arbeitsgruppe Boden 2005). Soil sampling to determine soil characteristics (Table 2) was carried

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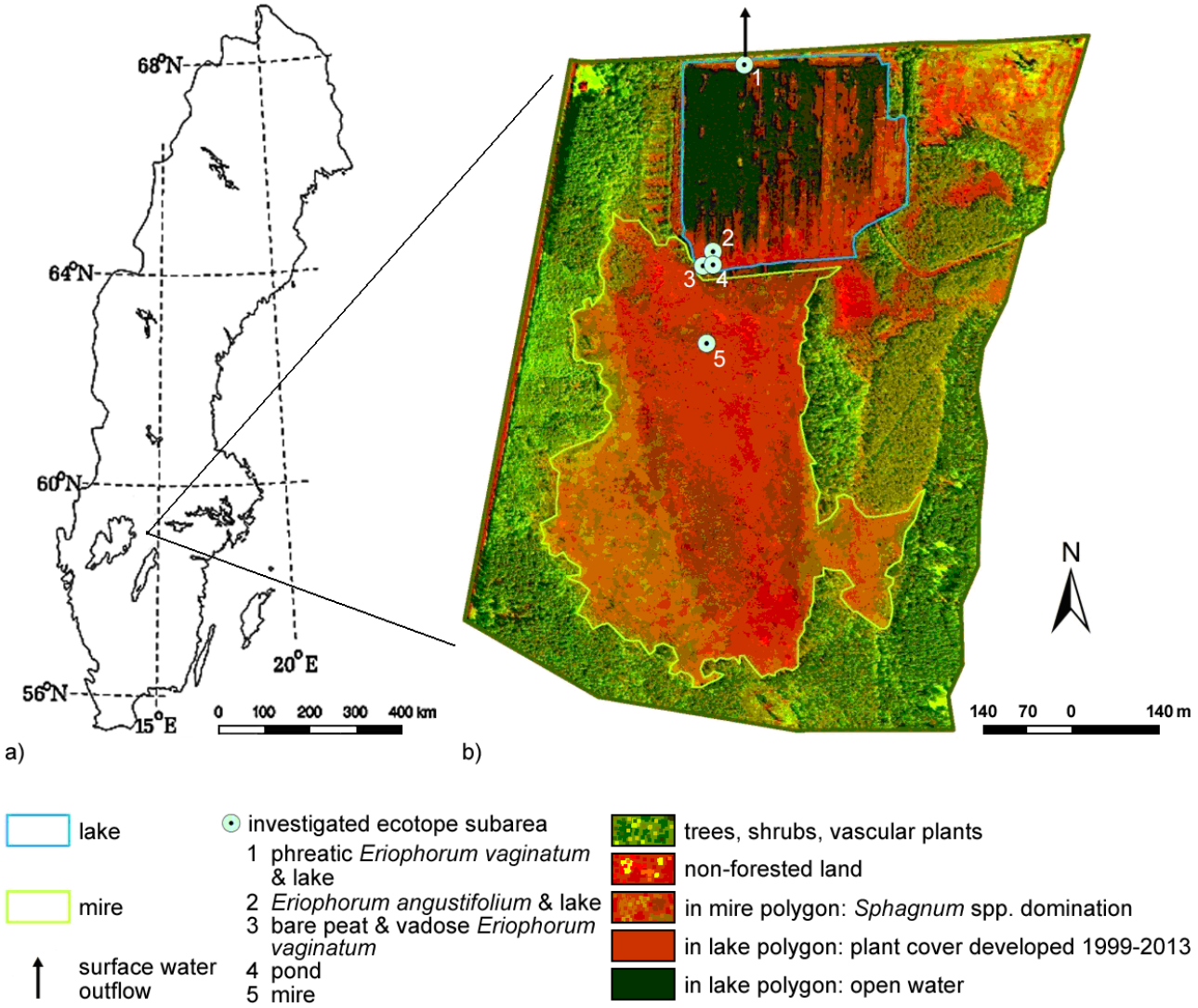

Figure 1. a) Map of Sweden showing the location of the Porla peatland; b) visualised Principal Component Analysis (PCA) layer of orthophoto (Lantmäteriet 2013) over the Porla study site, created as a RGB raster composite with red and green channels of Band 1 and Band 2 (PCA tool in ArcMap 10.2.1).

out horizon-wise in October 2009, 2011 and 2012. The pH values were determined from 2 g dry peat in 25 ml deionised water. Total C and total nitrogen (N) were quantified by dry combustion in a C/N analyser (CN2000, Leco, USA) according to ISO 10694 and ISO 13878. Surface water samples were collected at monthly intervals from 2009 to 2012 from the outflow of the lake (Figure 1b) for determination of pH, electrical conductivity, dissolved organic carbon (DOC) and total C according to EN 1484, EN 27888 and ISO 10523.

Measurement of GHG fluxes

The CO_2, CH_4 and N_2O measurements were made using the opaque closed chamber method (Parkin & Venterea 2010, Pumpanen *et al.* 2010) and, as such, only ecosystem respiration was measured for CO_2. For gas sampling on peat and *Sphagnum* spp., permanent round PVC frames (inner base diameter 18.7 cm) were installed at each GHG flux measurement position. To avoid lateral gas exchange in the soil, the insertion depth of the frames varied due to different soil water conditions (cf. Hutchinson & Livingston 2001, Davidson *et al.* 2002). In the mire, *Sphagnum* did not overgrow the frames during the 3½ years of chamber measurements. However, some of the *Eriophorum vaginatum* ecotope measurement positions were moved in 2011 because the tussocks had overgrown the frames.

For gas flux measurements, a non-steady-state flow-through opaque respiration chamber was attached to the frame and sealed with a rubber gasket. The chamber was made of PVC with 18.7 cm inner base diameter and 16 cm height and had an effective

Table 1. Descriptions of the seven ecotopes investigated.

Ecotopes	Description	Soil water conditions	Mean annual water table depth	Number of GHG flux measurement positions
Mire	Open poor fen subdivided into hollows, lawns and hummocks; covered by *Sphagnum* spp.; not subject to peat extraction.	Saturated to inundated	~ 0 cm	9
Vadose *Eriophorum vaginatum*	*Eriophorum vaginatum* tussocks on bare peat surfaces at the lake's southern shore.	Drained topsoil surface, often wet or saturated	~ 40 cm	8
Bare peat	Bare peat inter-tussocks at the lake's southern shore.			8
Phreatic *Eriophorum vaginatum*	*Eriophorum vaginatum* tussocks on water-saturated peat with mud overlay at the lake's northern shore.	Saturated to inundated	~ 0 cm	8
Eriophorum angustifolium	*Eriophorum angustifolium* on water-saturated peat at the lake's southern littoral zone; often with floating peat.	Saturated to inundated	~ 0 cm	8
Pond	Open water between mire and lake; established before rewetting (Lode 2001).	Inundated	---	2
Lake	Constructed lake; open water; often floating peat carpets occur; maximum depth 1.5 m.	Inundated	---	2

chamber air volume of 4.3 L. Air samples were taken in crossflow through the chamber headspace with polysiloxane tubing. Frame air volume was determined on each GHG measurement occasion to obtain the headspace air volume (sum of chamber and frame air volumes) by measuring the height of the headspace in the frame at five evenly spaced points inside each frame with a folding ruler and a level; calculating the average height $\bar{h}$ and finally computing the headspace air volume of each frame as $\pi r^2 \bar{h}$, r being the frame radius. Measurement of the headspace air volume in frames with *Eriophorum vaginatum* tussocks was done by placing the folding ruler vertically into the tussock (cf. Mahmood & Strack 2011). A chamber installed in the centre of a life buoy (i.e. floating chamber), identical in dimensions and with an effective headspace air volume of 3.0 L, was used for GHG measurements on open water.

The CO_2 concentration in the headspace air was determined using a portable infra-red gas analyser (GMP343 and MI70, Vaisala, Finland) connected to the chamber. The analyser was calibrated by the manufacturer in 2007, 2010 and 2012 and was occasionally checked with CO_2 standards (AGA, Sweden) of 298 mol-ppm (± 2 %) and 599 mol-ppm (± 2 %). An external membrane pump (flow rate 0.4 L min^{-1}) circulated the air between the chamber headspace and the CO_2 probe during the 4.5 minutes of chamber closure. CO_2 concentration values were stored every 30 seconds (October 2011: 15 seconds) as the mean of the previous 10 seconds.

