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Impact of water table level on annual carbon and greenhouse gas balances of a restored peat extraction area

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Abstract

Peatland restoration may provide a potential after-use option to mitigate the negative climate impact of abandoned peat extraction areas; currently, however, knowledge about restoration effects on the annual balances of carbon (C) and greenhouse gas (GHG) exchanges is still limited. The aim of this study was to investigate the impact of contrasting water table levels (WTL) on the annual C and GHG balances of restoration treatments with high (Res-H) and low (Res-L) WTL relative to an unrestored bare peat (BP) site. Measurements of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) fluxes were conducted over a full year using the closed chamber method and complemented by measurements of abiotic controls and vegetation cover. Three years following restoration, the difference in the mean WTL resulted in higher bryophyte and lower vascular plant cover in Res-H relative to Res-L. Consequently, greater gross primary production and autotrophic respiration associated with greater vascular plant cover were observed in Res-L compared to Res-H. However, the means of the measured net ecosystem CO_2 exchanges (NEE) were not significantly different between Res-H and Res-L. Similarly, no significant differences were observed in the respective means of CH_4 and N_2O exchanges in Res-H and Res-L, respectively. In comparison to the two restored sites, greater net CO_2, similar CH_4 and greater N_2O emissions occurred in BP. On the annual scale, Res-H, Res-L and BP were C sources of 111, 103 and 268 $g\,C\,m^{-2}\,yr^{-1}$ and had positive GHG balances of 4.1, 3.8 and 10.2 $t\,CO_2\,eq\,ha^{-1}\,yr^{-1}$, respectively. Thus, the different WTLs had a limited impact on the C and GHG balances in the two restored treatments three years following restoration. However, the C and GHG balances in Res-H and Res-L were considerably lower than in BP owing to the large reduction in CO_2 emissions. This study therefore suggests that restoration may serve as an effective method to mitigate the negative climate impacts of abandoned peat extraction areas.

1 Introduction

Peatlands are widely distributed across the Northern Hemisphere covering 5–30 % of national land areas in northern Europe, North-America and Russia and play a key role in the global carbon (C) cycle (Gorham, 1991; Joosten and Clarke, 2002; Vasander et al., 2003; Charman et al., 2013). Throughout the Holocene, northern peatlands have accumulated ~ 270–450 Gt C as peat and presently store about a third of the global soil C pool (Gorham, 1991; Turunen et al., 2002). They also provide a small but persistent long-term C sink (between 20 and 30 $g C m^{-2} yr^{-1}$) (Gorham, 1991; Vitt et al., 2000; Roulet et al., 2007; Nilsson et al., 2008). Carbon accumulation in peatland ecosystems occurs mainly due to the slow decomposition rate under the anoxic conditions caused by high water table levels (Clymo, 1983). Within the past century, a large fraction of peatlands has been exploited for energy production and horticultural use. Since commercial peat extraction requires initial vegetation removal and drainage, harvested peatlands are turned into C sources by eliminating the carbon dioxide (CO_2) uptake during plant photosynthesis and increasing CO_2 emission due to enhanced aerobic decomposition of organic matter. Thus, following the cessation of peat extraction activities, after-use alternatives that mitigate the negative climate impacts of these degraded and abandoned areas are required.

Among different after-use alternatives, re-establishment of peatland vegetation, which is essential for returning the extracted peatlands back into functional peat-accumulating ecosystems, has been shown to provide climate benefits (Tuittila et al., 1999, 2000a; Graf and Rochefort, 2009; Waddington et al., 2010; Strack and Zuback, 2013) as well as high ecological value (Rochefort and Lode, 2006; Lamers et al., 2015). However, due to the harsh environmental conditions of bare peat surfaces and the lack of a propagule bank, spontaneous regeneration of self-sustaining ecosystems rarely occurs and thus, human intervention is necessary to initiate this process. For instance, active re-introduction of natural peatland vegetation communities (i.e. primarily fragments of *Sphagnum* mosses and companion species) combined with rewetting has been shown to be an effective method to initiate the recovery of *Sphagnum*-dominated ecosystems with resumed long-term peat accumulation (Quinty and Rochefort, 2003).

Re-establishment of peatland vegetation and raising the water table level (WTL) affect the ecosystem C balance and peat accumulation through their impact on the production and decomposition of organic matter. Specifically, vegetation development results in increased plant photosynthesis and respiration (i.e. autotrophic respiration) as well as in greater substrate supply for methanogenesis. In addition, restoring the hydrological regime affects the CO_2 uptake by vegetation and the microbial decomposition of organic matter (i.e. heterotrophic respiration) by increasing water availability and decreasing soil oxygen status of the upper peat layer. Moreover, an increase in the WTL also reduces the depth of the aerobic peat layer in which methane (CH_4) oxidation may occur. As a consequence, higher WTL following filling or blocking of the drainage ditches commonly results in decreased CO_2 emissions (Tuittila et al., 1999; Waddington and Warner, 2001), while increasing the emissions of CH_4 (Tuittila et al., 2000a; Waddington and Day, 2007; Vanselow-Algan et al., 2015) relative to the abandoned bare peat area. The depth of the WTL is therefore in addition to the vegetation biomass recovery a key controlling variable of the ecosystem CO_2 and CH_4 exchanges following peatland restoration.

Considering the strong effects of the WTL on plant succession and ecosystem C exchanges, differences in the depth of the re-established WTL baseline (i.e. the mean WTL) due to the varying effectiveness of initial restoration activities (e.g. ditch blocking, surface peat stripping) may have implications for the trajectories of vegetation development and recovery of the C sink function following restoration. To our knowledge, no study to date has investigated the impact of contrasting WTLs on the subsequent ecosystem C balance within the same restoration site. Understanding the sensitivity of the C balance to differences in the re-established WTL baseline is however imperative when evaluating the potential of restoration for mitigating the negative climate impacts of drained peatlands. Moreover, estimates of the C sink-source strength of restored and unrestored peatlands have been limited to the growing season period in most previous

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studies (Tuittila et al., 1999, 2000a, 2004; Waddington et al., 2010; Samaritani et al., 2011; Strack et al., 2014). In contrast, data on annual budgets, which are required to evaluate the full climate benefits of peatland restoration relative to the abandoned peat extraction area, are currently scarce and to our knowledge only reported in a few studies (e.g. Yli-Petäys et al., 2007; Strack and Zuback, 2013).

Furthermore, the full ecosystem greenhouse gas balance (GHG) also includes emissions of nitrous oxide (N_2O), a greenhouse gas with an almost 300 times stronger warming effect relative to CO_2 (IPCC, 2013). Highly variable N_2O emissions ranging from < 0.06 to $26\ \mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ have been previously reported for drained organic soils, with highest emissions occurring from mesic and nutrient rich sites (Martikainen et al., 1993; Regina et al., 1996; Maljanen et al., 2010). In contrast, N_2O emissions are generally low in natural peatlands because environmental conditions (i.e. uptake of mineral N by the vegetation and anaerobic conditions due to high WTL favoring the complete reduction of N_2O to dinitrogen) diminish the potential for N_2O production (Martikainen et al., 1993; Regina et al., 1996; Silvan et al., 2005; Roobroeck et al., 2010). Thus, while the focus of most previous studies in restored peatlands has been limited to the CO_2 and CH_4 exchanges, accounting for N_2O emissions might be imperative when assessing the climate benefits of peatland restoration as an after-use option for abandoned peat extraction areas. To our knowledge, however, N_2O fluxes in restored peatlands have not been quantified to date.

This study investigated the GHG fluxes (i.e. CO_2, CH_4 and N_2O) and their biotic and abiotic controls in a restored peat extraction area with high (Res-H) and low (Res-L) WTLs and in an unrestored bare peat (BP) site. The two main objectives were (i) to investigate the impact of contrasting WTLs on the annual C and GHG balances of a restored peatland and (ii) to assess the potential of peatland restoration for mitigating the C and GHG emissions from abandoned peat extraction areas. Our hypotheses were that (i) the C and GHG balances are improved in Res-H relative to Res-L since the increased net CO_2 uptake, as a result of reduced peat mineralization and greater water availability enhancing gross primary production, outweighs the increase in CH_4

emissions under high WTL conditions and (ii) the C and GHG balances of the two restoration treatments are ameliorated relative to BP due the decreased CO_2 emissions from peat mineralization and lower N_2O emissions under more anoxic conditions following rewetting of drained peatlands.