For measurements of CH_4 and N_2O concentration in the chamber headspace, 20 ml air samples were collected in septum bottles (glass vials with 20 mm/3.0 mm butyl-PTFE septum in aluminium seal cap, Scantec Nordic, Sweden) at 10, 20, 30, 40 and 50 minutes after chamber closure (April 2009 to May 2012) or 10, 20 and 30 minutes after chamber closure (June to October 2012). Air was circulated with an external membrane pump (volume flow rate 0.4 L min^{-1}) between the chamber and vial over 20 seconds (7 air exchanges in the vial). The CH_4 and N_2O samples were stored in the dark at room

Table 2. Ecotopes (excluding pond) with main soil characteristics at different profile depths. H = degree of peat decomposition according to von Post (1924).

Ecotope	Peat type	Degree of peat decomposition	Median bulk density in g cm^{-3} (min.–max.)	Median peat pH (min.–max.)	Median C/N ratio (min.–max.)	Additional plants
Mire	*Sphagnum* spp.	0–10 cm: recent *Sphagnum* 10–23 cm: H 2 23–32 cm: H 3–4 32–50 cm: H 2	0–7 cm: 0.02 (0.02–0.03) 10–22 cm: 0.05 (0.04–0.05)	4.1 (4.0–4.1)	0–10 cm: 93 (68–121) 10–20 cm: 39 (32–45)	Dry parts and hummocks: *Sphagnum fuscum*; hollows: mats of *Sphagnum angustifolium*, *Rhynchospora alba*, *Andromeda polifolia*, *Drosera anglica*, *Drosera intermedia*.
Vadose *Eriophorum vaginatum*	*Sphagnum* spp. / *Eriophorum* spp.	0–5 cm: H 5–6 5–17 cm: H 4 17–24 cm: H 3 24–70 cm: H 2	0–5 cm: 0.12 (0.09–0.15) 17–24 cm: 0.12 (0.09–0.17) 30–42 cm: 0.11 (0.08–0.13)	3.7 (3.5–3.7)	0–20 cm: 60 (43–88) 20–70 cm: 101 (77–114)	Some small *Betula pubescens*, *Pinus sylvestris* and *Erica tetralix*.
Bare peat						
Phreatic *Eriophorum vaginatum*	*Carex* spp.	0–6 cm: H 6–7 6–24 cm: H 3	0–20 cm: 0.09 (0.06–0.12)	4.0 (3.9–4.0)	0–21 cm: 40 (38–43)	Some small *Betula pubescens*, *Pinus sylvestris* and *Drosera intermedia*.
Eriophorum angustifolium	*Carex* spp. / *Sphagnum* spp.	Often floating peat (H 6–7) on fluctuating water table -17 cm to 0 cm: water 0–11 cm: H 6–7 11–24 cm: H 7 24–43 cm: H 8	0–19 cm: 0.12 (0.11–0.13)	4.2 (4.2–4.3)	0–16 cm: 36 (---)	---
Lake (bottom peat in littoral zone)	*Carex* spp.	H 3–6	---	4.4 (4.2–4.7)	---	---

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temperature (storage conditions determined in leakage tests by the authors) and analysed between one day and two weeks after sampling with a gas chromatograph (Clarus 500, Perkin Elmer, USA) equipped with a flame ionisation detector, an electron capture detector and an automatic vial headspace injector (Turbo Matrix 110, Perkin Elmer, USA). CH_4 standards of 2, 10, 20 and 350 mol-ppm and N_2O standards of 0.3, 1.7 and 4.7 mol-ppm (AGA, Sweden) were used for calibration. Separate calibration functions were established for concentrations below and above 20 mol-ppm CH_4.

GHG flux estimation and evaluation

CO_2, CH_4 and N_2O fluxes were estimated according to $F = f'(t_0) \cdot p \cdot V / (A \cdot R \cdot T)$, where F is the molar flux to the atmosphere. The first functional derivative $f'(t_0)$ at the moment of chamber closure t_0 is estimated from the regression function $f(t) = y_{gas}(t)$ of the change in concentration y_{gas} in headspace air over time t and given as concentration per unit time; p is the atmospheric pressure, V the headspace air volume, A the chamber base area, R the molar gas constant and T the sample air temperature (measured during CO_2 sampling only).

If the range of y_{gas} during chamber closure was less than two-fold larger than the gas analyser's repeatability (CO_2: ± 2 ppm) or 95 % confidence interval (CH_4: ± 5 % of the range's mean, N_2O: ± 0.12 ppm), or if the y_{gas} time series failed the *von Neumann* trend test (Doerffel 1990; $P \geq 95$ %; test only applicable for series with $n \geq 4$ values), the resulting flux value was classified for further linear mixed effects analysis as a non-detectable flux and as a flux estimated from a headspace composition change without a significant trend.

Regression analysis of headspace CO_2 concentrations

In general, the time series of headspace CO_2 concentration during chamber closure contained eight (minimum number of seven) values. Following the biophysical model from Kutzbach *et al.* (2007), non-linearity in the rate of CO_2 exchange across the soil-atmosphere interface is assumed in an opaque non-steady-state chamber. Hence, a morphologically convex upward curvature of the concentration time series is expected for CO_2 release from the soil surface to the headspace air. Non-linear regressions of the headspace concentration time series have also been shown empirically to be a sometimes more suitable way to estimate CO_2 fluxes than linear regression (Pihlatie *et al.* 2013). Therefore, exponential and, as an empirical alternative, quadratic regressions (cf. Koskinen *et al.* 2014) were estimated in addition to the linear regression.

Before regression analysis, all y_{gas} values within the first 50 seconds after chamber closure were rejected due to potential disturbances caused by chamber attachment (cf. Davidson *et al.* 2002, Kutzbach *et al.* 2007). All regression functions had to fulfil some empirical plausibility criteria (cf. Baker *et al.* 2003, Görres *et al.* 2014) to be accepted as valid for flux estimation (Table 3). However, functions not in line with the expected curvature in the biophysical model were accepted (cf. Kutzbach *et al.* 2007). For each concentration time series measurement, the result with the least residual standard deviation (cf. Kutzbach *et al.* 2007) from the valid regression was used to estimate the CO_2 flux. Non-detectable CO_2 fluxes were estimated by linear regression only (cf. Parkin & Venterea 2010).

Regression analysis of headspace CH_4 and N_2O concentrations

From all measured series of headspace CH_4 or N_2O concentrations, 51 % consisted of five valid values, 11 % of four and 38 % of three valid values. For that reason, only linear regression was used to estimate CH_4 and N_2O fluxes (cf. Kutzbach *et al.* 2007, Parkin & Venterea 2010, de Klein & Harvey 2012). Eight obvious invalid y_{gas} values below the detection limit of the gas chromatograph (0.09 ppm for CH_4 and 0.10 ppm for N_2O) and ten values from obviously leaky vials (vials with fissure or neck breakage, damaged crimp cap or creased internal septum surface) were discarded. Disturbances obviously due to ebullition were detected in any single CH_4 concentration time series measurement by testing some simple plausibility criteria (cf. Silvola *et al.* 1992, Granberg *et al.* 2001, Alm *et al.* 2007, Forbrich *et al.* 2010). These criteria are based on various CH_4 concentrations that were measured or estimated with the obtained linear regression function (Table 4). If a disturbance in the flux estimation due to ebullition was plausible, the related CH_4 flux estimate was marked for the purpose of further linear mixed effects analyses.

GHG flux detection limits

The flux detection limit (F_{DL}) was estimated by a simple approach according to detection limit estimation and time series analysis (cf. Doerffel 1990, VDI 2449 Part 1, Baker *et al.* 2003, Günther *et al.* 2014). It was assumed that a concentration change in the chamber headspace air had to exceed the width of the gas analyser's confidence or repeatability band (see above) to be detectable. Therefore, this band width was set as the concentration change between the first and last measurements of a presumed

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Table 3. Criteria for acceptable regression functions for headspace carbon dioxide (CO_2) concentrations.

Type of regression	Criteria		
	Threshold for $y(t_0)$ related to ambient CO_2 concentrations [a]	Non-exaggerated estimation of $f'(t_0)$	Monotony between t_0 and t_{end}
Linear	360 ppm $\leq y(t_0) \leq$ 440 ppm	---	---
Quadratic		$(y_{min} - y(t_0) \leq y_{max} - y_{min})$	$f'(t_0), f'(t_{end}) > 0$ or $f'(t_0), f'(t_{end}) < 0$
Exponential			---

where: y_{min} = measured minimum CO_2 concentration in headspace air;
y_{max} = measured maximum CO_2 concentration in headspace air;
$y(t_0)$ = estimated initial CO_2 concentration in headspace air;
$f'(t_0)$ = slope of the regression function at t_0;
$f'(t_{end})$ = slope of the regression function at t_{end};
t_0 = moment of chamber closure;
t_{end} = moment of last CO_2 concentration measurement in headspace air.

[a] 360 ppm and 440 ppm CO_2 were set as thresholds representing the limits of an acceptable initial headspace CO_2 concentration range with regard to uncertainties of measurement and regression and to fluctuations in ambient concentration, boundary layer effects in plants and PVC frames, microscale cold air layers and katabatic winds.

Table 4. Plausibility decisions on disturbance of flux estimation by ebullition and related criteria in headspace methane (CH_4) concentration time series: If all criteria within one row are fulfilled, the flux estimate is considered to be sufficiently free of disturbance by CH_4 ebullition. If in all rows at least one respective criterion is not fulfilled, the flux estimate is considered to be disturbed by CH_4 ebullition.

Criteria		
Threshold for $y(t_0)$ related to ambient CH_4 concentration[a]	Relationship of $y(t_0)$ uncertainty to ambient CH_4 concentration[b,c]	Relationship of difference between $y(t_0)$ and ambient CH_4 concentration to range of headspace CH_4 concentration [b,d]
1 ppm $\leq y(t_0) \leq$ 4 ppm	---	---
$y(t_0) <$ 1 ppm	$y(t_0) + \Delta\, y(t_0) \geq$ 1.55 ppm	1.55 ppm $- y(t_0) \leq y_{max} - y_{min}$
$y(t_0) >$ 4 ppm	$y(t_0) - \Delta\, y(t_0) \leq$ 2.35 ppm	$y(t_0) -$ 2.35 ppm $\leq y_{max} - y_{min}$

where: y_{min} = measured minimum CH_4 concentration in headspace air;
y_{max} = measured maximum CH_4 concentration in headspace air;
$y(t_0)$ = estimated initial CH_4 concentration in headspace air;
$\Delta\, y(t_0)$ = 95 % confidence interval to $y(t_0)$;
t_0 = moment of chamber closure.

[a] 1 ppm and 4 ppm CH_4, about half or twice the typical ambient CH_4 concentration (~ 2 ppm), were set as thresholds representing the limits of an acceptable initial headspace concentration range with regard to uncertainties of measurement and regression and to fluctuations in ambient CH_4 concentration and boundary layer effects in plants and PVC frames.
[b] 1.95 ppm ± 0.4 ppm = 1.55 ppm ∨ 2.35 ppm are the average and range of measured CH_4 concentration in ambient air sampled and determined in the same way as headspace air.
[c] As long as the uncertainty range of $y(t_0)$ overlaps the range of measured CH_4 concentration in ambient air, the related flux estimate is not suspected to be disturbed by ebullition.
[d] As long as the range of measured headspace CH_4 concentration fits or exceeds the absolute value of the difference between $y(t_0)$ and the nearest range limit of measured CH_4 concentration in ambient air, the related flux estimate is not suspected to be disturbed by ebullition.

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headspace air determination to calculate the slope $f'(t_0)$ in a linear regression. F_{DL} was estimated depending on the effective V of each flux measurement position.

Statistical analyses of GHG flux

For the calculation of means and quartiles of fluxes from the various ecotopes, flux estimates classified as non-detectable fluxes and CH_4 flux estimates for which disturbance by ebullition was plausible (Table 4) were included.

A linear mixed effects analysis (cf. Bates 2010, Gries 2012, Winter 2013) was performed to investigate GHG fluxes based on the individual flux estimates of all measurement positions by means of the packages lme4 and car in R x64 3.2.2 (Fox & Weisberg 2011; Bates *et al.* 2015a,b; R Core Team 2015). The linear mixed effects models built in this analysis combined the flux to the atmosphere as the response variable with observations of some adjacent environmental conditions (e.g. temperature, ecotope type) as independent variables that were set as fixed or random effects. Herewith, soil and water temperatures from the various ecotopes were pooled in a single data set. To identify the best fitting model for a GHG flux, *P*-values and *Akaike's Information Criterion* were obtained by likelihood ratio tests comparing a model with the effect in question against the respective model without the effect in question (cf. Gries 2012, Winter 2013). The models were also checked and compared for good approaches to homoscedasticity and normality. Contrasts among the predictions in the obtained linear mixed effects models were pairwise tested by least-squares means, using the lsmeans package in R x64 3.2.2 (Lenth & Hervé 2015, R Core Team 2015).

In the linear mixed effects analysis, the natural logarithm of the flux was needed to meet normality and homoscedasticity requirements and to improve the significance of the obtained models. To permit the flux values to be transformed into logarithms, all non-detectable fluxes were replaced with a value of half the detection limit F_{DL} (Baker *et al.* 2003) and fluxes estimated from headspace composition changes without a significant trend were neglected to prevent negative flux values in these two categories. Adding a constant to all flux values to avoid negative values was not an option, because of the non-linear relationship between such modified values and soil /water temperature in the model.

CH_4 flux estimates were not included in the linear mixed effects analysis if disturbance by ebullition was plausible (Table 4). The pond was not considered in CH_4 analysis as the water temperature range represented in the data was too small. N_2O was not included in the linear mixed effects analyses as the majority of N_2O flux values were below the detection limit.

RESULTS

Soil physical and chemical conditions

The main peat types in the observed ecotopes were *Sphagnum*, *Carex* and *Eriophorum* peat (often mixed with each other) with H 2–8, bulk density 0.02–0.12 g cm^{-3} and pH 3.7–4.4 (Table 2). Surface water conditions were characterised by pH 5, electrical conductivity ~30 µS cm^{-1}, DOC concentration of 34 mg L^{-1} and total C concentration of 36 mg L^{-1} (mean values 2009–2012).

Soil temperature and soil water conditions

Soil water conditions and soil/water temperature varied between measurement occasions and between the ecotopes. All ecotopes were usually saturated or inundated dependent on precipitation levels. However, April 2009 was very dry (6.3 mm $month^{-1}$ precipitation, 4 × 4 km gridded data; SMHI 2014) and the otherwise saturated bare peat with *Eriophorum vaginatum* tussocks became merely wet. Due to an exceptionally warm and dry summer in 2010 (45 mm cumulated precipitation between 01 June and 06 July, 4 × 4 km gridded data; SMHI 2014), soil water conditions in the same area became dry (i.e. the upper 5 cm of the peat were dried out). Soil temperature at 10 cm depth ranged from 0.5 °C (at three measurement positions on 16 April 2009) to 20.8 °C (at one measurement position on 05 July 2010).

Linear mixed effects analyses

Soil/water temperature and ecotope type (with interaction term for CH_4) were obtained as significant fixed effects in the linear mixed effects analyses of the relationship between CO_2 or CH_4 fluxes and some adjacent environmental conditions in the respective models. For the CO_2 model, the soil water condition was also a significant fixed effect. The inclusion of measurement position and measurement occasion as random effects made significant improvements to the models. The random effect of measurement occasion (expressed in the models as intercepts) represents seasonal influences and the influences of previous and present weather conditions that were not expressed in soil/water temperature and soil water categories. The random effect of measurement position (also expressed as intercepts) represents the differences between the positions within an ecotope that were not expressed in soil/water temperature and

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soil water categories.

In both models there was a significant linear relationship between soil/water temperature and the natural logarithm of the GHG fluxes as a response variable. Thus, the models estimated the fluxes to the atmosphere from an ecotope at a given soil/water temperature and soil water category as $F_i = e^{(a \cdot |T_i| + b)}$, generalised over measurement position and occasion, where F_i is the flux to the atmosphere in µmol m^{-2} h^{-1} at soil/water temperature T_i in °C at a flux measurement *i*. The constants were $a = a_1$ and $b = b_{1,eco} + b_{2,sw} + b_3$ for CO_2, and $a = (a_1 + a_{2,eco})$ and $b = b_{1,eco} + b_3$ for CH_4, where a_1, $a_{2,eco}$, $b_{1,eco}$, $b_{2,sw}$ and b_3 were coefficients of the models; among these $a_{2,eco}$ and $b_{1,eco}$ were dependent on the ecotope type *eco* and $b_{2,sw}$ was dependent on the soil water condition *sw*. The constant *a* may be expressed as $a = \ln(TS_{10})/10$, where TS_{10} is a soil or water temperature sensitivity coefficient that is mathematically analogous to the temperature coefficient Q_{10} in the van 't Hoff reaction-rate-temperature rule (Holleman & Wiberg 1958). Therefore $TS_{10} = (F_i / F_0)^{10\ K / (T_i - T_0)}$, where F_i and F_0 are the fluxes at soil/water temperatures T_i and $T_0 = 0$ °C.

Visual inspection of residual plots did not reveal any obvious deviation from homoscedasticity for the CO_2 model, but there was a slight deviation for the CH_4 model due to flux estimates below the detection limit. The approach to normality was fair in the CO_2 model but poor in the CH_4 model. All fixed effects tested were significant, but some regression coefficients were not (Tables 5 and 6). The models

Table 5. Parameters of the linear mixed effects model for CO_2 flux to the atmosphere from the ecotopes. Significant fixed effects and coefficients in bold. Reference level for ecotope: mire; reference level for soil water condition: saturated. Est. = estimate; *SE* = standard error; *t* = *t* value.