2 Material and methods

2.1 Experimental area

The study was conducted in the Tässi peat extraction area located in central Estonia (58°32′16″ N; 25°51′43″ E). The region has a temperate climate with long-term mean (1981–2010) annual temperature and precipitation of 5.8 °C and 764 mm, respectively (Estonian Weather Service, 2015). Peat extraction in the peatland started in late 1960's and today peat is continued to be harvested for horticultural purposes using the milling technique on about 264 ha.

The current study was carried out on a 4.5 ha area which was set aside from peat extraction in the early 1980's. The residual *Sphagnum* peat layer depth is about 2.5 m. A section in the size of approximately 0.24 ha within the abandoned site was restored in April 2012. The restoration was done following a slightly modified protocol of the moss layer transfer technique (Quinty and Rochefort, 2003) aiming at restoring the growth of *Sphagnum* mosses and initiating the development of a natural bog community. The first restoration steps included stripping the uppermost oxidized peat layer (20 cm) and flattening the freshly exposed surface. In addition, the peat along the borders of the restoration area was compressed and the outflow drainage ditch was dammed with peat material to reduce the lateral water outflow from the experimental site.

To study the impact of water table level on restoration success in terms of vegetation development and greenhouse gas fluxes, the restoration site was divided into wetter and drier sections by lowering the peat surface by 10 cm for approximately one third of the area. This resulted in restoration treatments with high (Res-H) and low (Res-L) water table levels. In addition, an unrestored bare peat (BP) site was included in the study as a reference. Two replicate plots (20 m × 20 m) were established for each of the Res-H, Res-L and BP treatments.

To enhance vegetation succession, living plant fragments from *Sphagnum*-dominated hummocks were collected from a nearby (10 km) donor site (Soosaare bog) and spread out in the ratio of 1 : 10 (i.e. 1 m^2 of collected plant fragment were spread over 10 m^2) in the Res-H and Res-L treatments. As the last step, straw mulch was applied to protect plant fragments from solar radiation and to improve moisture conditions. Further details about the restoration procedure at this study site have been given in Karofeld et al. (2015).

Three years following restoration, the bryophyte species found at the restored site were dominated primarily by *Sphagnum* mosses (e.g. *S. fuscum*, *S. rubellum* and *S. magellanicum*). The common vascular plant species observed post-restoration included shrubs and trees such as common heather (*Calluna vulgaris* L.), common cranberry (*Oxycoccus palustris* Pers.), downy birch (*Betula pubescens* Ehrh.), bog-rosemary (*Andromeda polifolia* L.), scots pine (*Pinus sylvestris* L.) with a minor cover of accompanying herbaceous sedge and forb species such as tussock cottongrass (*Eriophorum vaginatum* L.) and round-leaved sundew (*Drosera rotundifolia* L.) (Karofeld et al., 2015).

2.2 Environmental measurements

A meteorological station to continuously monitor environmental variables was set up on-site in June 2014. This included measurements of air temperature (T_a; model CS 107, Campbell Scientific Inc., Logan, UT, USA), photosynthetically active radiation (PAR; model LI-190SL, LI-COR Inc., Lincoln, NE, USA) and precipitation (PPT; tipping bucket model 52 202, R. M. Young Company, Traverse City, MI, USA) at 1.2 m height above the ground. Soil temperature (T_s; depths of 5 and 30 cm) was measured with CS temperature probes (model CS 107, Campbell Scientific Inc., Logan, UT, USA) and volumetric soil moisture (VWC; depth 5 cm) with CS water content reflectometers (model

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CS615, Campbell Scientific Inc., Logan, UT, USA). All automated abiotic data were collected in 1 min intervals and stored as 10 min averages on a CR1000 datalogger (Campbell Scientific Inc., Logan, UT, USA). In addition, continuous 30 min records of the WTL relative to the soil surface were obtained with submerged HOBO Water Level Loggers (Onset Computer Corporation, Bourne, MA, USA) placed inside perforated 1.0 m long PVC pipes (Ø 5 cm; sealed in the lower end).

The on-site meteorological measurements were complemented by Estonian Weather Service data to obtain complete time series of T_a, PAR and PPT over the entire year. Hourly means of T_a and daily sums of PPT were obtained from the closest (~ 20 km away) Viljandi meteorological station. In addition, global radiation (hourly sums) data from the Tartu meteorological station (~ 40 km away) was converted to PAR based on a linear correlation relationship to on-site PAR.

In addition, manual measurements of soil temperature (depths 10, 20, 30 and 40 cm) were recorded by a handheld temperature logger (Comet Systems Ltd., Rožnov pod Radhoštěm, Czech Republic) and volumetric soil water content (depth 0–5 cm) using a handheld soil moisture sensor (model GS3, Decagon Devices Inc., Pullman, WA, USA) during each sampling campaign. Furthermore, groundwater temperature, pH, redox potential, dissolved oxygen content, electrical conductivity as well as ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were measured in observation wells (Ø 7.5 cm, 1.0 m long PVC pipes perforated and sealed in the lower end) installed at each sampling location using YSI Professional Plus handheld instruments (YSI Inc.). In addition, soil samples (0–10 cm depth) in three replicates were taken from each of the treatments and analyzed for pH as well as total C, total N, P, K, Ca and S contents at the Tartu Laboratory of the Estonian Environmental Research Centre. Three additional samples were taken from the same depth to determine bulk density in each treatment. Mean values for these soil properties are summarized in Table 1.

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2.3 Vegetation cover estimation

To assess the effect of vegetation development on greenhouse gas fluxes, vegetation cover (%) and species composition were recorded inside each of the flux measurement collars (see Sect. 2.4) in late spring. In each collar, the cover was estimated visually for each species with an accuracy of 1 %. Bryophyte, vascular plant and total vegetation cover were computed as the sum of their respective individual species coverages.

2.4 Net ecosystem CO_2 exchange, ecosystem respiration, gross and net primary production measurements

To evaluate the impact of WTL on the net ecosystem CO_2 exchange (NEE) in the restored Res-H and Res-L treatments, flux measurements were conducted biweekly from May to December 2014 at three sampling locations within each replicate plot (i.e. 6 locations per treatment) using the closed dynamic chamber method. At each sampling location, a collar (Ø 50 cm) with a water-filled ring for air-tight sealing was permanently installed to a soil depth of 10 cm. NEE measurements were conducted in random plot order (to avoid diurnal effects) using a clear Plexiglas chamber (95 % transparency; h 50 cm, V 65 L) combined with a portable infra-red gas-analyzer (IRGA). The chamber was equipped with a sensor to measure photosynthetically active radiation and air temperature (TRP-2, PP Systems, Hitchin, UK) inside the chamber. Ambient air temperature was also recorded with an additional temperature sensor placed on the outside of the chamber. Cooling packs placed inside the chamber were used to avoid a temperature increase inside the chamber during measurements. The chamber was also equipped with a low-speed fan to ensure constant air circulation. After every NEE measurement, ecosystem respiration (RE) was determined from a subsequent measurement during which the transparent chamber was covered with an opaque and light reflective shroud. CO_2 concentrations, PAR, temperature, pressure and relative humidity were recorded by an EGM-4 IRGA (PP Systems, Hitchin, UK) system every 4.8 s over a 4 or 3 min chamber deployment period for NEE and RE measurements, respectively. Since the aim of this study was to assess the atmospheric impact of restoration, all fluxes are expressed following the atmospheric sign convention in which positive and negative fluxes represent emission to and uptake from the atmosphere, respectively.

Gross primary production (GPP) was derived from the difference between NEE and RE (i.e. GPP = NEE – RE). In addition, an estimate of net primary production (NPP) was derived from the difference between NEE and heterotrophic respiration (Rh; see Sect. 2.5) (i.e. NPP = NEE – Rh).

RE estimates during the non-growing season months of March to April 2014 and January to February 2015 were determined from closed static chamber measurements (described in Sect. 2.6). Air samples collected during these measurements were analyzed for their CO_2 concentrations on a Shimadzu GC-2014 gas chromatograph with an electron capture detector (ECD). These RE estimates also represented non-growing season NEE for all treatments.