Coefficient		*a*			$b_{1,eco}$			$b_{2,sw}$			b_3		
Fixed effect		**Soil/water temperature**			**Ecotope**			**Soil water condition**			**Intercept**		
Pr (> chi-square)		**0.02**			**$< 2 \cdot 10^{-16}$**			**0.04**					
Ecotope *eco*	Soil water condition *sw*	Est.	*SE*	*t*	Est.	*SE*	*t*	Est.	*SE*	*t*	Est.	*SE*	*t*
Mire	Saturated	**0.07**	0.028	**2.43**							**6.0**	0.39	**15.5**
	Inundated							-0.1	0.18	0.74			
Bare peat	Dry				**0.9**	0.21	**4.28**	0.1	0.33	0.24			
	Wet							**1.0**	0.39	**2.59**			
	Saturated												
Vadose *Eriophorum vaginatum*	Dry				**1.9**	0.19	**9.64**	0.1	0.33	0.24			
	Wet							**1.0**	0.39	**2.59**			
	Saturated												
Phreatic *Eriophorum vaginatum*	Saturated				**1.5**	0.18	**7.99**						
	Inundated							-0.1	0.18	0.74			
Eriophorum angustifolium	Saturated				**1.4**	0.22	**6.31**						
	Inundated							-0.1	0.18	0.74			
Pond	Inundated				0.6	0.44	1.44	-0.1	0.18	0.74			
Lake	Inundated				-0.3	0.40	0.67	-0.1	0.18	0.74			

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Table 6. Parameters of the linear mixed effects model for CH_4 flux to the atmosphere from the ecotopes. Significant fixed effects and coefficients in bold. Reference level for ecotope: mire. Est. = estimate; *SE* = standard error; *t* = *t* value.

Coefficient	a_1			$a_{2,eco}$			$b_{1,eco}$			b_3		
Fixed effect	**Soil/water temperature**			**Soil temperature · ecotope**			**Ecotope**			Intercept		
Pr (> chi-square)	**0.03**			**$1.7 \cdot 10^{-6}$**			**$< 2.2 \cdot 10^{-16}$**					
Ecotope *eco*	Est.	*SE*	*t*	Est.	*SE*	*t*	Est.	*SE*	*t*	Est.	*SE*	*t*
Mire	**0.22**	0.047	**4.82**							0.3	0.66	0.48
Bare peat				**-0.23**	0.045	**5.08**	0.6	0.67	0.95			
Vadose *Eriophorum vaginatum*				**-0.21**	0.047	**4.36**	**4.2**	0.68	**6.24**			
Phreatic *Eriophorum vaginatum*				**-0.17**	0.055	**3.12**	**4.9**	0.74	**6.69**			
Eriophorum angustifolium				-0.07	0.059	1.21	**4.3**	0.82	**5.23**			
Lake				0.01	0.092	0.08	1	1.3	0.43			

indicated that CO_2 and CH_4 fluxes were dependent on the ecotope properties and on soil/water temperature and, for CO_2, also somewhat on soil water conditions.

CO_2 fluxes to the atmosphere

In a total of 432 CO_2 flux values, 77 were non-detectable fluxes or fluxes estimated from headspace composition changes without a significant trend or were related to unacceptably high CO_2 concentration estimates (> 440 ppm) at the moment of chamber closure. All negative CO_2 flux estimates were classified as non-detectable fluxes.

Overall, CO_2 fluxes to the atmosphere were highest from the three *Eriophorum* spp. ecotopes (Figure 2). The highest fluxes were recorded during June and July for all vegetated ecotopes and the bare peat. Small CO_2 fluxes to the atmosphere occurred during April and May, and then again in September and October (Figure 2). In general, higher soil/water temperatures and a decrease in soil water content resulted in higher CO_2 fluxes (Figure 3). The range of variation within an ecotope's sample from an individual measurement occasion (except for lake and pond) was in general larger with high fluxes, e.g. in July 2010 (Figure 2).

CO_2 fluxes between the mire on the one hand and the three *Eriophorum* spp. ecotopes and the bare peat on the other hand, as well as between the lake and the three *Eriophorum* spp. ecotopes, were significantly different in the mixed model (Table 7). In general, the lake and the mire produced the lowest CO_2 fluxes in this study (Figures 2 and 3). In contrast, the three *Eriophorum* spp. ecotopes were high CO_2 emitting ecotopes on almost all measurement occasions. The model also significantly ($P < 0.0005$) distinguished between the CO_2 fluxes from the wet ecotopes and those from saturated and inundated ecotopes, which were highest from the vadose *Eriophorum vaginatum* ecotope and the bare peat under wet conditions (Figure 3).

CH_4 fluxes to the atmosphere

About one third (127) of the 382 CH_4 flux estimates were below the flux detection limit or did not show a significant trend in concentration change over the closure time. In 86 flux estimates, disturbance by CH_4 ebullition was plausible and 27 of these were non-detectable fluxes or fluxes estimated from headspace concentration change without a significant trend. Disturbances by ebullition occurred in all ecotopes except the bare peat and were present on all measurement occasions in the *Eriophorum angustifolium* ecotope. Moreover, 51 negative CH_4 flux estimates were either non-detectable fluxes or fluxes estimated from headspace composition changes without a significant trend or were plausibly disturbed by ebullition.

In general, CH_4 fluxes to the atmosphere were highest from the phreatic *Eriophorum vaginatum* and *Eriophorum angustifolium* ecotopes (Figures 4 and 5).

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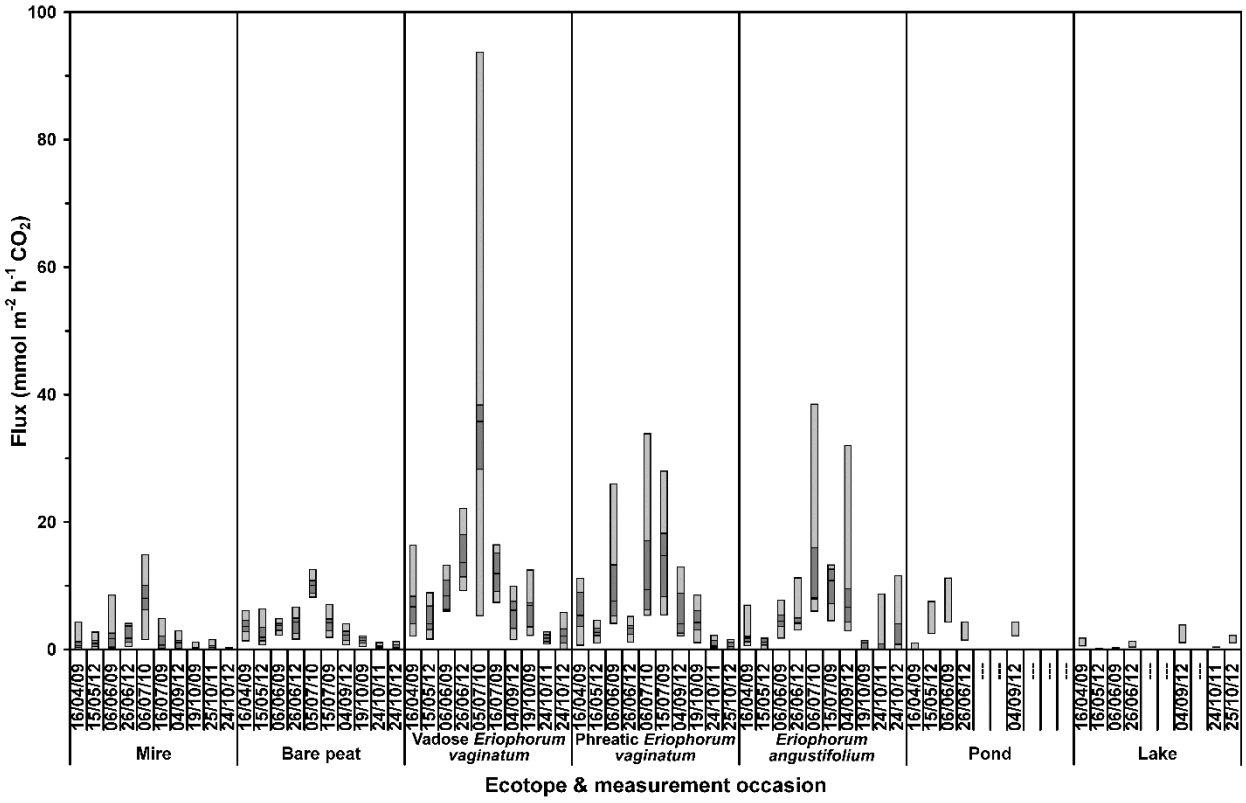

Figure 2. CO_2 fluxes to the atmosphere (mmol m^{-2} h^{-1}) within the ecotopes, shown in quartiles (bars) and listed in order of seasons.