In the BP treatment, RE was determined by measurements using a separate closed dynamic chamber set-up as described below in Sect. 2.5. Due to the absence of vegetation, GPP as well as NPP were assumed to be zero and NEE subsequently equaled RE in the BP treatment.

2.5 Heterotrophic and autotrophic respiration measurements

From May to December 2014, heterotrophic respiration was measured simultaneously with NEE measurements from separate PVC collars (Ø 17.5 cm) inserted to a depth of 10 cm beside each NEE collar. The area inside of the Rh collars was cleared from living moss and vascular plants in April 2014 and kept free of vegetation during the remaining year. For Rh measurements, a second set of instrumentation was used which included an opaque chamber (h 30 cm, V 0.065 L; equipped with a low-speed fan) combined with an EGM-4 infrared gas analyzer. During each Rh measurement, CO_2 concentration and air temperature inside the chamber were recorded every 4.8 s over a period of 3 min. Autotrophic respiration (Ra) was derived from the difference between the mea-

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sured RE and Rh fluxes (i.e. Ra = RE – Rh). Due to the absence of vegetation, Ra was not determined in BP.

2.6 Methane and nitrous oxide flux measurements

To assess the impact of WTL on methane (CH_4) and nitrous oxide (N_2O) exchanges in the restored Res-H and Res-L treatments, flux measurements were conducted with the closed static chamber method at a biweekly to monthly interval from March 2014 to February 2015 at the same locations (i.e. same collars) as were used for the NEE measurements (described in Sect. 2.4). During each chamber deployment period, a series of air samples were drawn from the chamber headspace (*h* 50 cm, *V* 65 L; white opaque PVC chambers) into pre-evacuated (0.3 mbar) 50 mL glass bottles 0, 0.33, 0.66 and 1 h after closing the chamber. The air samples were analyzed for CH_4 and N_2O concentrations with a flame ionization detector (FID) and an electron capture detector (ECD), respectively, using a Shimadzu GC-2014 gas chromatograph combined with a Loftfield automatic sample injection system (Loftfield et al., 1997).

2.7 Flux calculation

Fluxes of CO_2, CH_4 and N_2O were calculated from the linear change in gas concentration in the chamber headspace over time, adjusted by the ground area enclosed by the collar, volume of chamber headspace, air density and molar mass of gas at measured chamber air temperature. The linear slope in case of the dynamic chamber measurements was calculated for a window of 25 measurement points (i.e. 2 min) moving stepwise (with one-point increments) over the entire measurement period after discarding the first two measurement points (i.e. applying a 9.6 s "dead band"). The slope of the window with the best coefficient of determination (R^2) was selected as the final slope for each measurement. In the static chamber method, the linear slope was calculated over the four available concentration values.

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All dynamic chamber CO_2 fluxes with a $R^2 \geq 0.90$ ($p < 0.001$) were accepted as good fluxes. However, since small fluxes generally result in a lower R^2 (which is especially critical for NEE measurements), dynamic chamber fluxes with an absolute slope within $\pm 0.15\,\mathrm{ppm\,s^{-1}}$ were always accepted. The slope threshold was determined based on a regression relationship between the slope and respective R^2 values. For static chamber measurements, the R^2 threshold for accepting CO_2, CH_4 and N_2O fluxes was 0.90 ($p < 0.05$), 0.80 ($p < 0.1$) and 0.80 ($p < 0.1$), respectively, except, if the maximum difference among the four concentration values was less than the gas-specific GC detection limit (i.e., < 20 ppm for CO_2, < 20 ppb for CH_4 and < 20 ppb for N_2O), in which case no filtering criterion was used.

2.8 Annual balances

To obtain estimates for the annual CO_2 fluxes, non-linear regression models were developed based on the measured CO_2 flux, PAR, WTL and T_a data following Tuittila et al. (2004). As a first step, measured GPP fluxes were fitted to PAR inside the chamber using a hyperbolic function adjusted by a second term which accounted for additional WTL effects (Eq. 1):

$$\mathrm{GPP} = \frac{\alpha \times A_{\max} \times \mathrm{PAR}}{\alpha \times \mathrm{PAR} + A_{\max}} \times \exp\left[-0.5 \times \left(\frac{\mathrm{WTL} - \mathrm{WTL_{opt}}}{\mathrm{WTL_{tol}}}\right)^2\right]. \quad (1)$$

where GPP is gross primary production ($\mathrm{mg\,C\,m^{-2}\,h^{-1}}$), PAR is the photosynthetically active radiation ($\mathrm{\mu mol\,m^{-2}\,s^{-1}}$), α is the light use efficiency of photosynthesis (i.e. the initial slope of the light response curve, $\mathrm{mg\,C\,\mu mol\,photon^{-1}}$), $A_{\max}$ is maximum photosynthesis at light saturation ($\mathrm{mg\,C\,m^{-2}\,h^{-1}}$), WTL is the water table level (cm), $\mathrm{WTL_{opt}}$ is the WTL at which maximum photosynthetic activity occurs and $\mathrm{WTL_{tol}}$ is the tolerance, i.e. the width of the Gaussian response curve of GPP to WTL.

Secondly, RE fluxes were fitted to T_a using an exponential function (Eq. 2):

$$RE = R_0 \times \exp^{(b \times T_a)}. \quad (2)$$

where RE is ecosystem respiration ($mg\,C\,m^{-2}\,h^{-1}$), T_a is air temperature (°C), R_0 is the soil respiration ($mg\,C\,m^{-2}\,h^{-1}$) at 0 °C and b is the sensitivity of respiration to T_a. Both GPP and RE were modeled with hourly resolution using hourly PAR, WTL and T_a as input variables. Growing season (1 May to 31 October) GPP and annual RE were then derived from the cumulative sums of these modeled fluxes. The balance between growing season GPP and annual RE estimates resulted in the annual NEE in SH and SL, whereas annual RE represented annual NEE in BP. The GPP and RE model parameters for the different treatments are summarized in Table 2.

Annual sums of CH_4 and N_2O fluxes were estimated by scaling their hourly mean and median flux values, respectively, to annual sums. The median flux was used for N_2O to avoid a positive bias caused by episodic high peak fluxes measured directly after rainfall events. The annual sums were converted to CO_2 equivalents (CO_2 eq) using the global warming potentials (GWP, over a 100 year timeframe including carbon-climate feedbacks) of 34 and 298 for CH_4 and N_2O, respectively (IPCC, 2013).

2.9 Statistical analysis

Collar flux data were averaged for each plot before conducting further statistical analysis to avoid pseudoreplication. The non-parametric Friedman one-way analysis of variance (ANOVA) by ranks test for dependent samples was used to account for repeated measurements in time when testing for treatments effects (i.e. Res-H, Res-L and BP) on the growing season or annual means of the various component fluxes. This analysis was followed by a Bonferroni post-hoc comparison to determine significant differences among treatment means. The Mann–Whitney U test was used when comparing only the restoration treatments for significant effects (i.e. on GPP, NPP and Ra fluxes). Pearson's correlations were used to investigate the effects of vegetation cover on fluxes. The significance level was $P < 0.05$ unless stated otherwise. All calculations and statistics were computed using the Matlab software (Matlab Student version, 2013a; Mathworks, USA).

3 Results

3.1 Environmental conditions

The annual mean T_a and total PPT from March 2014 to February 2015 were 7.2 °C and 784 mm, respectively, which suggests warmer conditions with normal wetness when compared to the long-term climate normal (5.8 °C and 764 mm). PAR peaked in the first week of July while the seasonal T_a curve peaked at around 23 °C in late July (Fig. 1a). A prolonged warm and dry period occurred from early to late July with a mean T_a of 20.0 °C and total rainfall of 43.3 mm.

The WTL ranged from −2 to −52 and from −8 to −59 cm in the restored Res-H and Res-L treatments, respectively, while remaining between −26 and −69 cm in the unrestored BP site (Fig. 1b). The mean WTLs in Res-H and Res-L were −24 and −31 cm, respectively, resulting in a mean annual difference of 7 cm between the restored treatments. Throughout the year, the WTL in Res-H was always higher than in Res-L with the difference varying between 3 and 10 cm. The mean WTL in BP was −46 cm resulting in mean differences of −22 and −15 cm compared to Res-H and Res-L, respectively.

3.2 Vegetation cover and composition

The total surface cover, i.e. the fraction of re-colonized surface area, inside the flux measurement collars was higher in the wetter Res-H (63 %) than in the drier Res-L (52 %) treatment. Bryophytes were more abundant in Res-H (62 %) than in Res-L (44 %) (Table 3). The bryophyte cover consisted primarily of *Sphagnum* species which contributed 98 and 96 % in Res-H and Res-L, respectively. Vascular plants occurred

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more frequently in the drier Res-L (14 %) than in the wetter Res-H (4 %) treatment and were dominated by woody plants (i.e. shrubs and tree seedlings) (Table 3). The cover of sedges was < 1 % in both restored treatments.

3.3 Carbon dioxide fluxes

Daytime NEE was positive indicating CO_2 emissions during the non-growing season months (November to April) in all three treatments (Fig. 2a). During the early (i.e. June) and late (i.e. mid-August to September) summer, net CO_2 uptake occurred in both Res-H and Res-L with maximum rates of −42 and −41 $mg\,C\,m^{-2}\,h^{-1}$, respectively. However, during the warm and dry mid-summer period, CO_2 emissions of up to 36 and 27 $mg\,C\,m^{-2}\,h^{-1}$ were observed in Res-H and Res-L, respectively. In contrast, NEE remained positive in BP throughout the growing season and followed the seasonal pattern of T_a with maximum emission rates of 104 $mg\,C\,m^{-2}\,h^{-1}$ occurring in early August. The annual mean midday NEE in Res-H and Res-L were significantly lower than in BP, but not significantly different between the two restored treatments (Table 4).

Midday RE was similar for all treatments during the non-growing season months (Fig. 2b). During the growing season, however, midday RE differed among treatments with lowest and highest RE observed in Res-H and BP, respectively. RE in Res-H and Res-L reached maximum values of 74 and 96 $mg\,C\,m^{-2}\,h^{-1}$ during early July, respectively, whereas RE peaked at 104 $mg\,C\,m^{-2}\,h^{-1}$ in early August in BP. The annual mean midday RE was significantly lower in Res-H and Res-L than in BP (Table 4).

From early June to late August, both the daytime GPP and NPP were lower (i.e. representing greater production) in the drier Res-L than in the wetter Res-H treatment (Fig. 2c and d). Greatest GPP (i.e. most negative values) occurred in late June and mid-August reaching −90 and −98 $mg\,C\,m^{-2}\,h^{-1}$ in Res-H and Res-L, respectively. GPP temporarily decreased (i.e. resulting in more positive values) to −14 and −41 $mg\,C\,m^{-2}\,h^{-1}$ during the warm and dry mid-summer period in both Res-H and Res-L. The seasonal patterns in NPP followed closely those of GPP, reaching

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−65 and −68 $mg\,C\,m^{-2}\,h^{-1}$ in Res-H and Res-L, respectively. The growing season mean GPP in Res-H (−49.3 $mg\,C\,m^{-2}\,h^{-1}$) was significantly higher than that in Res-L (−65.5 $mg\,C\,m^{-2}\,h^{-1}$) (Table 4). The difference in the growing season means of NPP in Res-H and Res-L was not statistically significant.

Midday Ra was more than two times greater in the drier Res-L than in the wetter Res-H treatment for most of the growing season sampling dates (Fig. 2e). The seasonal pattern of Ra coincided with that of GPP in both restored treatments with greatest Ra occurring in late June and mid-August reaching maximum values of up to 27 and 36 $mg\,C\,m^{-2}\,h^{-1}$ in Res-H and Res-L, respectively. The growing season mean Ra was significantly higher (by about two times) in Res-L than in Res-H (Table 4). The ratio of Ra to Rh was on average 0.21 and 0.42 in Res-H and Res-L, respectively.

Midday Rh was consistently lower in Res-H and Res-L than in BP throughout the growing season (Fig. 2f). Maximum Rh of up to 61, 73 and 104 $mg\,C\,m^{-2}\,h^{-1}$ in Res-H, Res-L and BP, respectively, were observed in early July (restored treatments) and early August (unrestored BP). The growing season mean Rh was significantly lower (by about 50 %) in Res-H and Res-L than in BP (Table 4).

3.4 Methane fluxes

Throughout most of the year, CH_4 fluxes were observed in the range of −13 to 60 $\mu g\,C\,m^{-2}\,h^{-1}$ in all three treatments (Fig. 3a). Occasional peak CH_4 emission of up to 170 and 92 $\mu g\,C\,m^{-2}\,h^{-1}$ occurred in Res-H and Res-L, respectively. During the non-growing season months, CH_4 exchange was variable showing both small uptake as well as large emission (−6 to 138 $\mu g\,C\,m^{-2}\,h^{-1}$). The mean annual CH_4 exchange was about two times greater in the wetter Res-H than in the drier Res-L treatment, however, the differences among the three treatments were not statistically significant (Table 4).

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3.5 Nitrous oxide fluxes

N_2O fluxes in Res-H and Res-L remained within the range of −2.8 to 25 µg N m^{-2} h^{-1} for most of the year (Fig. 3b). In contrast, high N_2O emissions of 66 to 133 µg N m^{-2} h^{-1} occurred during July and August in BP. The annual mean N_2O exchanges of −0.12 µg N m^{-2} h^{-1} in Res-H and 2.13 µg N m^{-2} h^{-1} in Res-L were not significantly different (Table 4). Meanwhile, the mean N_2O exchanges in the two restored treatments were significantly lower (by 1–2 magnitudes) compared to the 27.1 µg N m^{-2} h^{-1} in BP (Table 4).

3.6 Biotic and abiotic controls of greenhouse gas fluxes

The differences in NEE, GPP, NPP and Ra among individual collars (i.e. the spatial variability) were significantly correlated to bryophyte but not to vascular plant cover in Res-H (Table 5). In contrast, spatial variations in NEE, GPP, NPP and Ra were significantly correlated to vascular plant but not to bryophyte cover in Res-L. In addition, RE was significantly correlated to vascular plant cover in Res-L. Meanwhile, the CH_4 and N_2O exchanges were not significantly correlated to vegetation cover neither in Res-H nor in Res-L.

Soil temperature measured at 10 cm depth was the abiotic variable that best explained variations in RE (R^2 = 0.79, 0.84 and 0.81 in Res-H, Res-L and BP, respectively) in form of an exponential relationship (Fig. 4) with higher temperatures resulting in higher respiration rates. The basal respiration and temperature sensitivity parameters were lowest in the wetter Res-H treatment and highest in BP.

N_2O fluxes correlated best with volumetric water content measured at 0–5 cm soil depth in Res-L (R^2 = 0.60) and in BP (R^2 = 0.39) (Fig. 5). In contrast, N_2O fluxes were not correlated to soil volumetric water content or any other abiotic variable in Res-H. Similarly, the CH_4 exchange did not show any significant relationships with any abiotic variable for any of the three treatments.

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3.7 Annual carbon and greenhouse gas balances

In the restored Res-H and Res-L treatments, the modelled annual RE estimates were 188.6 and 213.2 $g\,C\,m^{-2}\,yr^{-1}$, respectively, whereas in the unrestored BP treatment annual RE was 267.8 $g\,C\,m^{-2}\,yr^{-1}$ (Table 6). The annual GPP was estimated at −78.0 and −110.5 $g\,C\,m^{-2}\,yr^{-1}$ in Res-H and Res-L, respectively. This resulted in annual net CO_2 exchanges of 110.6, 102.7 and 267.8 $g\,C\,m^{-2}\,yr^{-1}$ in the wetter Res-H, drier Res-L and BP treatments, respectively. The growing season net CO_2 loss (i.e. NEE) represented 45 and 37 % of the annual net CO_2 loss in Res-H and Res-L, respectively, while it accounted for 67 % in BP. The additional carbon losses via CH_4 emission were 0.190, 0.117 and 0.137 $g\,C\,m^{-2}\,yr^{-1}$ in Res-H, Res-L and BP, respectively. In total, all treatments acted as carbon sources, however, the annual C balance was the lower in the restored Res-H (110.8 $g\,C\,m^{-2}\,yr^{-1}$) and Res-L (102.8 $g\,C\,m^{-2}\,yr^{-1}$) treatments than in the unrestored BP (268.0 $g\,C\,m^{-2}\,yr^{-1}$) treatment. The total GHG balance, including the net CO_2 exchange as well as CH_4 and N_2O emissions expressed as CO_2 eq, was 4.14, 3.83 and 10.21 $t\,CO_2\,eq\,ha^{-1}\,yr^{-1}$ in Res-H, Res-L and BP, respectively (Table 6). The GHG balance was driven by the net CO_2 exchange (96 to 98 %) in all three treatments. The contribution of CH_4 emission was highest (2.1 %) in the wetter Res-H treatment, while the contribution of N_2O emission was highest (3.9 %) in the unrestored BP treatment.