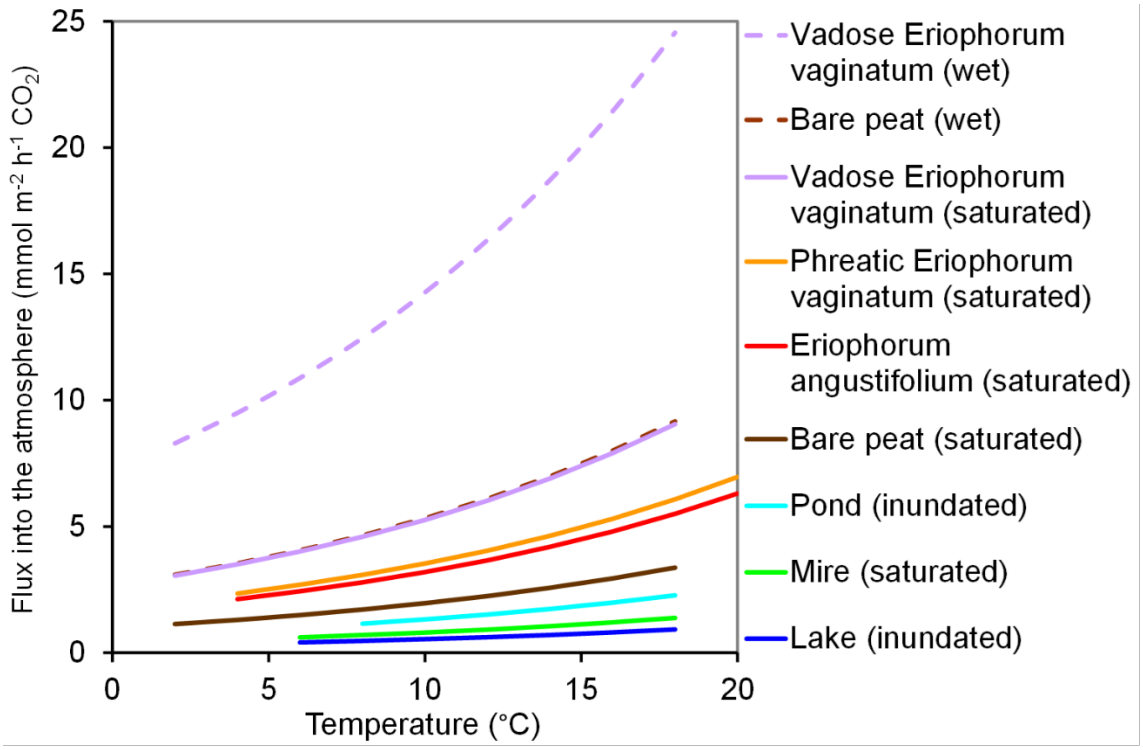

Figure 3. Ecotope CO_2 fluxes to the atmosphere (mmol m^{-2} h^{-1}) related to soil/water temperature (°C) and soil water conditions. Fluxes estimated with the linear mixed effects model (Table 5) based on measured temperature ranges.

Table 7. Ecotope pairs with significantly different CO_2 fluxes to the atmosphere ($P \leq 0.05$) based on the linear mixed effects model. (Pairwise comparisons among least-squares means; results were averaged over the levels of soil water condition; *P* value adjustment: *Tukey* method for comparing a family of seven estimates).

Leader	Joiner
Mire	Bare peat; Vadose *Eriophorum vaginatum*; Phreatic *Eriophorum vaginatum*; *Eriophorum angustifolium*
Lake	Vadose *Eriophorum vaginatum*; Phreatic *Eriophorum vaginatum*; *Eriophorum angustifolium*
Bare peat	Vadose *Eriophorum vaginatum*

For all vegetated ecotopes, the smallest fluxes occurred during April and May and the highest fluxes during June and July. The fluxes to the atmosphere were usually small in September and October, but on some measurement occasions the fluxes were as high as during the summer. In September 2012, comparatively high CH_4 fluxes were observed from all four vegetated ecotopes and the bare peat, but this was only evident in their maximum values (vadose *Eriophorum vaginatum*: 1.2 mmol m^{-2} h^{-1}, phreatic *Eriophorum vaginatum*: 8.9 mmol m^{-2} h^{-1}, *Eriophorum angustifolium*: 9.0 mmol m^{-2} h^{-1}, mire: 1.9 mmol m^{-2} h^{-1}, bare peat: 2.1 mmol m^{-2} h^{-1}). The same pattern was observed in June 2012 for the phreatic *Eriophorum vaginatum* and *Eriophorum angustifolium* ecotopes and in October 2012 for the *Eriophorum angustifolium* ecotope (Figure 4). The range of variation within an ecotope sample from an individual measurement occasion in the phreatic *Eriophorum vaginatum* and *Eriophorum angustifolium* ecotopes were in general larger with high fluxes. CH_4 fluxes from the mire and the vadose *Eriophorum vaginatum* ecotope were small (mean values from -0.21 to 0.32 mmol m^{-2} h^{-1} and 0.05 to

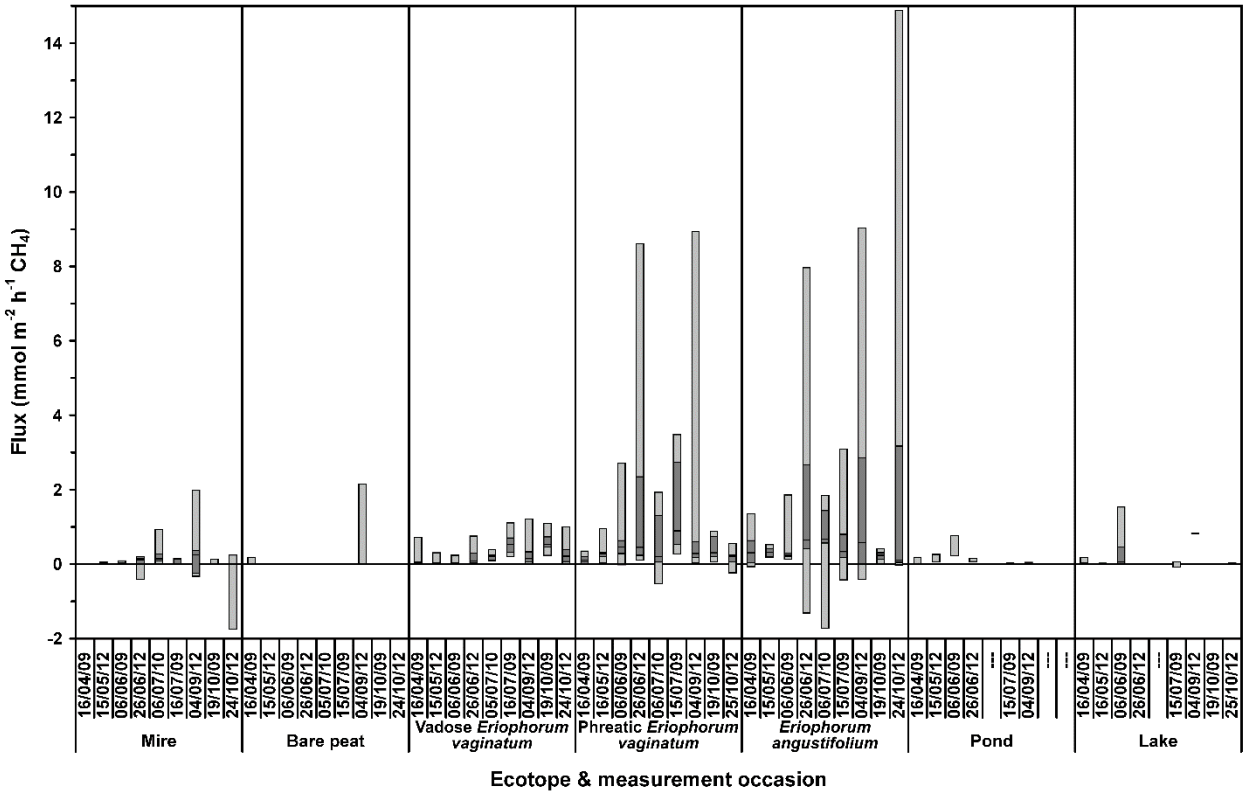

Figure 4. CH_4 fluxes (mmol m^{-2} h^{-1}) within the ecotopes, shown in quartiles (bars) and listed in order of seasons. Positive values show a flux from the peatland to the atmosphere and negative values are a flux from the atmosphere to the peatland.

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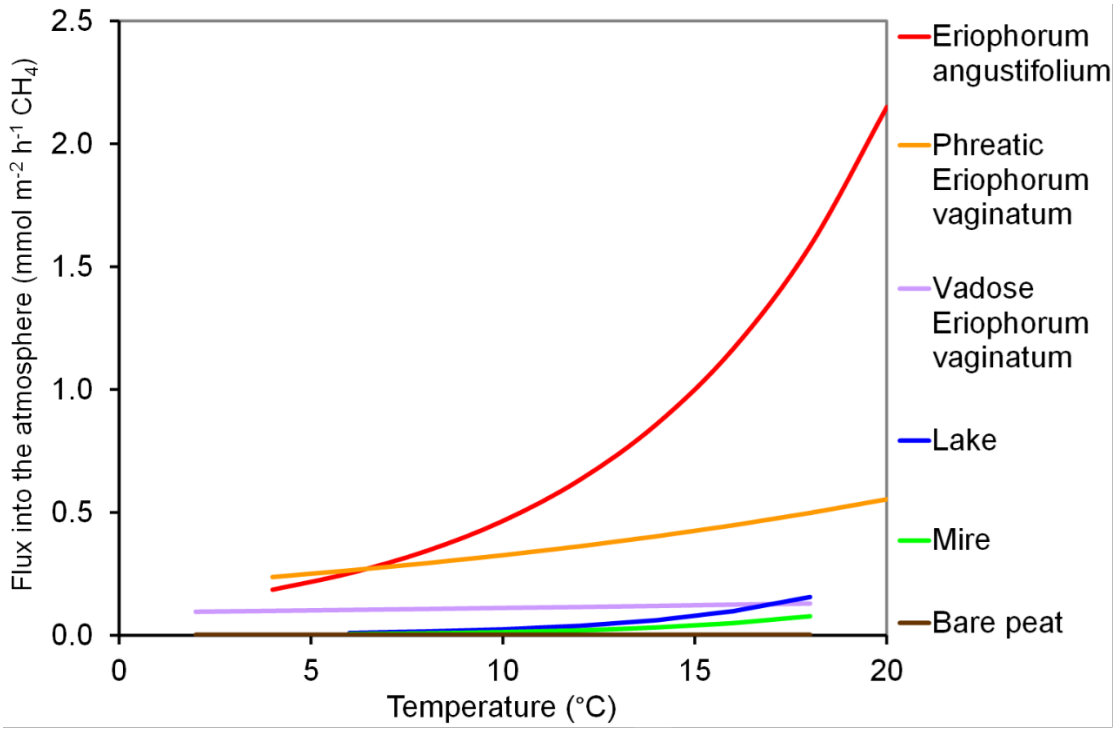

Figure 5. Ecotope CH_4 fluxes (mmol m^{-2} h^{-1}) related to soil or water temperature (°C). Fluxes estimated with the linear mixed effects model (Table 6) based on measured temperature ranges.

0.61 mmol m^{-2} h^{-1}, respectively) and those from the bare peat were very small (mean values from 0.00 to 0.27 mmol m^{-2} h^{-1}). Low CH_4 fluxes to the atmosphere were observed in the pond and lake on all occasions (Figure 4).

In the mixed model, the CH_4 fluxes between the mire on the one hand and the three *Eriophorum* spp. ecotopes and the bare peat on the other hand, and between all ecotopes and the bare peat, were significantly different (Table 8). CH_4 fluxes were higher in all ecotopes (except for the bare peat) with higher soil/water temperatures (Figure 5). Under these conditions, fluxes to the atmosphere from *Eriophorum angustifolium* ecotope increased considerably more than those from the other ecotopes. In general, the bare peat, the mire and the lake could be considered as low CH_4 emitting ecotopes (Figures 4 and 5).

N_2O fluxes to the atmosphere

N_2O fluxes to the atmosphere were very small (Figure 6) and below the flux detection limit, with the exception of 26 June 2012, when one of the bare peat measurement positions produced a N_2O flux of 12 µmol m^{-2} h^{-1}. However, the 95 % confidence interval associated with this estimate was ±10 µmol m^{-2} h^{-1} N_2O, thereby indicating the poor reliability of this flux value.

Table 8. Ecotope pairs with significantly different CH_4 fluxes to the atmosphere ($P \leq 0.05$), based on the linear mixed effects model. (Pairwise comparisons among least-squares means; results may be misleading due to involvement in interactions; *P*-value adjustment: *Tukey* method for comparing a family of seven estimates).

Leader	Joiner
Bare peat	Mire; Lake; Vadose *Eriophorum vaginatum*; Phreatic *Eriophorum vaginatum*; *Eriophorum angustifolium*.
Mire	Vadose *Eriophorum vaginatum*; Phreatic *Eriophorum vaginatum*; *Eriophorum angustifolium*.
Lake	Phreatic *Eriophorum vaginatum*; *Eriophorum angustifolium*.
Vadose *Eriophorum vaginatum*	*Eriophorum angustifolium*.

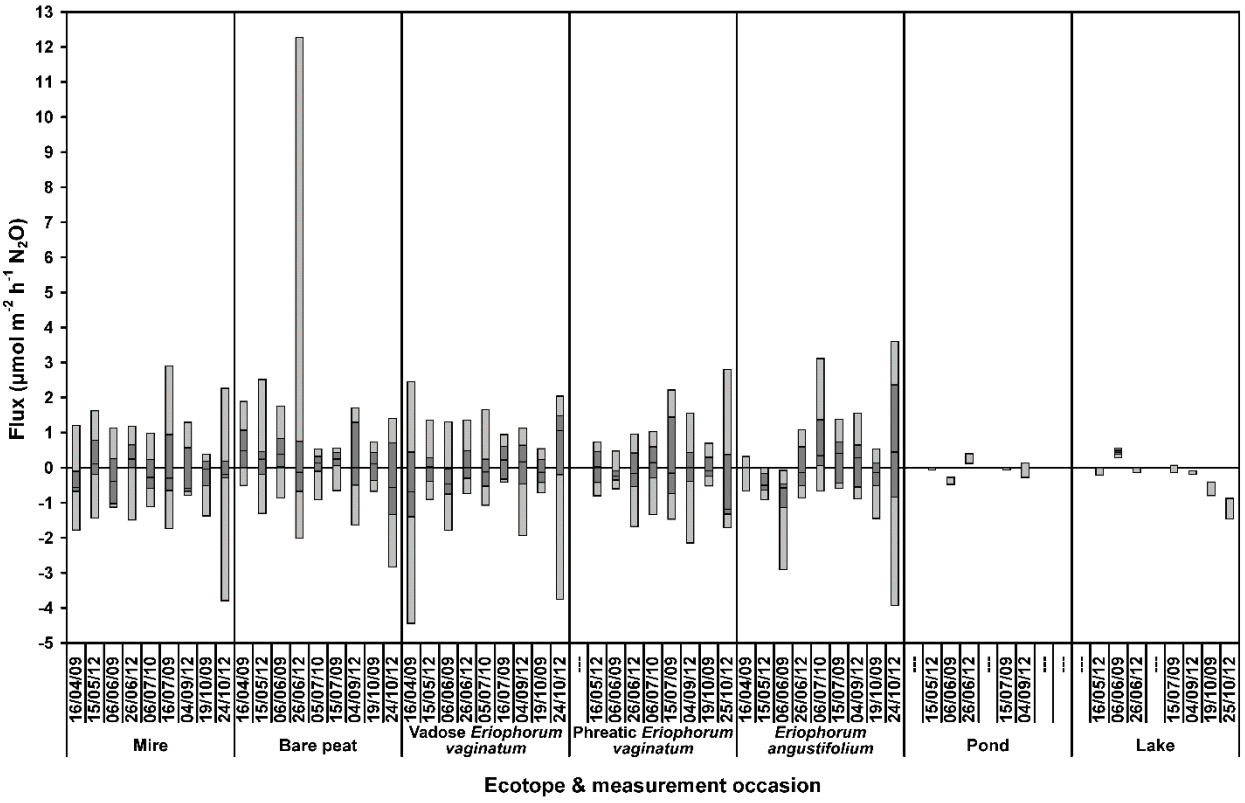

Figure 6. Nitrous oxide (N_2O) fluxes (µmol m^{-2} h^{-1}) within the ecotopes, shown in quartiles (bars) and listed in order of seasons. Positive values indicate fluxes from the peatland to the atmosphere and negative values indicate fluxes from the atmosphere to the peatland.