4 Discussion

4.1 Greenhouse gas fluxes and their controls in restored and abandoned peat extraction areas

4.1.1 Coupling of water table level and vegetation dynamics

Three years following restoration, contrasting vegetation communities in Res-H and Res-L had developed as a result of a mean annual WTL difference of 7 cm. Specifically, a greater cover of bryophytes (63 %) (primarily *Sphagnum* spp.), which rely on capillary forces for acquiring water and thus require moist conditions (Rydin, 1985), was present in the wetter Res-H treatment. In contrast, the lower WTL in Res-L resulted in a lower bryophyte cover (44 %) but greater abundancy of vascular plants, likely due to the extended zone of aeration for plant roots. Apart from having roots to absorb water and nutrients from the soil, vascular plants also differ from bryophytes by having leaf stomata to regulate water transport and CO_2 exchange (Turner et al., 1985; Schulze et al., 1994). Thus, the establishment of contrasting vegetation communities as a result of different WTL baselines has potential implications for the biogeochemical cycles and GHG fluxes following peatland restoration (Weltzin et al., 2000).

4.1.2 Carbon dioxide fluxes

In this study, the significantly higher GPP in Res-L was likely due to the greater vascular plant cover compared to Res-H, since vascular plants reach higher photosynthesis rates at higher light levels compared to mosses (Bubier et al., 2003; Riutta et al., 2007a). Similarly, Strack and Zuback (2013) reported a strong correlation between vascular plant cover and GPP in a restored peatland in Canada. In return, the greater GPP also explains the higher Ra observed in Res-L compared to Res-H. This highlights the implications of hydrological differences and the associated vegetation development on plant-related CO_2 fluxes. Furthermore, it has been suggested that the presence of vascular plants can facilitate greater survival and better growth of the re-introduced mosses as they can provide shelter from the intense solar radiation and wind and thus create a more favorable micro-climate (Ferland and Rochefort, 1997; Tuittila et al., 2000b; McNeil and Waddington, 2003; Pouliot et al., 2012). Since *Sphagnum* mosses are generally more sensitive to drought compared to vascular plants, restoration strategies allowing the development of a diverse vegetation cover (i.e. byrophytes accompanied by vascular plants) could therefore be considered to have greater potential for limiting CO_2 loss and regaining the C sink function (Tuittila et al., 1999). Nevertheless, despite the significant effects of the re-established WTL baseline on vegetation development and the associated CO_2 component fluxes (i.e. RE and GPP), the net CO_2 exchange of the two restored treatments was similar. Our study therefore suggests that the greater GPP was partly counterbalanced by greater Ra in Res-L compared to Res-H. However, while differences in the re-established WTL baseline had no significant effect on the CO_2 sink-source strength three years after restoration of the abandoned peat extraction area, vegetation characteristics are likely to further diverge in the future which might essentially result in contrasting net CO_2 balances over longer time spans (Weltzin et al., 2000; Yli-Petäys et al., 2007; Samaritani et al., 2011; Vanselow-Algan et al., 2015).

Compared to the unrestored BP treatment, growing season Rh, i.e. the decomposition of soil organic matter, was considerably reduced in the restored treatments which suggests that raising the WTL effectively mitigated C losses from the ecosystem by reducing the potential for aerobic peat decomposition (Silvola et al., 1996; Frolking et al., 2001; Whiting and Chanton, 2001). Furthermore, the significantly lower ecosystem respiration in Res-H and Res-L compared to BP demonstrates that the additional autotrophic respiration from the growing vegetation was negligible compared to the large reduction in Rh. Likewise, Strack and Zuback (2013) found a significantly lower Rh and RE in the restored compared to an unrestored site in Canada 10 years following peatland restoration. Furthermore, the lower RE in the restored treatments relative to BP might also result from the lower temperature sensitivity of Rh, i.e. soil organic matter decomposition, observed in this study which is likely due to greater oxygen limitation in the restored treatments following the raising of the WTL. Thus, our findings highlight the effectiveness of raising the WTL in reducing peat decomposition and CO_2 emissions from drained organic soils.

4.1.3 Methane fluxes

Both WTL and vegetation dynamics have been previously highlighted as major controls on the CH_4 exchange in natural, restored and drained peatlands (Bubier, 1995; Frenzel and Karofeld, 2000; Tuittila et al., 2000a; Riutta et al., 2007b; Waddington and Day, 2007; Lai, 2009; Strack et al., 2014). Specifically, the WTL determines the depth of the lower anaerobic and upper aerobic peat layers and thus the potential for CH_4 production and consumption occurring in these respective layers (Bubier, 1995; Tuittila et al., 2000a). Vegetation composition, on the other hand, affects the CH_4 production through substrate supply (i.e. quality and quantity) (Saarnio et al., 2004; Ström et al., 2005) and by offering a direct emission pathway for CH_4 from the deeper anaerobic layer to the atmosphere via the aerenchymatic cell tissue of deep rooting sedge species such as *Eriophorum* spp. (Thomas et al., 1996; Frenzel and Karofeld, 2000; Ström et al., 2005; Waddington and Day, 2007).

Given the considerable differences in WTL and vegetation composition, the lack of significant differences in CH_4 emissions among the restored and BP treatments in our study was therefore surprising. Most likely, similar CH_4 emissions in Res-H and Res-L were the result of opposing effects counterbalancing the production and consumption of CH_4. For instance, enhanced anaerobic CH_4 production due to higher WTL in Res-H could have been partly compensated by greater CH_4 oxidation within or immediately below the more developed moss layer (Frenzel and Karofeld, 2000; Basiliko et al., 2004; Larmola et al., 2010). In Res-L on the other hand, greater vascular plant substrate supply might have sustained substantial CH_4 production despite a reduction of the anaerobic zone (Tuittila et al., 2000a; Weltzin et al., 2000). Further noteworthy is that, while very few aerenchymatic sedge species (e.g. *Eriophorum vaginatum*) were

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established at the time of this study, a future increase in the sedge cover is likely to occur (Tuittila et al., 2000a; Weltzin et al., 2000; Vanselow-Algan et al., 2015) which could considerable increase the CH_4 emission in the restored treatments over longer time spans. Overall, the potential effects from enhanced anaerobic conditions due to raised WTL, CH_4 oxidation in the moss layer or greater vascular plant substrate supply on the net CH_4 fluxes were small, considering that CH_4 emissions were not significantly different from those in BP which was characterized by a considerably lower WTL and absence of vegetation. Thus, our study suggests that in non-flooded conditions WTL changes following peatland restoration have a limited effect on the CH_4 emissions during the initial few years.

4.1.4 Nitrous oxide fluxes

Soil moisture and WTL effects on the soil oxygen status have been previously identified as the main control on N_2O emissions from pristine and drained peatlands (Firestone and Davidson, 1989; Martikainen et al., 1993; Klemedtsson et al., 2005). Highest N_2O emissions commonly occur in mesic soils with intermediate water table levels, which allows both aerobic and anaerobic N_2O production during nitrification and denitrification, respectively, while avoiding the anaerobic reduction of N_2O to N_2 (Firestone and Davidson, 1989; Martikainen et al., 1993). In addition, substrate supply (i.e. C and inorganic N) is a key prerequisite for N_2O production (Firestone and Davidson, 1989). In our study, similar N_2O fluxes in the two restored treatments therefore suggest that the differences in WTL, soil moisture and substrate supply from mineralization of organic matter were too small to affect the magnitudes of N_2O emission three years following restoration with different WTL baselines. On the other hand, the enhanced anaerobic conditions due to higher WTL as well as lower soil N concentrations due to reduced mineralization and enhanced plant N uptake might explain both the reduced N_2O emissions and their lower sensitivity to soil moisture in the restored Res-H and Res-L treatments compared to BP. Thus, peatland restoration has the potential for reducing the N_2O emissions commonly occurring in drained, abandoned peatlands by altering both soil hydrology and N substrate supply.