DISCUSSION

Influence of ecotope and soil temperature on GHG fluxes to the atmosphere

CO_2 fluxes to the atmosphere

Since our measurement technique covered only ecosystem respiration, we were unable to estimate the net CO_2 uptake. Therefore, all high CO_2 emitting sites such as the *Eriophorum* spp. ecotopes might accumulate more C (cf. Wilson *et al.* 2013, Strack *et al.* 2014) than non-vegetated sites, water bodies and the mire. *Eriophorum angustifolium* is a very efficient CO_2 accumulator (Wilson *et al.* 2013) and as 'peat builders' *Eriophorum* spp. add new C as above- and below-ground tissues (Marinier *et al.* 2004) into the old and recalcitrant peat (Tuittila *et al.* 1999). It thus supports the re-establishment of peatland vegetation, such as *Sphagnum* mosses and vascular plants (Marinier *et al.* 2004, Siegenthaler *et al.* 2013).

CO_2 fluxes from the vegetated ecotopes followed the seasonal temperature pattern. The higher CO_2 fluxes observed with increasing temperature at the three *Eriophorum* spp. ecotopes were associated with a steeper slope than the other ecotopes in the linear mixed model function (Figure 3), which may be explained by better growth rates that result in higher fluxes. The exceptionally warm and dry weather conditions in July 2010 led to high soil temperatures and a decrease in soil water content and thus to high CO_2 fluxes to the atmosphere. Wilson *et al.* (2013) and Strack & Zuback (2013) found similar patterns for water table drop and higher CO_2 fluxes to the atmosphere for their study sites in Ireland and Québec, respectively, during the mid-summer period in 2010.

CO_2 fluxes from the mire and the newly established lake were lower than those from the three *Eriophorum* spp. ecotopes. For the lake, the CO_2 fluxes of 2–46 mmol m^{-2} d^{-1} can be explained by its dystrophic state, i.e. it is not controlled by primary production but is mostly affected by the bottom-peat material that could be released to form floating peat, and by the nutrient-poor water received from the mire. Waddington *et al.* (2001) observed low CO_2 fluxes to the atmosphere from highly decomposed peat in cutover peatlands after mining and attributed this to low substrate quality. Huttunen *et al.* (2003) reported high CO_2 fluxes, which ranged from 3.9 mmol m^{-2} d^{-1} up to 73 mmol m^{-2} d^{-1}, from boreal

eutrophic lakes, ponds and reservoirs, from lakes with high primary production and from humic lakes within peatlands or managed forest catchments. CO_2 fluxes varied widely between their study sites, e.g. 4.7–15 mmol m^{-2} d^{-1} from an oligotrophic lake and 0.4–52 mmol m^{-2} d^{-1} from mesotrophic reservoirs and ponds. Our findings in regard to CO_2 fluxes from the constructed lake fit well within the ranges of fluxes reported by Huttunen *et al.* (2003), even though the formation of the investigated water bodies differed.

CO_2 fluxes from the lake seemed to be largely unaffected by a temperature increase, although CO_2 solubility in water is strongly dependent on temperature. As a possible CO_2 retention medium or CO_2 source, a water body has an intermediate position between the peat at the lake bottom and the atmosphere. The total C in the lake water comprised 94 % DOC, but it is unclear whether this DOC mainly comes from water discharge from the mire and pond, or whether the residual bottom peat is not as recalcitrant as expected. Furthermore, DOC might not be involved in on-site CO_2 production in the lake at Porla, even though DOC conversion is generally most possible in rewetted peatlands and, therefore, off-site fluxes to the atmosphere must be investigated and included in C balances (Evans *et al.* 2016). Another reason for the low CO_2 fluxes could be the current absence of shallow lake vegetation that would enrich the water with CO_2 due to plant-mediated uptake from the atmosphere and to decomposition of plant material. Pelletier *et al.* (2015) found reduced CO_2 photosynthetic uptake and thus limited CO_2 loss through respiration for peatlands with pools. The pools in their study did not result from rewetting, which was the case for the shallow lake in Porla, although the mechanisms behind reduced CO_2 fluxes from such sites might be the same. The mire and lake, both low CO_2 emitters, constitute almost 95 % of the Porla study site. However, our flux measurement positions were only single points within a particular ecotope sub-area and, therefore, might not be totally representative for the entire ecotope.

CH_4 fluxes to the atmosphere

As has been found previously, water table position and the existence of aerenchymatous species are important controls on CH_4 fluxes from peatlands to the atmosphere (Bubier 1995, Le Mer & Roger 2001, Larmola *et al.* 2010, Mahmood & Strack 2011, Miller 2011). At our study site, a combination of water table position and the presence of vascular plants explained the spatial distribution of CH_4 fluxes, with low fluxes associated with low water tables and with the absence of vegetation (bare peat). Medium fluxes were associated with standing water and with the absence of vegetation in the lake and with water saturation and no vascular vegetation in the mire. The high fluxes from the three *Eriophorum* spp. ecotopes were sub-divided into high fluxes from the vadose *Eriophorum vaginatum* ecotope with a low water table and deep-rooting vascular plants, higher fluxes from the phreatic *Eriophorum vaginatum* ecotope with saturated-inundated conditions and deep-rooting vascular plants, and even higher fluxes from *Eriophorum angustifolium* with standing water and vascular plants with long tiller systems. Some authors (e.g. Juutinen *et al.* 2003, Wilson *et al.* 2009) have also observed a distinct contrast in CH_4 fluxes between the highly productive littoral zone (in Porla: the *Eriophorum angustifolium* ecotope) and the pelagic zone of a lake. Within the vegetated ecotopes at soil surface water level (mire, phreatic *Eriophorum vaginatum*, *Eriophorum angustifolium*), the mire emitted less CH_4 than the two *Eriophorum* spp. ecotopes. We attributed this to minimised plant-mediated CH_4 transport in the mire due to the absence of vascular plants and to simultaneous CH_4 oxidation as a result of the methanotrophic bacteria living in the aerobic *Sphagnum* spp. lawn (Whalen 2005, Hornibrook *et al.* 2009, Fritz *et al.* 2011).

Seasonal CH_4 fluxes in the Porla study site can also be considered to be related to soil/water temperature and to active plant growth that supplies fresh litter and thus forces aerenchymatous gas transport (Huttunen *et al.* 2003). The increase in CH_4 fluxes that was observed in all vegetated ecotopes in conjunction with increasing peat temperatures is in line with results from Komulainen *et al.* (1998) for a restored fen, where the highest CH_4 fluxes during summer were explained by the seasonal dynamics of microbial activity and substrate supply. For a boreal mire in northern Sweden, Granberg *et al.* (2001) observed higher CH_4 fluxes to the atmosphere from *Eriophorum* plants, during periods of increased air temperatures, as a result of increased photosynthetic C fixation rates due to increased above-ground biomass and shoot length, which in turn led to higher root exudate production rates. In contrast, sites with an oxic upper peat horizon (i.e. the bare peat ecotope in Porla) support CH_4 oxidation and, thus, low CH_4 fluxes to the atmosphere are observed. In addition to the increasing organic substrate supply after rewetting that may lead to high CH_4 emissions, ecotopes with *Eriophorum vaginatum* tussocks can also serve as CH_4 catalysts. Due to their wide below-ground network of roots and rhizomes they can absorb CH_4 (Frenzel & Rudolph 1998) and can thus lead to somewhat higher CH_4 fluxes to the atmosphere than the surrounding bare peat (Tuittila *et al.* 2000).

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While the limited data available for the lake prevented any conclusive analysis of the relationship between water temperature and CH_4 fluxes, the comparatively high CH_4 emissions from all *Eriophorum* spp. ecotopes in the September and October measurements are in line with results presented by Bellisario *et al.* (1999) for *Carex* spp. and by Saarnio *et al.* (1997), Moore *et al.* (2011) and Marinier *et al.* (2004) for *Eriophorum vaginatum*. They explained this 'end-of-season' CH_4 peak by the supply of new C from vegetation dieback into the surrounding recalcitrant peat and the continuation of root exudation even with declining air and peat temperatures.

Nevertheless, once rewetting has created a new hydro-environment that may lead to a growing mire and to a C accumulation ecosystem, the GHG balance should be estimated. Expressed in CO_2 mol-equivalents using the GWP_{100} factor of 12.4 mol CO_2 mol^{-1} CH_4 (converted from the original mass equivalents 34 g CO_2 g^{-1} CH_4, Myhre *et al.* 2013), the ratio of CH_4 to CO_2 fluxes to the atmosphere at the Porla study site was less than 3.9 for 90 % of all flux measurement pairs, less than 2.0 for 80 % of pairs and less than 0.3 for 50 % of pairs, excluding fluxes without a significant concentration change trend during chamber closure and CH_4 flux estimates plausibly disturbed by ebullition. Thus, the overall climate impact of CH_4 fluxes to the atmosphere in the Porla study site can be expected to be less than the impact of soil and plant respiration. Taking into consideration that Wilson *et al.* (2016b) found a negative GHG balance (net consumption) for *Eriophorum angustifolium* in a rewetted peatland, we speculate that CO_2 uptake by photosynthesis exceeds the GHG fluxes to the atmosphere in the *Eriophorum angustifolium* ecotope, the highest CH_4 emitter at the Porla study site.