4.2 The carbon and greenhouse gas balances of restored and abandoned peat extraction areas

Both restored treatments were C sources during the growing season which indicates that the CO_2 uptake by the re-established vegetation was not able to compensate for the C losses via respiration and CH_4 emissions three years following restoration. Several studies have previously reported estimates for the growing season C sink-source strength of restored peatlands, with contrasting findings owing to different restoration techniques, environmental conditions during the study year and time passed since the initiation of the restoration (Tuittila et al., 1999; Bortoluzzi et al., 2006; Yli-Petäys et al., 2007; Waddington et al., 2010; Samaritani et al., 2011; Strack et al., 2014). For instance, restored peatlands in Finland (Tuittila et al., 1999) and Canada (Waddington et al., 2010; Strack et al., 2014) were C sinks during the growing season three to six years after restoration. In contrast, other studies suggested that several decades may be required before restored peatlands resume their functioning as C sinks (Yli-Petäys et al., 2007; Samaritani et al., 2011). However, while growing season studies can provide important information on processes governing the fluxes, it is necessary to quantify and compare full annual budgets to better evaluate the climate benefits of peatland restoration relative to abandoned peatland areas (and other after-use options, e.g. afforestation or energy crop cultivation).

In our study, the annual C source strength of the two restored treatments and the bare peat site was about 1.5 to 2.5 times greater than on the growing season scale. This highlights the importance of accounting for the considerable non-growing season emissions when evaluating the C sink potential of restored peatlands. In comparison, the annual C source strength of the two restored treatments (111 and 103 $g\,C\,m^{-2}\,yr^{-1}$) was lower than the annual emissions of 148 $g\,C\,m^{-2}\,yr^{-1}$ reported for a restored cutaway peatland in Canada 10 years following restoration (Strack and Zuback, 2013).

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Similarly, the C balance of BP (268 $g\,C\,m^{-2}\,yr^{-1}$) in our study was about half of the 547 $g\,C\,m^{-2}\,yr^{-1}$ emitted at the Canadian unrestored site. However, high emissions in the study of Strack and Zuback (2013) were partly attributed to the dry conditions during the study year. Thus, this indicates that restored peatlands are unlikely to provide an annual C sink during the first decade following restoration of peat extraction sites. However, compared to naturally re-vegetating peatlands which may require 20–50 years to reach a neutral or negative C balance (Bortoluzzi et al., 2006; Yli-Petäys et al., 2007; Samaritani et al., 2011), initiating the restoration by rewetting in combination with re-introduction of peatland vegetation might reduce the time required for the ecosystem to return to being a C sink similar to that of a natural peatland (Tuittila et al., 2004; Roulet et al., 2007; Nilsson et al., 2008).

The similar GHG balances in the two restored treatments Res-H and Res-L suggest that the differences in the mean WTL had a limited effect on the GHG balance within few years following restoration of the peat extraction area. Moreover, the GHG balances in the restored treatments were driven primarily by the net CO_2 exchange, while that the contribution of CH_4 and N_2O exchanges remained minor in our study. In contrast, 30 years after rewetting of a German bog, high CH_4 emission were reported as the main component of the GHG balance (Vanselow-Algan et al., 2015). The same study also reported GHG balances ranging from 25–53 $t\,CO_2\,eq\,ha^{-1}\,yr^{-1}$ which are considerably higher compared to our study. This indicates that the GHG balances of restored peatlands may vary greatly over longer time spans. Moreover, this also suggests the GHG balance of peatland restoration with differing WTL baselines is likely to further diverge over time due to contrasting trajectories in vegetation development and changes in soil biogeochemistry (e.g. pH, nutrient contents and soil moisture dynamics).

While the two restored treatments had similar GHG balances, the difference between the GHG balances in restored and BP treatments was considerable. Only three years following restoration, the GHG balance in the restored treatments was reduced to about half of that in BP. This reduction was mainly due to lower annual CO_2 emissions (i.e. lower NEE) in the restored treatments compared to BP likely as a result of increased

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WTL and vegetation development. In addition, annual N_2O emissions were also significantly reduced in the restored treatments, although, compared to the differences in the CO_2 balance, the impact of the reduction in N_2O emissions on the GHG balance was relatively small. Overall, our study suggests that peatland restoration may provide an effective method to mitigate the negative climate impacts of abandoned peat extraction areas in the short-term. However, due to the lack of long-term observations and recent reports of potential high CH_4 emissions occurring several decades after rewetting (Yli-Petäys et al., 2007; Vanselow-Algan et al., 2015), it remains uncertain whether restoration of abandoned peat extraction areas may also provide an after-use solution with climate mitigation potential in the long-term.

5 Conclusions

We found that differences in the re-established water table level strongly affected the vegetation communities following restoration of the abandoned peat extraction area. Furthermore, the difference in vegetation cover and composition was identified as the main control of within- and between-site variations in GPP, NPP and plant respiration. We therefore conclude that variations in WTL baselines may have important implications for plant-related CO_2 fluxes in restored peatlands. In contrast, differences in the WTL baseline had only small effects on the net CO_2 exchange due to the concurrent changes in plant production and respiration in the wet and dry restoration treatments. Moreover, since CH_4 and N_2O exchanges were also similar in the two restored treatments, this study suggests that differing water table levels had a limited impact on the C and GHG balances three years following restoration. Furthermore, we observed a considerable reduction of heterotrophic respiration in the restored treatments which advocates rewetting as an effective method to reduce aerobic organic matter decomposition in drained peatlands. In contrast, our study suggests that the effects of rewetting on CH_4 fluxes were negligible three years following restoration. However, rewetting reduced the N_2O emissions by 1–2 magnitudes which indicates a high potential of

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peatland restoration in reducing the N_2O emissions commonly occurring in drained peatlands. Three years following restoration, the C and GHG balances of the restored treatments were reduced by approximately half relative to those of the abandoned bare peat area. We therefore conclude that peatland restoration may effectively mitigate the negative climate impacts of abandoned peat extraction areas; however, longer time spans may be needed to return these sites into net C sinks.

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Table 1. Soil properties in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP); numbers in parenthesis indicate standard error.

Soil property	Res-H	Res-L	BP
pH	4.0 (0.07)	3.9 (0.07)	3.9 (0.06)
Bulk density ($g\,cm^{-3}$)	0.08 (0.002)	0.09 (0.003)	0.13 (0.004)
C (%)	49 (0.6)	50 (0.3)	48 (0.6)
N (%)	0.61 (0.04)	0.76 (0.05)	0.85 (0.04)
C/N	80.3	65.8	56.5
P ($mg\,g^{-1}$)	0.2 (0.03)	0.2 (0.02)	0.4 (0.03)
K ($mg\,g^{-1}$)	0.2 (0.007)	0.2 (0.003)	0.1 (0.004)
Ca ($mg\,g^{-1}$)	2.1 (0.07)	2.1 (0.07)	3.4 (0.23)
S ($mg\,g^{-1}$)	0.9 (0.12)	1.0 (0.05)	1.4 (0.09)

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Table 2. Parameters for the gross primary production (GPP) and ecosystem respiration (RE) models in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP); α is the quantum use efficiency of photosynthesis (mg C µmol photon^{-1}), A_{max} is the maximum rate of photosynthesis at light saturation (mg C m^{-2} h^{-1}); WTL_{opt} is the WTL at which maximum photosynthetic activity occurs; WTL_{tol} is the tolerance, i.e. the width of the Gaussian response curve of GPP to WTL; R_0 is the soil respiration (mg C m^{-2} h^{-1}) at 0 °C, b is the sensitivity of respiration to air temperature; numbers in parenthesis indicate standard error; Adj. R^2 = adjusted R^2.

Model parameter	Res-H	Res-L	BP
GPP model			
α	−0.20 (0.07)	−0.23 (0.07)	n/a
A_{max}	−98.0 (39.9)	−121.9 (43.4)	n/a
WTL_{opt}	−18.7 (8.4)	−24.9 (6.4)	n/a
WTL_{tol}	16.4 (10.0)	21.0 (9.7)	n/a
Adj. R^2	0.58	0.61	n/a
RE model			
R_0	13.0 (1.5)	13.4 (1.5)	18.6 (2.7)
b	0.056 (0.005)	0.064 (0.005)	0.055 (0.005)
Adj. R^2	0.62	0.71	0.60

n/a = not applicable.

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Table 3. Vegetation cover (%) inside the collars for greenhouse gas flux measurements in restoration treatments with high (Res-H) and low (Res-L) water table level. Total surface cover represents the area of bare peat surface re-colonized by vegetation; numbers in parenthesis indicate the range among individual collars.

Species	Res-H	Res-L
Bryophytes	62 (32 to 93)	44 (15 to 74)
Sphagnum mosses	61 (31 to 91)	43 (12 to 70)
Vascular plants	4 (2 to 9)	14 (5 to 22)
Shrubs and tree seedlings	2 (0 to 7)	13 (5 to 22)
Sedges	< 1	< 1
Total surface cover	63 (35 to 95)	52 (20 to 85)

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Table 4. Means of measured CO_2 fluxes ($mg\,C\,m^{-2}\,h^{-1}$) including net ecosystem exchange (NEE), ecosystem respiration (RE), gross primary production (GPP), net primary production (NPP), autotrophic respiration (Ra) and heterotrophic respiration (Rh) as well as means of measured methane (CH_4; $\mu g\,C\,m^{-2}\,h^{-1}$) and nitrous oxide (N_2O; $\mu g\,N\,m^{-2}\,h^{-1}$) fluxes in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP). Negative and positive fluxes represent uptake and emission, respectively. Numbers in parenthesis indicate standard error; different letters indicate significant ($P < 0.05$) differences among treatments.

Component flux	Res-H	Res-L	BP
NEE	0.57 (4.9)[c]	−2.82 (4.9)[c]	44.9 (8.2)[ab]
RE	29.9 (5.1)[c]	35.1 (6.4)[c]	44.9 (8.2)[ab]
GPP*	−49.3 (7.4)[a]	−65.5 (7.3)[b]	n/a
NPP*	−41.5 (5.3)	−48.1 (4.2)	n/a
Ra*	7.9 (2.6)[a]	16.2 (3.4)[b]	n/a
Rh*	37.0 (5.1)[c]	38.5 (5.9)[c]	71.2 (8.4)[ab]
CH_4	23.0 (10.7)	10.9 (6.1)	14.7 (3.7)
N_2O	−0.12 (0.25)[c]	2.13 (1.29)[c]	27.1 (9.1)[ab]

* Growing season mean (1 May to 31 October).
n/a = not applicable.

Table 5. Correlation coefficients of vegetation (bryophytes and vascular plants) cover (%) with CO_2 fluxes including the net ecosystem CO_2 exchange (NEE), ecosystem respiration (RE), gross primary production (GPP), net primary production (NPP) and autotrophic respiration (Ra) and with methane (CH_4) and nitrous oxide (N_2O) fluxes in restoration treatments with high (Res-H) and low (Res-L) water table level. Total vegetation represents the sum of bryophyte and vascular plant cover.

	Res-H							Res-L						
Vegetation cover	NEE	RE	GPP	NPP	Ra	CH_4	N_2O	NEE	RE	GPP	NPP	Ra	CH_4	N_2O
Bryophytes	−0.95[b]	0.74	−0.95[b]	−0.84[a]	0.97[b]	−0.53	−0.56	−0.75	0.67	−0.81[a]	−0.70	0.78	−0.33	−0.34
Vascular plants	−0.70	0.49	−0.76	−0.68	0.60	−0.07	−0.05	−0.92[b]	0.93[b]	−0.97[b]	−0.93[b]	0.89[a]	0.13	0.22
Total vegetation	−0.95[b]	0.74	−0.95[b]	−0.84[a]	0.96[b]	−0.50	−0.53	−0.82[a]	0.72	−0.84[a]	−0.75	0.88[a]	−0.21	−0.19

Significant correlations are marked with [a] indicates $P < 0.05$ and [b] indicates $P < 0.01$.

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Table 6. Growing season (GS; 1 May to 31 October) and annual (A) sums of the carbon balance components ($g\,C\,m^{-2}$) including gross primary production (GPP), ecosystem respiration (RE), net ecosystem exchange (NEE) of CO_2, and methane (CH_4) fluxes as well as of the greenhouse gas (GHG) balance components ($t\ CO_2\ eq\,ha^{-1}$) including NEE, CH_4 and nitrous oxide (N_2O) exchanges (using global warming potentials of 34 and 298 for CH_4 and N_2O, respectively) in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP). Negative and positive fluxes represent uptake and emission, respectively.

	Res-H		Res-L		BP	
Component flux	GS	A	GS	A	GS	A
C balance components						
GPP	−78.0	−78.0	−110.5	−110.5	n/a	n/a
RE	127.5	188.6	148.8	213.2	180.5	267.8
NEE	49.5	110.6	38.3	102.7	180.5 [a]	267.8 [a]
CH_4	0.130	0.190	0.036	0.117	0.076	0.137
Total C balance[b]		110.8		102.8		268.0
GHG balance components						
NEE	1.81	4.05	1.40	3.76	6.62	9.82
CH_4	0.059	0.086	0.016	0.053	0.035	0.062
N_2O	0.002	0.004	0.010	0.020	0.167	0.332
Total GHG balance[c]		4.14		3.83		10.21

[a] GPP for BP was assumed to be zero and NEE therefore equal to RE.
[b] The total C balance ($g\,C\,m^{-2}\,yr^{-1}$) is the sum of NEE and CH_4 fluxes.
[c] The total GHG balance ($t\ CO_2\ eq\,ha^{-1}\,yr^{-1}$) is the sum of NEE, CH_4 and N_2O fluxes.
n/a = not applicable.

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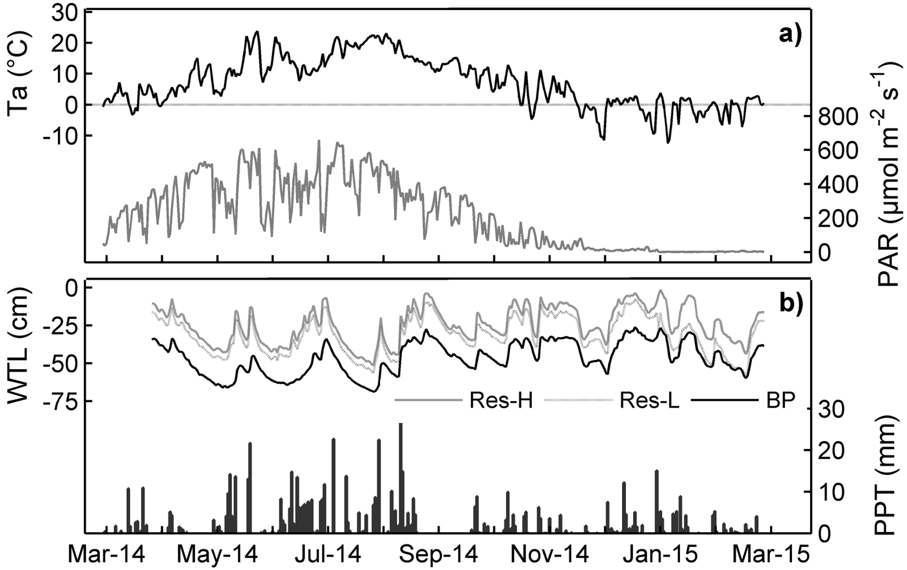

Figure 1. Daily means of **(a)** air temperature (T_a) and photosynthetically active radiation (PAR), **(b)** water table level (WTL) in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP) and daily sums of precipitation (PPT) from March 2014 to February 2015; T_a, PAR and PPT data are taken from the Pärnu meteorological station (until 17 June) and measured at the study site (from 18 June onward).