N_2O fluxes to the atmosphere

The estimated flux detection limits for N_2O release were in the range 0.5-3.9 mmol m^{-2} h^{-1} CO_2-equivalents. As almost all N_2O fluxes in the Porla study site were below these limits, the fluxes were negligible compared with the measured CO_2 and CH_4 fluxes to the atmosphere, which were in the range of 0–94 and 0–179 mmol m^{-2} h^{-1} CO_2-equivalents, respectively. This implies that N_2O fluxes to the atmosphere from the Porla peatland weakly contribute to the overall GHG fluxes as the site is nutrient poor (C:N ratio >25). We are aware that we might have missed "hot moments" (Butterbach-Bahl *et al.* 2013) of N_2O fluxes given our sampling campaign and that the available N might have been taken up by the vegetation, thus contributing to the low N_2O fluxes observed (Silvan *et al.* 2005). N_2O fluxes below the flux detection limit have also been reported from other studies in rewetted extracted peatlands (Wilson *et al.* 2013, 2016b).

Temperature sensitivity of ecotopes in regard to CO_2 and CH_4 fluxes

The mixed models assumed a linear relationship between soil/water temperature and the natural logarithm of the flux to the atmosphere over the entire observed soil/water temperature span ΔT_{sw} of typically 16–18 K (Figures 3 & 5). However, such linearity has mostly been reported to be limited to a smaller temperature range (Lloyd & Taylor 1994, Kirschbaum 1995, Davidson *et al.* 2006). The estimates of the soil temperature sensitivity coefficient TS_{10} obtained from the mixed models for a temperature span ΔT_{sw} up to 18 K in various ecotopes in Porla (Table 9) are in line with the Q_{10} temperature coefficients for peat soils or organic substrates presented in Lloyd & Taylor (1994), Silvola *et al.* (1996), Frolking *et al.* (2001) and Wang

Table 9. Estimates of soil temperature sensitivity coefficient TS_{10} for CO_2 and CH_4 fluxes to the atmosphere from different ecotopes based on the linear mixed effects models. Due to limited data material, no TS_{10} estimates are shown for the lake and pond ecotopes.

Ecotope *eco*	TS_{10} for CO_2	$TS_{10,eco}$ for CH_4	Related soil temperature range in °C
Mire	2.0	9.4	5-19
Bare peat		0.9	2-19
Vadose *Eriophorum vaginatum*		1.2	1-19
Phreatic *Eriophorum vaginatum*		1.7	4-20
Eriophorum angustifolium		4.6	4-20

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et al. (2015). However, these and other studies (Kirschbaum 1995, Kätterer *et al.* 1998, Reichstein *et al*. 2003, Davidson *et al.* 2006) show that Q_{10} for GHG release from soil-plant systems is not a constant, but is often strongly dependent on soil temperature itself, encompassing various biochemical reactions with individual speeds and changing contributions to the total reaction rate at different temperatures. In principle, a Q_{10} estimation by linear mixed effects models for more restricted temperature ranges would be suitable to approximate to the non-linearity of temperature sensitivity (Lloyd & Taylor 1994), but here the available data material, with some soil temperature clusters, was deemed too small to be split up into two or more soil temperature groups.

The mixed model indicated that the CO_2 fluxes to the atmosphere from ecotopes without vascular plants (mire and bare peat) had the same relative sensitivity to warmer temperatures as those from the three *Eriophorum* spp. ecotopes (Table 9). However, the increase in the flux to the atmosphere was larger for ecotopes with vascular plants than for the mire, lake and pond, where fluxes remained at a lower level over the observed temperature range (Figure 3).

The CH_4 fluxes from the mire and the *Eriophorum angustifolium* ecotopes appeared to be very sensitive to temperature increases (Table 9), although the fluxes from the mire remained at a low level (Figure 5). The increase in fluxes was larger for the phreatic *Eriophorum vaginatum* and *Eriophorum angustifolium* ecotopes than for the other ecotopes, where fluxes remained at a lower level over the studied temperature range, indicating that a combination of vascular plants, high water tables and relatively high soil temperatures enhanced CH_4 fluxes to the atmosphere.

CH_4 ebullition

Ebullition is a non-diffusive emission process that can be divided into steady and episodic ebullition (Lai 2009, Green & Baird 2013). Steady ebullition can often be constant enough to be correctly measured with discontinuous sampling of headspace air (using vials) during a chamber closure period < 60 minutes; but episodic ebullition, which is obviously non-constant over chamber closure, cannot easily be recorded using a vial sampling method. Observations of CH_4 headspace concentrations measured by infrared laser absorption at the Porla study site (unpublished data) revealed that ebullition mostly occurs as a result of the shock caused by chamber closure on the water-saturated soil or as an irregular series of single bubble fluxes to the atmosphere resulting in a step-like curvature of headspace concentration on a level high above the ambient concentration.

As CH_4 was routinely determined by vial sampling at time intervals of ten minutes, the brief bubble fluxes to the atmosphere were integrated (masked) into the relatively long-term averages of increasing headspace concentration. Thus, an initial CH_4 bubble probably resulted in a strong under-estimation of the real CH_4 flux to the atmosphere, while an irregular series of single bubbles most likely resulted in either under- or over-estimation of the real CH_4 flux to the atmosphere by our routine flux measurement method. To prevent false flux estimation caused by CH_4 ebullition, it was necessary to detect obvious episodic ebullition processes in each single headspace concentration time series. The experience of laser measurements and the visual analysis of the times series of CH_4 concentrations (cf. Baker *et al.* 2003, Parkin & Venterea 2010) led to some simple plausibility criteria for flux measurement disturbances caused by ebullition. These criteria are based on the relationships between measured ambient CH_4 concentrations, measured minimum and maximum values of CH_4 headspace concentration and estimated initial headspace concentration in cases of ebullition-free diffusive flow to the atmosphere or steady ebullition flow to the atmosphere. The criteria were uniformly used with all CH_4 datasets as described in the Methods section. Detection of flux measurement disturbances caused by ebullition is still problematic. Our regression analysis and flux estimation only revealed a reasonable suspicion of disturbance by ebullition, rather than proof or a result based on statistical probability. However, high CH_4 concentrations in the frames are not necessarily caused by ebullition. In tall frames, e.g. for the detection of fluxes from tall plants or from sites with frequent water table fluctuations, a potent boundary layer may develop that could have a high CH_4 concentration. Thus, the measurement starts at a high CH_4 concentration level at the moment of chamber closure and, for this reason, little or no regression slope will be observed. This sampling artefact should not be interpreted as ebullition.

CONCLUSIONS

The ecotopes had a significant impact on CO_2 and CH_4 fluxes to the atmosphere with low fluxes observed from the bare peat, the constructed shallow lake and the open poor fen and high fluxes from *Eriophorum vaginatum* tussocks and *Eriophorum angustifolium*. N_2O fluxes were negligible. In the

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restoration of the extracted peatland at Porla, the construction of a nutrient-poor shallow lake showed great potential for lowering GHG fluxes to the atmosphere.

Lake construction may eventually result in a CH_4 hotspot in the littoral zone, but the transition from extracted peatland to wetland ecosystem may reduce the overall climate warming impact. Establishment of vascular and pioneer plants, such as *Eriophorum* spp., in the littoral zone and along the lake shore is essential in paving the way for other peatland vegetation. If the shallow lake develops into bog or poor fen with *Sphagnum* spp. as the main vegetation form, CH_4 fluxes to the atmosphere from vascular plants directly after rewetting would be balanced by CO_2 uptake some years after rewetting, even though *Sphagnum* spp. lawns emit some CH_4. Furthermore, CO_2 fluxes to the atmosphere from ongoing peat extraction sites could be balanced by rewetting of abandoned sites. More data are now needed for water bodies in peatlands in general and for shallow lakes in rewetted peatlands in particular.

When planning a post-extraction landform, it can be important to know in advance which new ecotopes are potentially high GHG emitters. Therefore, previous data on net ecosystem CO_2 exchange at similar sites may be more helpful than ecosystem respiration flux data. Bearing in mind that the restoration goal for former extracted peatlands is the re-establishment of peatland ecosystem functions, any negative climate impact of rewetting can be tolerated as long as the plants can compensate for CH_4 and CO_2 fluxes to the atmosphere by CO_2 uptake. Knowledge of the chemistry of the residual peat can provide valuable information with regard to GHG fluxes dynamics after rewetting. Therefore, multi-year monitoring of ecosystem processes following the rewetting of extracted peatlands should be performed.

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