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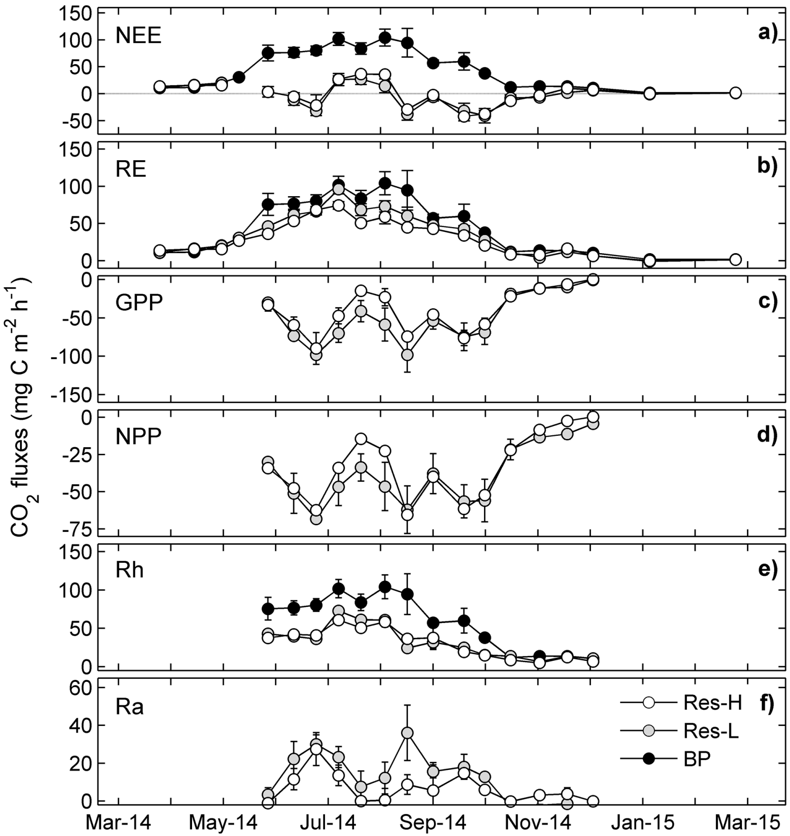

Figure 2. (a) Net ecosystem exchange (NEE) of carbon dioxide, **(b)** ecosystem respiration (RE), **(c)** gross primary production (GPP), **(d)** net primary production (NPP), **(e)** autotrophic respiration (Ra) and **(f)** heterotrophic respiration (Rh) in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP); error bars indicate standard error; the horizontal dotted line in **(a)** visualizes the zero line above and below which CO_2 emission and uptake occur, respectively.

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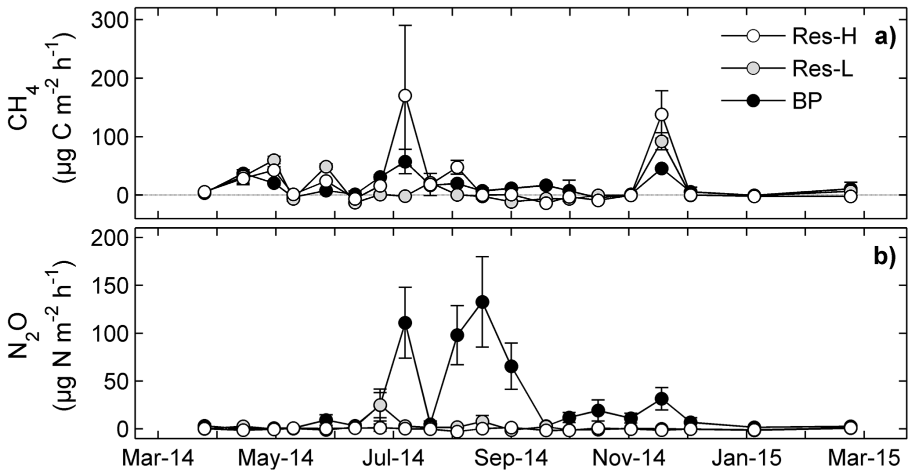

Figure 3. Measured fluxes of **(a)** methane (CH_4; $\mu g\,C\,m^{-2}\,h^{-1}$) and **(b)** nitrous oxide (N_2O; $\mu g\,N\,m^{-2}\,h^{-1}$) in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP); error bars indicate standard error; the horizontal dotted line in **(a)** visualizes the zero line above and below which CH_4 emission and uptake occur, respectively.

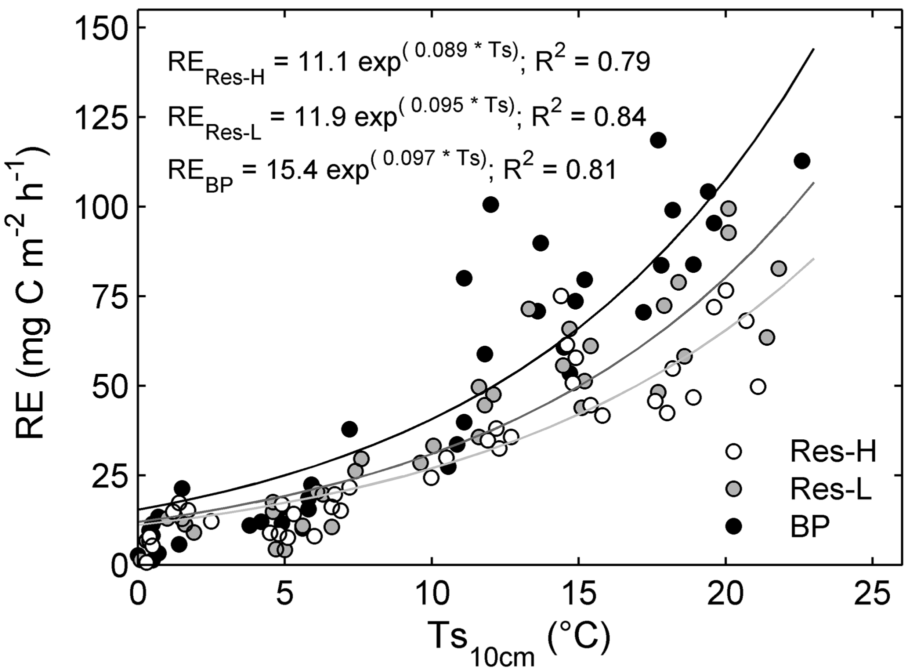

Figure 4. Response of ecosystem respiration (RE; $mg\,C\,m^{-2}\,h^{-1}$) to changes in soil temperature (T_s) measured at 10 cm soil depth in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP).

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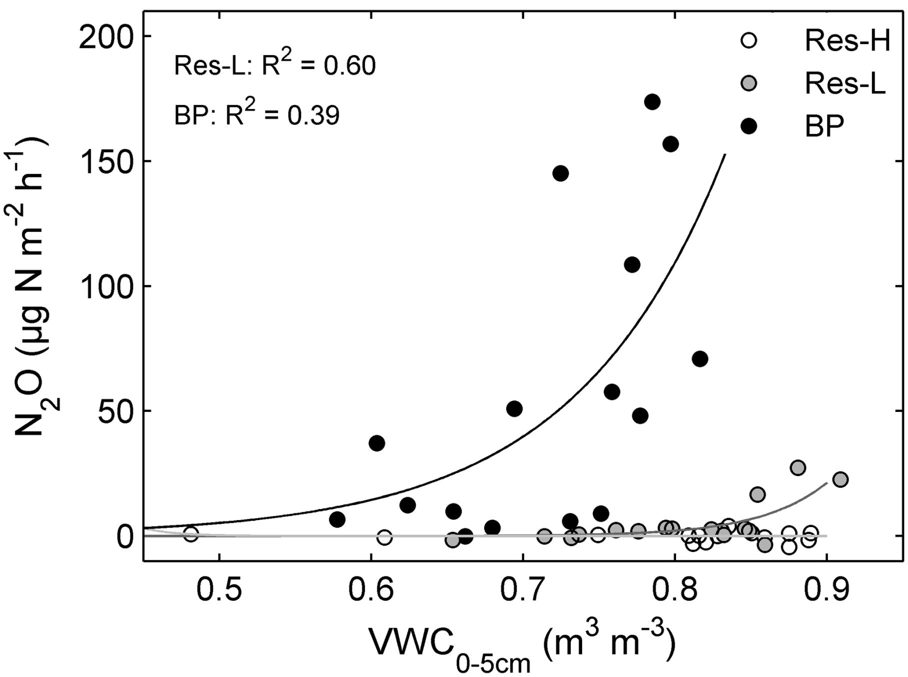

Figure 5. Response of nitrous oxide (N_2O) fluxes (µg N m^{-2} h^{-1}) to changes in volumetric water content (VWC) measured at 0-5 cm soil depth during the growing season in restoration treatments with high (Res-H) and low (Res-L) water table level and bare peat (BP).

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